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Article

Response of Understory Avifauna to Annual Flooding of Amazonian Floodplain Forests

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Abstract: The annual flooding in the Amazon basin transforms the understory of floodplain forests into an aquatic environment. However, a great number of non-aquatic bird species occupy the understory and midstory of these forests. In general, these birds are thought to be sedentary and territorial, but the way they adapt to this dramatic seasonal transformation has never been described in detail. In this study, we describe avifaunal strategies to cope with seasonal flooding in the lower Purus region, central Amazonia, Brazil. We conducted focal observations of five insectivorous species occupying the lowest forest strata in two types of floodplain forest (black- and whitewater) during the low- and high-water seasons. For each observation, the height of the bird above the substrate (ground or water), its vertical position in the forest, and vegetation density around the bird were noted. All species remained present in the floodplain forests during the two seasons and were not recorded in adjacent unflooded (*terra firme*) forest. In general, birds migrated vertically to higher forest strata and most species (three of the five) occupied similar vegetation densities independent of water level. Despite the tendency of all species to rise in relative vertical position at high water, there was a reduction in height above substrate for four of the five species, suggesting that their position relative to water was not an important microhabitat element for them. Responses were similar in the two floodplain forest types. It is likely that the decrease in available space during the flood, combined with similar vertical displacement in arthropods, leads to increased prey density for understory insectivorous birds and permits year-round territoriality without major habitat shifts.

Keywords: birds; microhabitat; Rio Purus; seasonality; tropical forest; vertical migration

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1. Introduction

The massive annual inundation of Amazonian floodplain forests is as drastic an example of seasonality as found anywhere on the planet. The entire ground surface and up to fourteen vertical meters of vegetation go underwater for as long as six months or more, annually converting terrestrial ecosystems to aquatic and back again [1–3]. Adaptations of the biota to this natural flooding cycle are as spectacular as the phenomenon itself, varying from dormancy [4,5] to migration of various types [5]. Migration can occur horizontally to adjoining unflooded *terra firme* forest or vertically to higher forest strata. Strictly terrestrial species vacate the floodplain forest as the water levels start to rise [6,7], whereas some spiders and pseudoscorpions have been observed to migrate vertically [8,9].

Food availability may also drive lateral seasonal movements between floodplain and *terra firme* forest, such as fruits for macaws and other large frugivores/granivores [6]. Most large-bodied piscivorous bird species take advantage of fish concentrations in receding waters but disappear from the floodplains as the water level rises and their fish prey disperse into the floodplain forests [10].

Amazonian floodplains are important for the diversity of birds in the Amazon, with approximately 15% of the non-aquatic Amazonian avifauna considered floodplain specialists [11]. Most of these species are typical passerine insectivores and are not known to be migratory [12]. Specialization on particular vegetation types (macrohabitat) and particular forest strata or vegetation density and structure (microhabitat) is common in birds throughout the world, including in Amazonia [13]. Even within floodplains, certain bird species may occur preferentially depending on water characteristics, which determine forest type. Forests inundated by sediment-rich, "whitewater" rivers, such as the Amazon itself, differ in tree species composition [14], vegetation structure [15,16], and bird species composition [17] from forests flooded by the nutrient-poor "blackwater" found in some Amazonian tributaries (e.g., Rio Negro) [1,3]. Although these habitat associations are reasonably well established, how most birds endure the flooding cycle is poorly known. In fact, we are unaware of any prior systematic study attempting to understand the specific responses of understory Amazonian floodplain birds to the annual flood pulse.

In this paper, we attempt to redress this shortfall by focusing on the behavioral responses of floodplain understory birds to annual flooding. To describe these responses, we performed bird censuses in three major forest types (blackwater and whitewater floodplains and *terra firme*) and measured specific habitat parameters during the low- and high-water seasons in a representative set of five floodplain understory bird species. Specifically, we asked: (1) Do the birds remain in floodplain forests at high water, move to upland forest, or leave the area altogether? (2) If they remain in the floodplains, do they move vertically? (3) Do they use specific microhabitats associated with height above ground or water, forest stratification, or vegetation density? (4) Do bird responses differ between black- and whitewater floodplain forests? We discuss our findings in the context of known natural history of these species and the generalizability of these results to other Amazonian floodplain forest birds.

2. Methods

2.1. Study Area

This study was conducted in the vicinity of Lago Uauaçu, near the confluence of the Purus and Solimões (upper Amazon) rivers, in the central Brazilian Amazon (04°20′ S, 62°28′ W; Figure 1). The region presents an ideal opportunity to investigate the responses of understory floodplain birds to seasonal flooding in a closed-canopy forest matrix, because it contains an extensive mosaic of juxtaposed *terra firme* and floodplain forests inundated by white- and blackwater. The Lago Uauaçu itself is a typical blackwater ria lake fed by rainfall in an upland catchment consisting primarily of *terra firme* forest. Blackwater floodplain forest occurs along the lake margins and along the banks of perennial streams, whereas extensive whitewater floodplain forests cover the confluence of the Solimões and Purus rivers, with a large number of lakes and channels. The lowest and highest water levels in the region are in November and June, respectively [15]. The Piagaçu-Purus Extractive Reserve (10,000 km^2) protects part of the study area, and sampling locations remain almost entirely undisturbed. Human population density is low, with the few communities present dependent on fishing and forest resources (e.g., Brazil nuts) for subsistence and income. Nearest cities (not shown) are Beruri, in the lower Rio Purus, and Codajás, on the Rio Solimões, both west of Manaus (Figure 1).

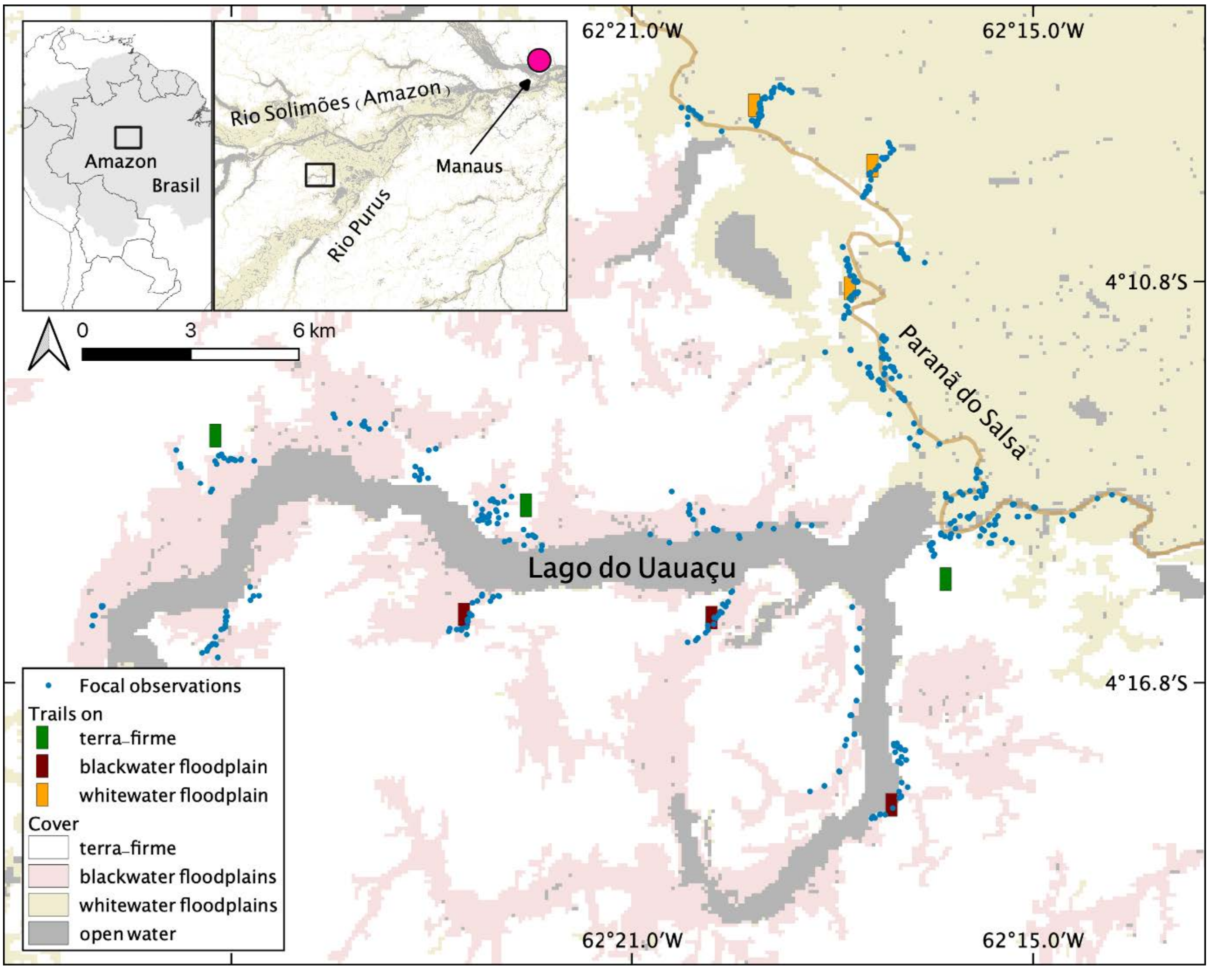

Figure 1. Study area at Lago Uauaçu (main map), near the confluence of the Solimões (upper Amazon) and Purus rivers (right inset), in the central Brazilian Amazon (left inset). Main forest types occurring in the region include extensive tracts of *terra firme* (white), whitewater floodplain (beige), and blackwater floodplain forest (pink). Three established trails (colored rectangles) in each forest type were used for standardized bird sampling, while focal floodplain bird observations were conducted throughout the region (blue dots), wherever focal species were encountered.

2.2. Focal Bird Species

Our focal observations targeted five Amazonian-endemic, floodplain-specialized, bird species that are considered resident and restricted to the forest understory [12]: *Galbula tombacea* (Galbulidae); *Myrmotherula assimilis*, *Myrmoborus leucophrys*, and *Hypocnemoides melanopogon* (Thamnophilidae); and *Hemitriccus minor* (Rhynchocyclidae). These were chosen from a longer list of possible species during the first field season, when we determined that they were common enough to be encountered on virtually every outing and so would yield reasonable sample sizes (see Results).

2.3. Sampling Design and Field Measurements

We conducted two field seasons, one at low water (October 2018) and one at high water (May–June 2019). Observations were performed on foot during low water and from a canoe during the flood season.

To determine if the target species move seasonally between floodplains and *terra firme*, i.e., move horizontally, we conducted systematic avifaunal point-count surveys in all three forest types in both seasons as part of a larger study on habitat specialization by Amazonian birds. Three transects were surveyed within each forest type (Figure 1). Along each transect, we conducted ten 15 min point-counts located 200 m apart. Within a given transect, all ten points were surveyed on the same morning (approx. 5:30–9:30), noting all bird species seen or heard. Detailed survey protocols [17] and results for the entire bird community, including non-flooded habitats, are presented elsewhere [18].

To detect possible seasonal changes by birds in microhabitat use within a given forest type, we also actively searched for individual birds during the morning (up to midday) and late afternoon (after 15:00). For each encounter with an individual of our target species, we took a series of measurements used to generate three indices of microhabitat—two related to height and one to vegetation density (see below). We measured the height at which the bird was perched above the nearest substrate (ground or water), height (above substrate) of the forest canopy (tallest vegetation) directly over the bird, and water depth directly under it (Figure 2). Heights were obtained using a laser rangefinder (Nikon Forestry 550 hypsometer) and water depth using a marked rope with a weight to sink to the ground. To avoid pseudo-replication and any effect of observer presence, we conducted the measurements of the bird's position when initially encountered. We did not use playback to attract birds. When multiple individuals of the same species were detected simultaneously, we took measurements of only one (the first detected).

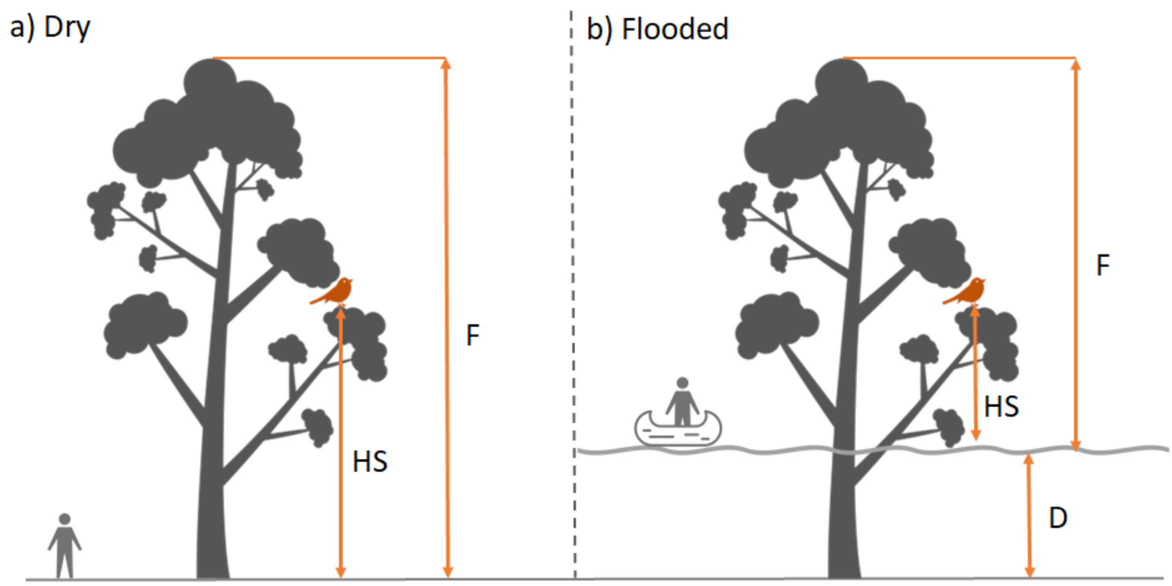

Figure 2. Schematic representation of measurements used to calculate two independent vertical indices of bird microhabitat in the floodplains of the Lago Uauaçu region, central Amazonia. Height above the substrate (HS) was measured directly from the ground at low water (**a**), and from the water surface at high water (**b**). The second index, bird's relative vertical position (P) in the forest vegetation column, is simply the bird's height above ground divided by the total height of the forest. At low water, it was calculated as P = HS/F, and at high water as P = (HS + D)/(F + D), where F is the height of the tallest vegetation above the substrate and directly over the bird and D is the depth of the water below the focal bird.

In addition to height and depth measurements, we also estimated vegetation density for each bird detected. Adapting a method described by Borghesio and Laiolo [19], we imagined a sphere with a one-meter radius around the individual and categorized the proportion of the volume of that sphere filled by vegetation (branches, lianas or leaves) in one of three density classes: low (<1/3 of the sphere filled with vegetation), medium (1/3–2/3 full), and high (>2/3 full).

2.4. Data Analyses

Using the height and depth measurements above, we calculated two complementary metrics: each individual bird's relative vertical position within forest strata (P in Figure 2 caption) and its absolute height above the substrate (ground or water, depending on season; HS in Figure 2). Relative vertical position is the bird's height divided by the forest height, resulting in a standardized value (from zero at ground level to one at the top of the canopy).

This variable treats vertical stratification as a structural feature proportional to forest height and is independent of flooding. In the high-water period, water depth was added to the bird's height and to canopy height to complete the calculation (Figure 2).

The two vertical indices calculated in this study were intended to capture different possible responses to the seasonal presence of water in the environment. Relative vertical position is a proportion of the entire column of vegetation, from the ground to the top of the tree crowns, regardless of flooding or total vegetation height. It was motivated by the concept of vegetative strata being a structural element of the forest thought to be perceived by birds as distinct microhabitats. Constancy in this measure, in the face of rising water level, thus would reflect a microhabitat preference by the birds for a particular forest stratum. Height above the substrate, on the other hand, was intended to reveal the use by birds of the rising base level as a relevant feature, trigger, or reference to determine their vertical position, irrespective of forest stratum per se. Finally, vegetation density was our measure of microhabitat structure independent of any vertical component.

We used a model-ranking approach (mixed generalized linear models, with Gaussian, Gamma or Tweedie distributions, depending on the species; see Supplementary Materials) to characterize variation in the vertical component of microhabitat use by our focal bird species. Within this approach, we considered two response variables: relative position (P) and height above the substrate (HS). For each response variable, we contrasted simple and multiple (additive and interaction) models, including (i) season (low- or high-water), (ii) water depth, as measured locally for every bird observation, (iii) water type (black or white), and (iv) a constant (null model) as predictor variables.

Note that water depth is a potential predictor variable because it changes between seasons. However, it differs from flood stage (the height of the river surface above sea level), which varies gradually over the annual cycle, but is uniform throughout the study area on any particular date. By contrast, depth is a local phenomenon and varies from point to point on the same date, due to the "rise and swale" ground topography typical of Amazonian floodplains [20]. Thus, the spatial variation in water depth at a local scale replicates the intermediate flooding stages that were not sampled by our simple two-season design.

A total of 13 models were contrasted for each response variable for each species. Models for each response variable were ranked using the Akaike information criterion, with adjustment for small sample size (AICc) [21]. Most-plausible models were considered those with dAICc ≤ 2 [21]. Among those, we selected the simplest models (with lowest degrees of freedom) to determine and graphically visualize variation in this vertical component of bird location.

We used Chi-squared tests to compare use of different vegetation density classes by each species between seasons. All analyses were performed using R version 3.3. [22]. Models to investigate changes in birds' height variables were constructed using the glmmTMB function in the glmmTMB package [23] and the model ranking using the *AICctab* function of *bbmle* package [24]. We ran the Chi-squared tests using the chisq.test function. All graphs were generated using the ggplot function in the *ggplot2* package [25].

3. Results

Throughout the study, the focal species were found exclusively in floodplain forests; no individuals were detected from any of the *terra firme* forest transects at either season. We measured habitat parameters of a total of 660 individuals of the five focal species, including 175 during low-water and 485 during the high-water season. Four of the five species occurred in both floodplain forest types; *Galbula tombacea* was detected only in whitewater forest (Table 1).

Table 1. Number of observations of each species in white- and blackwater floodplain forests in the Lago Uauaçu region of the central Amazon.

Species	Low-Water		High-Water		
	Blackwater	Whitewater	Blackwater	Whitewater	Total
Galbula tombacea	0	25	0	77	102
Hemitriccus minor	27	13	73	45	158
Hypocnemoides melanopogon	44	12	96	53	205
Myrmotherula assimilis	10	10	35	54	109
Myrmoborus leucophrys	18	16	17	35	86
Total	99	76	221	264	660

All five bird species changed their vertical position (relative position and height above the substrate) according to water depth or season (Figures 3 and 4), and the best (simplest among most plausible) models included one or both of these predictors (tables in Supplementary Materials). Floodplain forest type (black- or whitewater) was also important to explain the response of *Myrmoborus leucophrys* and, specifically, relative position in *Myrmotherula assimilis*.

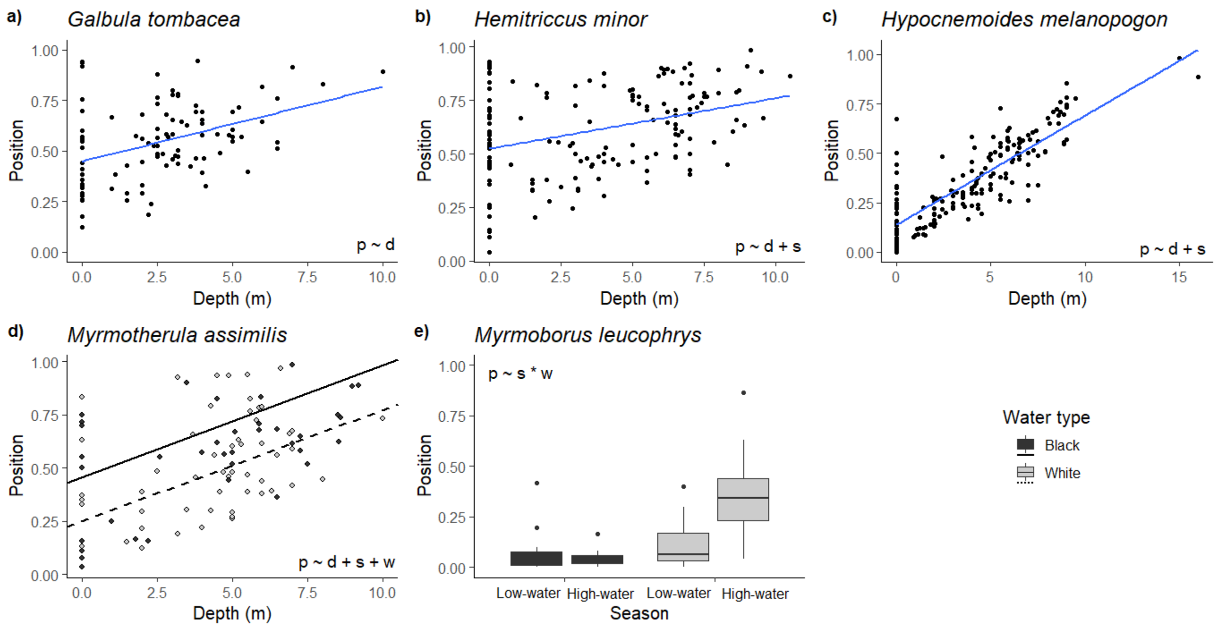

Figure 3. Variation in relative vertical position for five floodplain forest bird species in the Lago Uauaçu region of the central Amazon. The best model to predict vertical position (p) is shown for each species (**a**–**e**) as a line or boxplots and as a written formula, including the predictor variables depth (d), season (s), or water type (w), which is depicted graphically only where it affected results (species d and e). Points in scatterplots (**a**–**d**) represent all individual observations; in boxplots (species e), points are outliers. For *M. assimilis* (species d), black points and solid line represent observations in blackwater, and white points and dashed line represent whitewater. Where both season and depth are included in the best model (**b**–**d**), for clarity only depth is depicted graphically.

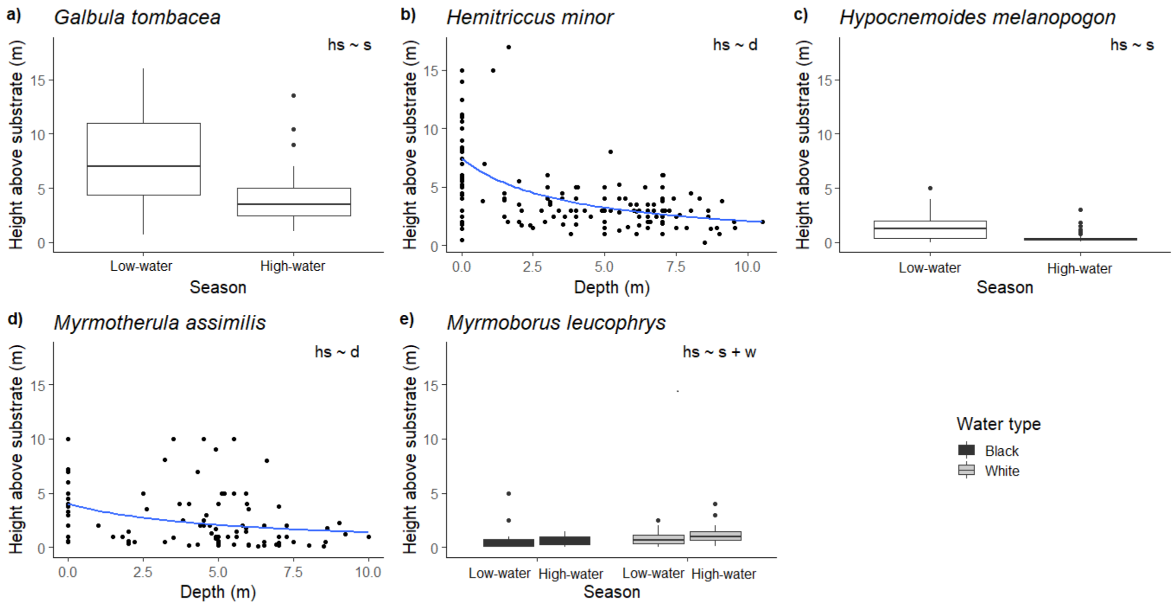

Figure 4. Variation in height above substrate (ground or water) for five floodplain forest bird species in the Lago Uauaçu region of the central Amazon. The best model to predict height above substrate (hs) is shown for each species (**a**–**e**) as a line or boxplots and as a written formula, including the predictor variables depth (d), season (s), or water type (w), which is depicted graphically only where it affected results (species e). Points in scatterplots (**b**,**d**) represent all individual observations; in boxplots (**a**,**c**,**e**), points are outliers.

The relative position of all bird species, except *M. leucophrys*, was related to the local water depth (Figure 3a–d). For *M. assimilis*, the position was higher in whitewater than in blackwater floodplain forests, but showed a similar correlation with local water level in both forest types (Figure 3d). For *M. leucophrys*, relative position only changed in whitewater floodplain forest (Figure 3e).

Height above substrate diminished with increased water depth for *Hemitriccus minor* and *M. assimilis* (Figure 4b,d). For *Galbula tombacea* and *Hypocnemoides melanopogon*, height above substrate was best related to season and the local water level was not relevant (Figure 4a,c). For *M. leucophrys*, there was a slight increase in height above the substrate from the low- to high-water season, and these differences varied slightly between black- and whitewater (Figure 4e).

The vegetation density around each bird differed between seasons for only two species (Figure 5a,c). *Galbula tombacea* frequented more open forest perches in the high-water season than in the low-water season ($p < 0.001$, $x^2 = 30.49$), and *H. melanopogon* preferred perches with intermediate vegetation density during high-water compared to denser vegetation at low-water ($p < 0.001$, $x^2 = 14.2$). The remaining three species did not change their preferences—all most frequently occupied perches with highly dense vegetation during both seasons (Figure 5b,d,e). No species showed any significant difference between floodplain forest types in vegetation density occupied ($p > 0.05$).

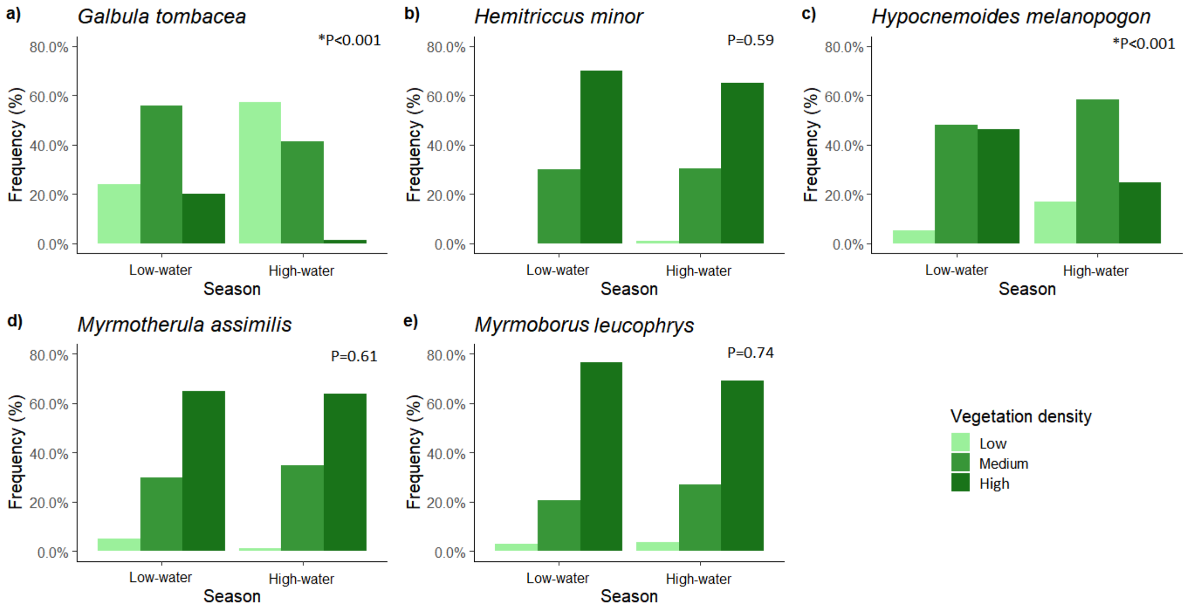

Figure 5. Frequency for each category of vegetation density during the low-water and high-water season for five floodplain bird species (**a**–**e**) in the Lago Uauaçu region of the central Amazon. *p*-values are for the chi-squared analysis of difference between seasons in frequency distributions of density classes for each species. Asterisk (*) indicates significant seasonal difference.

4. Discussion

The objective of this study was to document the response of resident floodplain forest bird species to the annual flood pulse. Results from the five species studied were remarkably consistent and suggest that a typical response of floodplain forest understory birds to the flood pulse is to remain in floodplain forest throughout the year, rise with flooding to somewhat higher forest strata, and maintain vegetation density preferences throughout both seasons, irrespective of water type. However, despite their overall similarities, the exact responses among species were not identical. For example, two species showed some seasonal variation in vegetation density, which may be adaptive or simply a function of vegetation structure available at different flood stages. Considering that the study species represent three different bird families and exhibit distinct sizes, morphologies, and foraging behaviors [11,12], they are expected to occupy unique ecological niches. The extent to which the response of a given species differs from this typical pattern may reflect important aspects of its natural history.

Among our study species, the White-browed Antbird (*Myrmoborus leucophrys*) showed just such an interesting deviation from the typical response to flooding. On the whitewater floodplain, it rose slightly with flooding and maintained a greater height above water than over land. In blackwater, however, it maintained roughly the same vertical position in the forest and the same height above the substrate, regardless of flooding. This seemingly impossible result was due to a behavior that our indices did not capture; all of our observations of this species at high-water in blackwater floodplains were at the water's edge over dry ground. Considering that our blackwater sites were mostly in narrow floodplains adjacent to *terra firme* forest on higher ground, whereas the whitewater floodplains at our study area extend for many kilometers and are far from uplands, individuals in whitewater during the high-water season did not have dry land within easy reach. Apparently, given the choice, *M. leucophrys* prefers to stay over land. Like the other members of its genus, this species is practically terrestrial on dry ground. It nests on the forest floor [26] and so, in floodplain forest, surely must do so only during the low-water season. Perhaps it would even occupy *terra firme* forest at Lago Uauaçu (as the species does in some other parts of the Amazon [26]) were it not for the presence of a very similar congener, *M. myotherinus*, common in the uplands [18].

With the exception of *M. leucophrys* in blackwater (which remained over dry ground at all times), no species maintained constant vertical position in the forest, presumably because flooding forced an average rise. However, most species also did not maintain a constant height over the substrate, implying that flooding simply reduced the vertical space available to birds and that exact positioning was determined by some other factor. Vegetation density as measured here apparently reflected that criterion accurately for three of the five species studied. An implication of this result is that vertical stratification, common in birds everywhere and in virtually all vegetation types [27], reflects the relative availability of specific vegetation densities or structure, rather than the importance of a particular height (either above ground or below the canopy). Thus, given the possibility of finding enough of their preferred microhabitat, birds will tolerate considerable reduction in overall available space and stay put. Monitoring marked individuals will be necessary to determine if territories are constant year-round in these species. Another implication is that vertical habitat stratification should be more prevalent and more finely subdivided in *terra firme* forests, where the available vegetation remains constant throughout the year, than in the floodplains. This may be an important factor in the former's greater bird species richness [11,28].

The reduction in spatial volume available to a bird caused by flooding certainly causes greater spatial overlap among individuals and species relative to the non-flooded season. However, this will not necessarily make finding food more difficult or promote stronger competition. On the contrary, the known vertical migration of non-aquatic insects into this same reduced space might facilitate foraging by insectivorous birds such as those we studied [8]. Measures of insect abundances and densities, and of agonistic interactions among birds and their rates of foraging success and possible changes in diet compostion, would be useful to explore this possibility more fully. We suspect, for example, that *H. melanopogon*, which remained close to the water at all times and nested at high water, takes advantage of a possible concentration of certain insects near the surface forced by the rising waters—much as army ant followers in *terra firme* concentrate at the leading edge of the antswarm to prey on fleeing insects. If flooding indeed facilitates predation on insects, then reduced competition for food resources in the floodplains, made possible by drastic environmental change through the year, may also promote greater coexistence of congeneric or ecologically similar species in the floodplain forests and less fine niche partitioning relative to the *terra firme* avifauna.

Flood stage (water height above sea level) is uniform throughout a given region within the central Amazon, because all these riverine bodies of water are interconnected with no significant waterfalls. Thus, the annual cycle of rising and falling water levels is identical in adjacent forests, regardless of water type. Consistent with this pattern, the effect of water type, where notable at all, was merely in the average vertical position of birds, but not in their response to flooding. The only significant interaction between water type and flooding was in *M. leucophrys*, which we believe to be explained by differences between black- and whitewater floodplains in their distance of our sample sites to non-flooded areas, not by any differences in the forests themselves. The differences between black- and whitewater in average vertical position found in some other species, however, are likely an effect of overall forest height. Blackwater forests tend to be lower in stature than those in whitewater and, thus, to project less above high water [14]. This in turn will force birds in blackwater to maintain higher relative positions in the forest, as found here.

An unexpected result of this study was that water depth at the point of each observation explained our vertical measures better than season in most cases. Flood season observations were all made in the same few-week period, so flood level (water height above sea level) did not vary meaningfully during this period. The variability in depth detected, was therefore strictly a function of ground level, which varies considerably over short distances (<15 m) in the ridge and swale landscape typical of Amazonian floodplains [20]. Birds are unlikely to evaluate water depth directly. Rather, depth of flooding (determined by height of the land) determines height of the trees [29], which in turn is related to how much vegetation projects above the water and what kind of microhabitat a bird will encounter. Thus, at any specific spot, a bird may rise or descend in the forest in search of its preferred microenvironment. In most cases, this very local-scale habitat selection appears to outweigh the simple phenomenon of presence or absence of water in the forest (as recognized by season). Only for *M. leucophrys*, for which we suspect the mere presence of water covering the forest floor is a crucial factor, did season consistently explain vertical variables better than water depth. These results once more appear to emphasize the importance of vegetation structure rather than flooding *per se* for these non-aquatic bird species.

This was the first study to measure and describe the responses of floodplain forest understory birds to the flood pulse. We found a predominant pattern of persistence of resident birds within the floodplain forest, accompanied by a tendency to forage higher in the forest at high water and to seek preferred microhabitat in the reduced space available. Within this general phenomenon, individual species showed unique specific aspects to their responses. To further advance our understanding, future studies should emphasize more species of different foraging guilds, monitor throughout the year using marked and tracked individuals, and quantify prey availability and selection. Understanding the responses of fauna to natural flood cycles is crucial to evaluating impact of activities and processes that alter this cycle, such as hydroelectric dams, irrigation and water diversion, sediment input from agriculture, mining and deforestation, flood control and filling of wetlands, and climate change. Additionally, only establishing a clear understanding of natural baseline behaviors and populations will enable us to recognize the pervasive effects of anthropogenic pollution, already suspected to affect insectivorous bird populations worldwide [30].

Supplementary Materials: The following are available online at https://www.mdpi.com/article/10.3390/f12081004/s1, Table S1. Ranking of all models of relative vertical position for each study species. Models are ordered from lowest to highest value of Δ AICc, which represents the difference in AIC relative to the best model. The simplest model, with lowest degrees of freedom (df) among those with Δ AICc ≤ 2, is shown in bold and was used for the figures. Letters represent model parameters: p = relative vertical position, d = depth, s = season, w = water. Table S2. Ranking of all models of height above substrate for each study species. Models are ordered from lowest to highest value of Δ AICc, which represents the difference in AIC relative to the best model. The simplest model, with lowest degrees of freedom (df) among those with Δ AICc ≤ 2, is shown in bold and was used for the figures. Letters represent model parameters: hs = height above substrate, d = depth, s = season, w = water.

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Data Availability Statement: Data available on request.

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References

1. Junk, W.J.; Piedade, M.T.F.; Schöngart, J.; Cohn-Haft, M.; Adeney, J.M.; Wittmann, F. A classification of major naturally-occurring Amazonian lowland wetlands. *Wetl. Ecol. Manag.* **2011**, *31*, 623–640. [CrossRef]
2. Orians, G.H. The number of bird species in some tropical forests. *Ecology* **1969**, *50*, 783–801. [CrossRef]
3. Goulding, M.; Barthem, R.; Ferreira, E.J.G. *The Smithsonian Atlas of the Amazon*; Smithsonian Institution Press: Washington, DC, USA, 2003.
4. Adis, J.; Mahnert, V. On the natural history and ecology of Pseudoscorpiones (Arachnida) from an Amazonian blackwater inundation forest. *Amaz. Limnol. Oecologia Reg. Syst. Fluminis Amaz.* **1985**, *9*, 297–314.
5. Adis, J. Estratégias de sobrevivência de invertebrados terrestres em florestas inundáveis da amazônia central: Uma resposta à inundação de longo período. *Acta Amaz.* **1997**, *27*, 43–54. [CrossRef]
6. Haugaasen, T.; Peres, C.A. Vertebrate responses to fruit production in Amazonian flooded and unflooded forests. *Biodivers. Conserv.* **2007**, *16*, 4165. [CrossRef]
7. Costa, H.C.M.; Peres, C.A.; Abrahams, I.M. Seasonal dynamics of terrestrial vertebrate abundance between Amazonian flooded and unflooded forests. *PeerJ* **2018**, *6*, e5058. [CrossRef] [PubMed]
8. Adis, J.; Mahnert, V.; Morais, J.W.; Rodrigues, J.M.G. Adaptation of an Amazonian Pseudoscorpion (Arachnida) from dryland forests to inundation forests. *Ecol. Soc. Am. Esa* **1988**, *69*, 287–291. [CrossRef]
9. Platnick, N.I.; Höfer, H. Systematics and ecology of ground spiders (Araneae, Gnaphosidae) from central Amazonian inundation forests. *Am. Mus. Novit.* **1990**, *2971*, 1–16.
10. Davenport, L.C.; Goodenough, K.S.; Haugaasen, T. Birds of two oceans? Trans-Andean and divergent migration of Black Skimmers (*Rynchops niger cinerascens*) from the Peruvian Amazon. *PLoS ONE* **2016**, *11*, e0144994. [CrossRef] [PubMed]
11. Remsen, J.V.; Parker, T.A. Contribution of river-created habitats to bird species richness in Amazonia. *Biotropica* **1983**, *15*, 223–231. [CrossRef]
12. Stotz, D.F.; Fitzpatrick, J.W.; Parker, T.A.; Moskovitz, D.K. *Neotropical Birds: Ecology and Conservation*; University of Chicago Press: Chicago, IL, USA, 1996.
13. Terborgh, J. Habitat selection in Amazonian birds. In *Habitat Selection in Birds*; Cody, M.L., Ed.; Academic Press: Orlando, FL, USA, 1985; pp. 311–338.
14. Pires, J.M.; Prance, G.T. The vegetation types of the Brazilian Amazon. In *Key Enviroments: Amazonia*; Pergamon Press: Oxford, UK, 1985; pp. 109–145.
15. Haugaasen, T.; Peres, C.A. Floristic, edaphic and structural characteristics of flooded and unflooded forests in the lower Rio Purús region of central Amazonia, Brasil. *Acta Amaz.* **2006**, *36*, 25–36. [CrossRef]
16. Haugaasen, T.; Peres, C.A. Tree phenology in adjacent Amazonian flooded and unflooded forests. *Biotropica* **2005**, *37*, 620–630. [CrossRef]
17. Laranjeiras, T.O.; Naka, L.N.; Cohn-Haft, M. Using river color to predict Amazonian floodplain forest avifaunas in the world's largest blackwater river basin. *Biotropica* **2019**, *51*, 330–341. [CrossRef]
18. Gilmore, B.M. Species Richness and Composition of Avifaunal Communities in a Complex Amazonian Landscape. Master's Thesis, University of Salford, Manchester, UK, 2020; 43p.
19. Borghesio, L.; Laiolo, P. Seasonal foraging ecology in a forest avifauna of northern Kenya. *J. Trop. Ecol.* **2004**, *20*, 145–155. [CrossRef]
20. Junk, W.J. General aspects of floodplain ecology with special reference to Amazonian floodplains. In *The Central Amazon Floodplain*; Springer: Berlin/Heidelberg, Germany, 1997; pp. 3–20.
21. Burnham, K.P.; Anderson, D.R. Model selection and multimodel inference. In *A practical Information-Theoretic Approach*, 2nd ed.; Springer: Berlin/Heidelberg, Germany, 2002.
22. R Core Team. Nlme: Linear and Nonlinear Mixed Effects Models. R Package Version 3.1-131. 2017. Available online: https://CRAN.R-project.org/package=nlme (accessed on 25 September 2020).
23. Brooks, M.E.; Kristensen, K.; van Benthem, K.J.; Magnusson, A.; Berg, C.W.; Nielsen, A.; Bolker, B.M. Modeling zero-inflated count data with glmmTMB. *BioRxiv* **2017**, 132753. [CrossRef]
24. Bolker, B.; Bolker, M.B. bbmle: Tools for General Maximum Likelihood Estimation. R Package Version 1.0.20. 2020. Available online: https://rdrr.io/cran/bbmle/ (accessed on 25 September 2020).
25. Wickham, H.; Chang, W.; Wickham, M.H. Package 'ggplot2'. *Creat. Elegant Data Vis. Using Gramm. Graph.* **2016**, *2*, 1–189.
26. Zimmer, K.; Isler, M.L. White-browed Antbird (*Myrmoborus leucophrys*), version 1.0. In *Birds of the World*; del Hoyo, J., Elliott, A., Sargatal, J., Christie, D.A., de Juana, E., Eds.; Cornell Lab of Ornithology: Ithaca, NY, USA, 2020. [CrossRef]

27. Walther, B.A. Grounded ground birds and surfing canopy birds: Variation of foraging stratum breadth observed in Neotropical forest birds and tested with simulation models using boundary constraints. *Auk* **2002**, *119*, 658–675. [CrossRef]
28. Vale, M.M.; Marques, T.L.; Cohn-Haft, M.; Vieira, M.V. Misuse of bird digital distribution maps creates reversed spatial diversity patterns in the Amazon. *Biotropica* **2017**, *49*, 636–642. [CrossRef]
29. Ferreira, L.V. Effects of flooding duration on species richness, floristic composition and forest structure in river margin habitat in Amazonian blackwater floodplain forests: Implications for future design of protected areas. *Biodivers. Conserv.* **2000**, *9*, 1–14. [CrossRef]
30. Powell, L.L.; Cordeiro, N.J.; Stratford, J.A. Ecology and conservation of avian insectivores of the rainforest understory: A pantropical perspective. *Biol. Conserv.* **2015**, *188*, 1–10. [CrossRef]