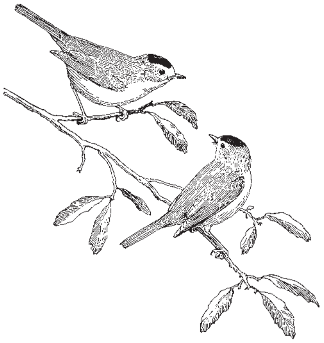

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Understanding the occupancy patterns of Amazon floodplain birds

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ABSTRACT—In the Amazon basin, several species are restricted to or occur primarily in habitats along rivers. However, little is known about habitat occupancy over time and how seasonal fluctuations in the level of rivers affect bird species occurrence in floodplains. In this study, we verified if the occupancy and detection probability of 10 floodplain bird specialist species are related to 3 environmental variables considered to be important for floodplain birds: the number of *Tessaria* shrubs, the number of *Cecropia* trees, and the number of other tree species. We also tested if occupancy and detection probabilities changed among flood pulse seasons. Our study was conducted at 19 sampling sites in the Madeira River floodplain in Rondônia, Brazil, including sites impacted by the Santo Antonio dam. Sampling was done with autonomous recorders and subsequent development of semi-automatic identification models for each species. The best occupancy models show that the number of *Tessaria* shrubs was positively related to occupancy probability for 4 species: Black-and-white Antbird (*Myrmochanes hemileucus*), Parker's Spinetail (*Cranioleuca vulpecula*), White-bellied Spinetail (*Mazaria propinqua*), and Plain-crowned Spinetail (*Synallaxis gujanensis*). The number of *Cecropia* trees was positively correlated with the occupancy of a single species, the Spotted Tody-Flycatcher (*Todirostrum maculatum*). The number of other trees was positively correlated for White-browed Antbird (*Myrboborus leucophrys*), Peruvian Warbling-Antbird (*Hypocnemis peruviana*), and Band-tailed Manakin (*Pipra fasciicauda*). Occupancy probability is similar among sampling periods, which indicates that species remain onsite. The detection probability, however, varied in 9 of the 10 species, probably related to seasonal variation in vocal activity. This variation in detectability needs to be considered in bird surveys in floodplains. In addition, the classification of floodplain species according to the type of habitat specialization can help define the species most vulnerable to environmental changes, such as those caused by hydroelectric plants in the Amazon. *Received 24 October 2021. Accepted 7 March 2022.*

Key words: Amazon dams, automated identification models, Madeira River, passive acoustic monitoring, pattern matching, riparian, vegetation structure.

Entendendo os padrões de ocupação das aves de várzea na Amazônia

RESUMO (Portuguese)—Na Bacia Amazônia, diversas espécies são restritas ou ocorrem primariamente em habitats ao longo dos rios. Entretanto, pouco se conhece sobre a ocupação do habitat ao longo do tempo e como as flutuações sazonais no nível dos rios afeta as espécies de aves que ocorrem nas várzeas. Nesse estudo, nós verificamos se a ocupação e a probabilidade de detecção de 10 espécies de aves especialistas em várzea são relacionadas com 3 variáveis ambientais consideradas importantes para aves de várzea: o número de arbustos do gênero *Tessaria*, o número de árvores do

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gênero *Cecropia* e o número de outras espécies de árvores. Nós também testamos se a ocupação e detectabilidade das espécies muda entre os períodos do pulso de inundação. Nosso estudo foi realizado em 19 sítios amostrais nas várzeas do rio Madeira no estado de Rondônia, Brasil, incluindo sítios impactados pela barragem de Santo Antonio. A amostragem foi feita com gravadores autônomos e posteriormente desenvolvido um modelo de identificação semi-automática para cada espécie. O melhor modelo de ocupação mostrou que o número de arbustos de *Tessaria* é positivamente relacionado a ocupação de 4 espécies: *Myrmochanes hemileucus*, *Cranioleuca vulpecula*, *Mazaria propinqua* e *Synallaxis gujanensis*. O número de árvores do gênero *Cecropia* foi positivamente relacionado a ocupação de uma única espécie, em *Todirostrum maculatum*. O número de outras árvores foi positivamente relacionado a ocupação de *Myrmoborus leucophrys*, *Hypocnemis peruviana* e *Pipra fasciicauda*. A probabilidade de ocupação é similar entre os períodos de amostragem, o que indica que as espécies permanecem nos locais. A probabilidade de detecção, porém, teve uma variação significante para 9 das 10 espécies, provavelmente relacionada a variação sazonal na atividade vocal. Essa variação na detectabilidade deve ser considerada nas amostragens de aves nas várzeas. Adicionalmente, a classificação das espécies de aves de várzea de acordo com o tipo de especialização em habitat pode ajudar a definir quais são as espécies mais vulneráveis a impactos ambientais, como os causados por usinas hidroelétricas.

Palavras-chave: barragens na Amazônia, correspondência de padrões, estrutura da vegetação, modelos de identificação automática, monitoramento acústico passivo, rio Madeira, ripário.

Floodplains are a fundamental component of the high diversity of bird species in the Amazon basin, with more than 400 species recorded in them. It is assumed that at least 15% are restricted to these environments (Remsen and Parker 1983, Cohn-haft et al. 2007a, Laranjeiras et al. 2019). An important feature that explains the patterns of species richness and distribution in floodplains is the gradient of different habitats formed along rivers, influenced by the strong effect of erosion and sediment deposition resulting from water energy and flood pulses (Remsen and Parker 1983).

The seasonal and natural amplitude of fluctuation in rivers' water levels can flood areas that vary from a few meters to kilometers, and many species that occur in these habitats have developed unique behavioral and ecological adaptations that allow them to cope with constant environmental changes caused by water fluctuations (Remsen and Parker 1983, Rowedder et al. 2021). The duration and intensity of rains vary geographically and cause changes in water level among periods of high and low precipitation featuring a flood pulse (Junk et al. 1989). When water levels rise, rivers deposit sediments and nutrients in floodplains, favoring the establishment of vegetation. This intense dynamism, caused by the constant destruction and creation of the substrate on which the floodplain develops, creates complex landscapes (Junk et al. 2011).

Floodplain landscapes are composed by vegetation formations of different stages of the ecological succession process (Remsen and Parker 1983, Robinson and Terborgh 1997, Junk et al. 2011). In white-water rivers (Amazonian rivers with a high concentration of sediments from the Andes), the initial stage of succession after the initial deposition of sediments is characterized by rapid colonization of herbaceous vegetation (Wittmann et al. 2010, Junk et al. 2011). After establishing grasses, shrubs and pioneer trees develop, forming monospecific clusters that characterize the second stage of succession. At this point, the establishment of this arboreal vegetation reduces the impact of erosion, stabilizes the substrate, and provides shading, favoring the establishment of secondary plant species (Wittmann et al. 2010, Junk et al. 2011). Finally, the mature floodplain forest is found in the highest places, which have shorter flooding periods. This mature floodplain forest has developed understory and a greater diversity of large tree species and characterizes an advanced stage of succession (Wittmann et al. 2002).

Understanding this dynamic of ecological succession is important, as some floodplain bird species are associated with particular microhabitats, with specific environmental conditions and vegetation structure elements (Rosenberg 1990, North and Reynolds 1996, Petermann 1997, Robinson and Terborgh 1997). For example, Pearly-breasted Conebill (*Conirostrum margaritae*) and Brownish Elaenia (*Elaenia pelzelni*) have a strong relationship with the distribution of the 2 tree species of the genus *Cecropia* that occur in floodplains: *C. membranacea* and *C. latiloba* (Urticaceae; Rosenberg 1990, Melo et al. 2020). White-bellied Spinetail (*Mazaria propinqua*) and Black-and-white Antbird (*Myrmochanes hemileucus*), among others, are considered strongly associated with herbaceous and shrubby vegetation on river islands, especially with the shrub *Tessaria integrifolia* (Asteraceae; Rosenberg 1990). Although ornithologists commonly categorize bird habitats (e.g., tall floodplain forest, upland forest; Remsen and Parker 1983, Rosenberg 1990, Petermann 1997, Cohn-Haft et al. 2007b), bird species distribution in the floodplains seems to follow continuous and subtle gradients (Laranjeiras et al. 2019, Naka et al. 2020). Furthermore, knowledge about how species occupy these habitats has continually changed. For example, bird species previously recognized as obligate river island specialists (Rosenberg 1990) were recorded in areas of small-scale agriculture on the Amazon River banks (Armacost and Capparella 2012).

A poorly studied feature of floodplain birds is their response to the flood pulse, especially for species that occupy habitats in the early stages of ecological succession (Schulenberg and Rosenberg 2020a, 2020b, 2020c). One study reported the behavioral responses of 5 specialist birds in floodplain forests between the dry and rainy seasons in Amazonia and observed a vertical movement upwards in the vegetation when water level rose, with permanence in the same sites (Rowedder et al. 2021). However, there is still a gap in our knowledge of the temporal and spatial variation patterns in habitat occupancy of practically all floodplain species.

Currently, the construction and operation of dams and hydroelectric plants have caused changes in the natural dynamics of rivers in the Amazon and caused the loss and degradation of floodplain habitats. More than 400 dams are either operating or in the planning stages throughout the Amazon basin (Latrubesse et al. 2017). However, we know little about how bird species restricted to floodplains respond to environmental impacts, such as the construction of hydroelectric dams (Latrubesse et al. 2020). River disruption and regulation by dams can cause habitat loss, decrease, or even suppress ecological connectivity among populations of organisms dependent upon seasonally flooded environments (Latrubesse et al. 2020). Increased knowledge about how species occupy the landscape, especially those restricted to floodplains, can help define priorities for conservation in these environments.

To understand bird spatial and temporal occupancy patterns in the floodplains, we selected 10 birds known to have different habitat affinities and degrees of dependence on floodplain vegetation. Our main goals were to determine (1) the probability of occupancy given 3 environmental variables known for their importance in the occurrence of floodplain species (number of *Tessaria integrifolia* shrubs, number of *Cecropia* trees, and number of "other" trees [trees different from the previous 2 species]); and (2) if the probability of occupancy and detectability changed over the 4 periods that characterize the flood pulse (dry season, beginning of rains, rainy season, and ebbing).

Methods

Study area

Our study took place in 19 sites in the Madeira River floodplain, in the municipality of Porto Velho (10 sites) and the district of Jaci-Paraná (9 sites; Fig. 1). There, patches of *Tessaria* shrubs are considered early stages of succession, while *Cecropia* sp. forests are found in more advanced stages (Robinson and Terborgh 1997). Because some floodplain birds are specialized in habitats with a high density of *Tessaria* shrubs or *Cecropia* trees (Rosenberg 1990), and some are dependent on floodplain forests (which have a high density of different species of trees; Remsen and Parker 1983, Petermann 1997), we established plots of 20 × 100 m, using the recorder as a central point. We counted the number *Tessaria* shrubs, *Cecropia* trees, and the number of tree species different from *Cecropia* or *Tessaria* that had a diameter at breast height (dbh) $\geq$ 10 cm (Supplemental Table S1, Fig. S1).

Mean annual rainfall throughout the Madeira River basin ranges from 2,000 to 2,500 mm, with a rainy season between December and April, and a peak flood (in Porto Velho) between March and April followed by a decrease in the water levels in June. In this region, the amplitude of the flood pulse in the Madeira River varies from 10.8 to 12.4 m between the periods of lowest and highest water levels (Goulding et al. 2003).

Acoustic recording

We used autonomous recorders (LG-brand smartphone wrapped in a water-resistant case and connected to a Monoprice external condenser microphone) at each site, installed in the vegetation at the height of 1.80 m from the ground or water surface depending on the sampling season. The minimum distance between recorders/sites was 400 m. Previous studies using the same recorder model found that the detection distance

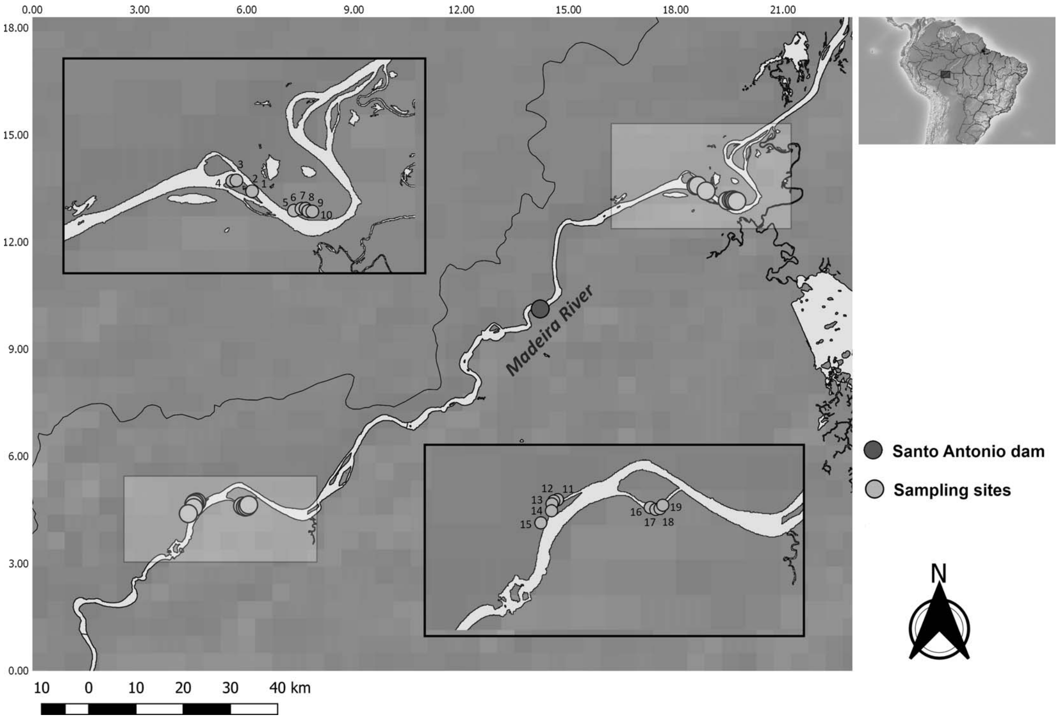

Figure 1. Study sites along the Madeira River in Brazil.

for most species is 100 m from the recorder (Campos-Cerqueira et al. 2019), so this is the distance we considered as sufficient to avoid pseudoreplication.

We programmed recorders to obtain 1 min-long recordings every 10 min, which corresponds to 144 recordings/recorder/d. We sampled for 20 d during each of the 4 seasons of the flood pulse: starting in September 2017 (dry season, with the lowest water level), December 2017 (beginning of the rainy season), March 2018 (top of the rainy season and the water level), and June–July 2018 (ebb season), totaling 80 d of sampling. Recordings were deposited on the RFCx Arbimon platform in the public project Birds of Madeira Flooded Habitats (https://arbimon.rfcx.org/project/birds-of-madeira-flooded-habitats/dashboard).

Selection of bird species

We selected species that were restricted or that occur mainly in Amazon floodplain habitats or that have different degrees of dependence on these environments based on information available in *Birds of the World* (Billerman et al. 2020; Table 1).

Semi-automated identification models

We used semi-automated classification algorithms in the RFCx ARBIMON platform (https://arbimon.rfcx.org) to determine each species' presence and absence in audio recordings. The semiautomatic identification models were used in a set of 100,702 recordings. We had no detections during nighttime, so we only used recordings made between 0500 and 1850 h. Classifications of all recordings were based on a template matching procedure. This procedure searches through audio data for acoustic signals and detects regions highly correlated with a template selected by the user. Regions of interest (ROIs) with values above a correlation threshold are presented as potential detections (LeBien et al. 2020). We selected the threshold of 0.1 to increase the number of presences (although this increases the number of false positives and may capture variations in call types). We also tested the threshold of 0.3, but the number of presences for some species was low (Supplemental Table S2). We manually inspected all potential detections to eliminate false positives using the score filter on all matches resulting from

Table 1. Ten floodplain bird species selected for the study of occupancy and detection in floodplain habitats along the Madeira River in Rondônia, Brazil. We determined their affinity to riverine habitats in the Amazon according to information available in *Birds of the World* (Billerman et al. 2020).

Family	Common name	Scientific name	Habitat	Endemic to Amazonia
Dendrocolaptidae	Straight-billed Woodcreeper	*Dendroplex picus*	Several different habitat types	No
Furnariidae	Plain-crowned Spinetail	*Synallaxis gujanensis*	Floodplains	Yes
Furnariidae	White-bellied Spinetail	*Mazaria propinqua*	River island specialist	Yes
Furnariidae	Parker's Spinetail	*Cranioleuca vulpecula*	River island specialist	Yes
Thamnophilidae	Black-and-white Antbird	*Myrmochanes hemileucus*	River island specialist	Yes
Thamnophilidae	White-browed Antbird	*Myrmoborus leucophrys*	Mainly floodplain	Yes
Thamnophilidae	Silvered Antbird	*Sclateria naevia*	Floodplains, and locally along streams in upland forest	Yes
Thamnophilidae	Peruvian Warbling-Antbird	*Hypocnemis peruviana*	Mainly floodplain forest, less frequently in upland forest	Yes
Rhynchocyclidae	Spotted Tody-Flycatcher	*Todirostrum maculatum*	Associated with wet areas, also disturbed sites	Yes
Pipridae	Band-tailed Manakin	*Pipra fasciicauda*	Floodplain and gallery forest	No

the automated classification to validate the results, marking only the true positives as a presence. The score filter groups the highest-scoring matches in descending order, optimizing the time to find true positives with manual inspection.

Occupancy models

We use the presence/absence matrix (1 presence or absence per sampling day) generated after the semiautomatic identification model's classification to fit dynamic occupancy models through the *colext* function of the *Unmarked* package in R (MacKenzie et al. 2003). We organized our presence/absence matrix, including all sites as rows and each day of sampling as a column, for the 4 sampling seasons, with September as the first sampling season. We chose to use days as sampling units as they are suitable for occupancy analysis and reduce the volume of data that would become unfeasible when using recordings/minutes as units.

Dynamic occupancy models allow inferring about the occurrence of a species on all sampling sites considering changes in occurrence due to colonization, migration/extinction processes, and imperfect detection (MacKenzie et al. 2003, Kéry and Chandler 2016). The dynamic occupancy models include a sampling-level parameter describing the probability of detection conditioned to occupancy (p) and 3 biological-level parameters describing the probability of a site being occupied in the first sampling (psi), the colonization (gam), and migration/extinction (eps) probabilities (MacKenzie et al. 2003).

We included models with the first-sampling occupancy as a function of 1 of the 3 environmental variables (number of *Tessaria*, number of *Cecropia*, and number of other trees). We included detection probability as a function of the sampling period because species occurrence in the floodplain can vary according to the flood pulse period (Rosenberg 1990). For each species, we tested 9 models, with parameters and covariates, and a null model with only the intercept, with the probabilities estimated for all sampling sites together (Table 2).

We compared all models according to the Akaike information criterion, adjusting for small sampling sizes (ΔAICc), and we estimated occupancy by averaging all models with $\Delta\text{AICc} < 2.0$ using the function *modavgPred* from the *AICmodavg* package (Mazerolle 2020). To project each species' occupancy probability over the seasons, we used 1,000 nonparametric bootstrap iterations using the best model. The best model was also used to project the detection frequency by season. We did all analyses in R 4.0.3 (R Core Team 2020).

Results

The number of recordings with positive detections resulting from the classification of semiautomatic identification models ranged from 366 in White-browed Antbird (*Myrmoborus leu-*

Table 2. List of the dynamic occupancy models for 10 species of floodplain birds in the Madeira River, Rondônia, Brazil. Probability of a site being occupied in the first sampling (psi), the colonization (gam), migration/extinction (eps) probabilities, and probability of detection conditioned to occupancy (p). The Y argument means an effect on the model parameter.

Model	Description
psi(.)gam(.)eps(.)p(.)	Null model, without effect in occupancy, colonization, extinction, and detection
psi(.)gam(.)eps(.)p(Y)	No effect in occupancy, colonization, extinction, but season affecting the detection probability
psi(.)gam(Y)eps(Y)p(.)	Season affecting colonization and extinction, but not occupancy and detection probability
psi(.)gam(Y)eps(Y)p(Y)	Season affecting colonization, extinction, and detection probability
psi(Tessaria)gam(Y)eps(Y)p(Y)	Number of *Tessaria* affecting probability of a site being occupied in the first sampling, and season affecting colonization, extinction, and detection probability
psi(Cecropia)gam(Y)eps(Y)p(Y)	Number of *Cecropia* affecting probability of a site being occupied in the first sampling, and season affecting colonization, extinction, and detection probability
psi(Tree)gam(Y)eps(Y)p(Y)	Number of trees affecting probability of a site being occupied in the first sampling, and season affecting colonization, extinction, and detection probability
psi(Tessaria)gam(.)eps(.)p(Y)	Number of *Tessaria* affecting probability of a site being occupied in the first sampling, and season affecting the detection probability
psi(Cecropia)gam(.)eps(.)p(Y)	Number of *Cecropia* affecting probability of a site being occupied in the first sampling, and season affecting the detection probability
psi(Tree)gam(.)eps(.)p(Y)	Number of *Tessaria* affecting probability of a site being occupied in the first sampling, and season affecting the detection probability

cophrys) to 7,789 in Spotted Tody-Flycatcher (*Todirostrum maculatum*). The number of occupied sites varied from 3 in Silvered Antbird (*Sclateria naevia*) and Band-tailed Manakin (*Pipra fasciicauda*) to 16 in Straight-billed Woodcreeper (*Dendroplex picus*) (Supplemental Table S2).

The variable number of *Tessaria* shrubs explained the initial occupancy probability in 4 species: Plain-crowned Spinetail (*Synallaxis gujanensis*), White-bellied Spinetail, Parker's Spinetail (*Cranioleuca vulpecula*), and Black-and-white Antbird (Fig. 2, Table 3). The model with the number of *Cecropia* explained the initial occupancy probability for Spotted Tody-Flycatcher. The number of other trees explained the initial occupancy probability in 3 species: White-browed Antbird, Peruvian Warbling-Antbird (*Hypocnemis peruviana*), and Band-tailed Manakin (Fig. 2, Table 3). Two species, Silvered Antbird and Straight-billed Woodcreeper, did not have the initial occupancy probability explained by any of the variables (Fig. 2, Table 3).

Based on the best model, the pattern of occupancy and detection probability among flood pulse seasons varied among species. The probability of occupancy among seasons does not vary significantly for any species (Fig. 3). Silvered Antbird had the lowest and Straight-billed Woodcreeper had the highest probability of occupancy (Fig. 3). The detection probability among seasons varied for most species, but not for Straight-billed Woodcreeper. A considerable variation in detection probability among seasons was observed in White-browed Antbird, Silvered Antbird, Peruvian Warbling-Antbird, and Band-tailed Manakin (Fig. 4). Band-tailed Manakin had the lowest detection probability (0.00; 1 presence in March) at the top of the rainy season, but it also had the highest value at the beginning of the rainy season (1.00; 279 presences in Jun–Jul; Fig. 4).

Discussion

Our models explained the probability of occupancy for 4 species in *Tessaria* shrub habitat, 1 species in *Cecropia* tree habitat, and 3 species in habitats with other trees. The pattern of occupancy among seasons did not vary for any species; however, detection probability did for most of them.

One of the most notable characteristics of the Amazonian basin floodplains is the heterogeneity of habitats characteristic of different ecological succession stages (Remsen and Parker 1983). Some species are generalists and occupy diverse environments, but others have become microhab-

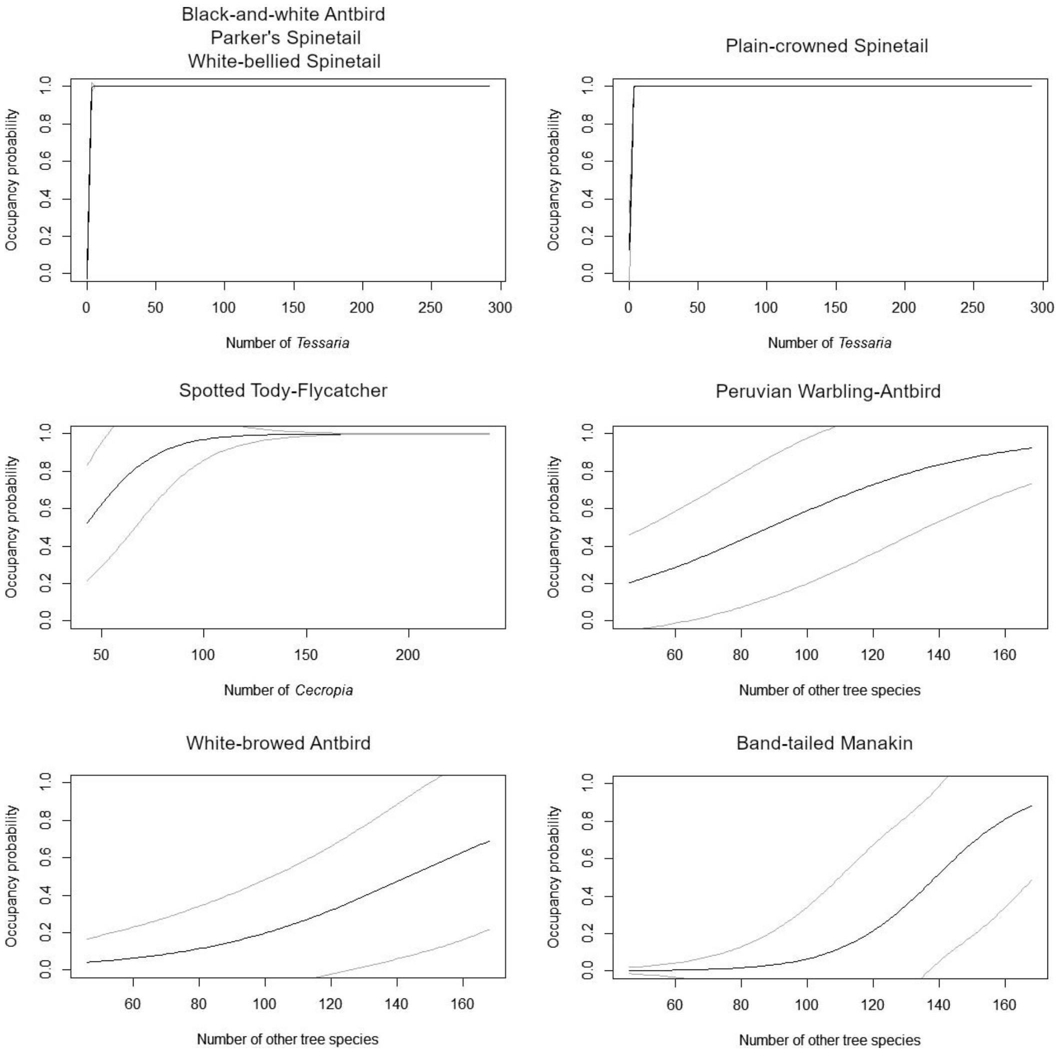

Figure 2. Predicted relationship between occupancy and environmental variables based on the best model. Gray lines represent the 95% confidence interval.

itat specialists (Rosenberg 1990, Robinson and Terborgh 1997). Similar to our study, Robinson and Terborgh (1997) also found more species restricted to habitats dominated by *Tessaria* shrubs than habitats with an abundance of *Cecropia* trees.

Our quantitative occupancy estimates agree with the association of White-bellied Spinetail, Parker's Spinetail, and Black-and-white Antbird with *Tessaria* (Rosenberg 1990; Schulenberg and Rosenberg 2020a, 2020b, 2020c). Shrubs of *Tessaria* occur in early successional stages of floodplain vegetation and are an essential habitat for some lowland species (Remsen and Parker 1983, Rosenberg 1990, Robinson and Terborgh 1997, Cohn-Haft et al. 2007b).

Species such as Black-and-white Antbird, Parker's Spinetail, and White-bellied Spinetail occasionally occur in other early successional habitats (Schulenberg et al. 2007, Billerman et al. 2020). However, they seem to be more common in areas with an abundance of *Tessaria* (Rosenberg 1990). For example, on river islands in Peru, White-bellied Spinetail practically occurred only in *Tessaria*, and 55% of the foraging behavior occurred associated with this shrub (Rosenberg 1990). The vegetation structure in these early

Table 3. All dynamic occupancy models with ΔAICc < 2 for each of 10 bird species that use floodplain habitats in the Madeira River, Rondônia, Brazil. Probability of a site being occupied in the first sampling (psi), the colonization (gam), migration/extinction (eps) probabilities, and probability of detection conditioned to occupancy (p). The Y argument means an effect on the model parameter.

Species	Best occupancy model	Number of parameters	AICc	ΔAICc	Weight	Cumulative weight
Straight-billed Woodcreeper	psi(.)gam(.)eps(.)p(.)	4	1285.07	0	0.84	0.84
Plain-crowned Spinetail	psi(Tessaria)gam(.)eps(.)p(Y)	8	485.72	0	0.91	0.91
White-bellied Spinetail	psi(Tessaria)gam(.)eps(.)p(Y)	8	388.08	0	0.98	0.98
Parker's Spinetail	psi(Tessaria)gam(.)eps(.)p(Y)	8	342	0	0.81	0.81
Black-and-white Spinetail	psi(Tessaria)gam(.)eps(.)p(Y)	8	311.14	0	0.88	0.88
White-browed Antbird	psi(Tree)gam(.)eps(.)p(Y)	8	338.1	0	0.52	0.52
	psi(.)gam(.)eps(.)p(Y)	7	338.66	0.56	0.39	0.52
Silvered Antbird	psi(.)gam(.)eps(.)p(Y)	7	189.11	0	0.87	0.87
Peruvian Warbling-Antbird	psi(Tree)gam(.)eps(.)p(Y)	8	495.29	0	0.88	0.88
Spotted Tody-Flycatcher	psi(Cecropia)gam(.)eps(.)p(Y)	8	457.66	0	0.49	0.49
	psi(Tessaria)gam(.)eps(.)p(Y)	8	459.5	1.84	0.2	0.69
Band-tailed Manakin	psi(Tree)gam(.)eps(.)p(Y)	8	176.48	0	0.80	−73.04

stages of succession is so distinctive from other Amazonian habitats that most of the birds restricted to floodplains in the Amazon occur there (Petermann 1997). Due to the strong association of these species with *Tessaria*, future studies investigating the persistence of this shrub in areas under the impact of hydroelectric plants may have important implications for the conservation of these bird species (Melo et al. 2021).

This strong association between birds and a dominant plant species also occurs in bamboo by some bird species in the Amazon. Some of these specialists occasionally occur in other habitats but are more common in areas with high bamboo density (Lebbin 2007, 2013). Although our results indicate that the occupancy of Plain-crowned Spinetail is associated with an increased number of *Tessaria*, this species occurs in several early successional stage habitats and prefers areas with dense vegetation, but its occurrence appears to be restricted to seasonally flooded habitats along rivers throughout its range (Remsen 2020).

In our study, we found the Spotted Tody-Flycatcher as the only species associated with an increased number of *Cecropia* trees, but the information available in the literature indicates that this species is a broader generalist, occurring in virtually all floodplain habitats and even in degraded habitats within cities (Lees and Moura 2017, Walther 2020). In our study, although Spotted Tody-Flycatcher is predicted to occupy areas impacted by the dam (sites 11–15 in Supplemental Fig. S2), its occupancy was higher in areas with more *Cecropia* and *Tessaria*.

Another group of highly specialized birds in floodplains is forest-dependent species (Remsen and Parker 1983). In our study, Peruvian Warbling-Antbird, White-browed Antbird, and Band-tailed Manakin had an occupancy probability related to a higher number of other tree species that characterize the floodplain forest. Studies indicate that some floodplain forest species tend not to occupy upland forest areas (Rowedder et al. 2021). Interspecific aggressiveness and territoriality between congeneric species that occupy different habitats in successional stages may be a hypothesis that explains why some floodplain species do not occur on terra firme (Robinson and Terborgh 1997). Forest species may have ecological and behavioral limitations that prevent them from crossing large areas of open habitats (Lees and Peres 2009), making the forest floodplain specialist species a priority for conservation since impacts such as dams can convert floodplain forests into open habitats (Cochrane et al. 2017, Melo et al. 2021).

In our study, 2 species did not have the probability of occupancy associated with any of the 3 variables. The Straight-billed Woodcreeper is a habitat generalist, occurring in various habitat types throughout its range (Marantz et al. 2020). In the case of Silvered Antbird, other essential elements of the landscape, which were not evaluated in our study, may be more associated with the occupancy patterns of this species, such as

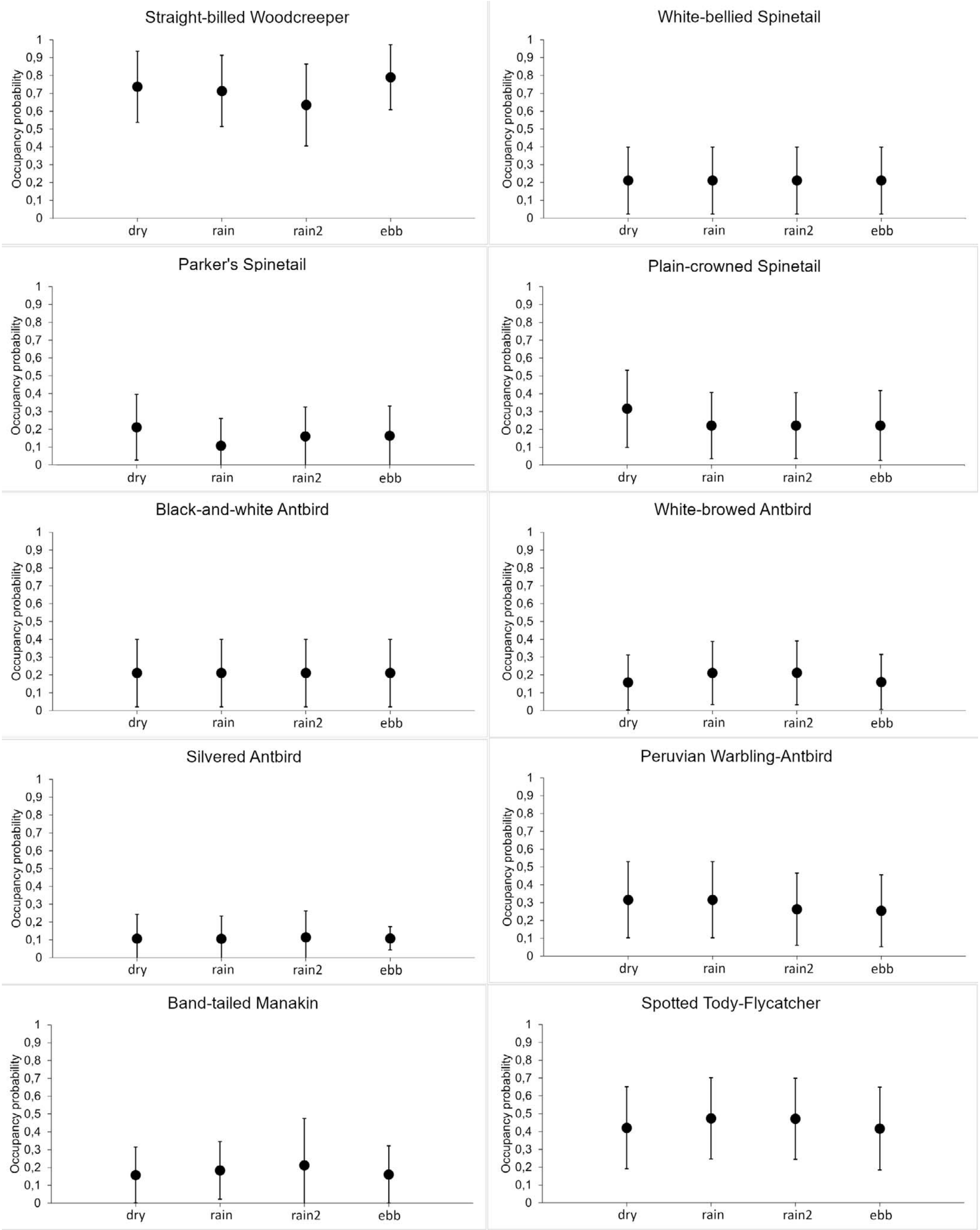

Figure 3. Occupancy probability and 95% confidence interval between the flood pulse seasons for each bird species predicted by the best model. Rain = beginning of the rainy season, rain2 = top of the rainy season.

the presence of vegetation above water (Zimmer et al. 2020). Likewise, future studies may further advance the understanding of these habitat relationships by testing the occupancy with more variables (e.g., *Gynnerium* spp. cane stands) that were not tested in our study.

The occupancy among the different periods of the flood pulse did not vary for any species,

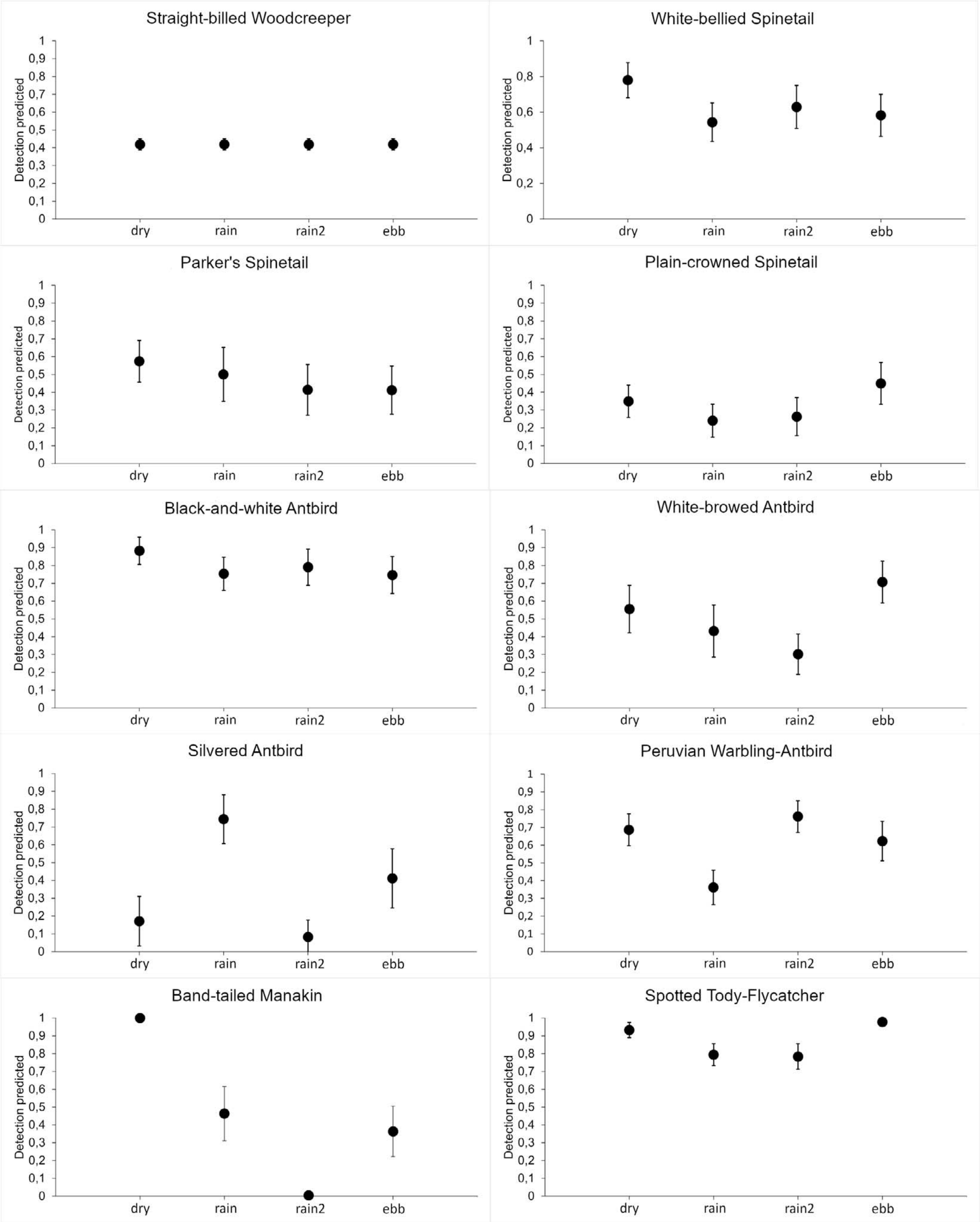

Figure 4. Detection predicted and 95% confidence interval between the flood pulse seasons for each bird species predicted by the best model. Rain = beginning of the rainy season, rain2 = top of the rainy season.

indicating that even floodplain understory species maintain their territories as long as there is still vegetation above the water. Recent studies have revealed that forest floodplain species change their foraging height following the rise in the water level in the rainy season (Rowedder et al. 2021). In the case of species that occupy habitats with naturally lower vegetation of the early successional stages of the floodplain, there is a gap in knowledge about the response of these birds to the decrease in available habitat during the rainy season. Our results demonstrate that the species we study remain on the same sites at different stages of the flood pulse seasons. This result is significant for the knowledge of the ecology of species considered specialists in floodplain fluvial islands (White-bellied Spinetail, Parker's Spinetail, and Black-and-white Antbird in our study), which already occupy a spatially limited environment.

The detection probability among seasons varied considerably for most species. In most birds, the detection probability is strongly related to vocal activity. It can vary throughout the day, throughout the year, and among years (Campos-Cerqueira and Aide 2016, Odom et al. 2016, Jahn et al. 2017, Demko and Mennill 2018, Peréz-Granados et al. 2021) and is influenced by both endogenous factors, such as hormonal changes during the reproductive period (Odom et al. 2016, Demko and Mennill 2018), and exogenous ones, such as moonlight and temperature (Pérez-Granados et al. 2021).

It is possible that the detection probability variation that we found in our study is related to the period of reproductive activity that differs among the species of our study. For example, Spotted Tody-Flycatcher has the highest detection probability in the ebb season, coinciding with the known reproductive period for this species in the floodplains of the Madeira River (Melo and Greeney 2019). In the Band-tailed Manakin, males vocalize in leks (Kirwan and Green 2011). The variation we found indicates that the peak of male vocalization in the Madeira River floodplains occurs during the dry season and decreases at the beginning of the rainy season, possibly due to the presence of active nests. During the rainy season, practically no vocal activity occurs, perhaps indicating the post-reproductive period. The 3 river island specialists closely associated with *Tessaria* had the highest probability of detection during the dry season, which may indicate the breeding season for birds specializing in this habitat type.

Our results provide more information about the habitat preferences of some floodplain species and highlight the importance of *Tessaria integrifolia* for the conservation and maintenance of species diversity in the floodplain. New studies using a larger number of variables and covering a larger region could deepen the patterns found here. Increasing our knowledge on the habitat requirements of species could be fundamental in a scenario of increasing threats to the floodplains, such as the planning for the implementation of several hydroelectric plants in the Amazon (Latrubesse et al. 2017, 2020).

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