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The width of riparian habitats for understory birds in an Amazonian forest

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Abstract. Riparian habitats are important for the maintenance of regional biodiversity. Many studies have compared bird distributions between riparian and non-riparian habitats but have not established how wide riparian habitats used by birds are, as measured by distance from the nearest stream. We investigated the distribution of understory birds along gradients of distance from streams, soil clay content, and slope in a central Amazonian forest, by mist-netting birds three times in 45 plots. We used nonmetric multidimensional scaling (NMDS) to reduce the dimensionality of species quantitative (abundance) and qualitative (presence–absence) composition to one multivariate axis. Estimates of the width of riparian habitats as indicated by understory birds depended on the community attribute considered, measuring 90 m for species quantitative composition and 140 m for species qualitative composition. Species distributions were correlated with clay content but were independent of slope, while distance from streams was positively correlated with clay content but independent of slope. Clay content affects plant species composition, which in turn, may influence bird species composition. However, distribution patterns of birds in relation to distance from streams are consistent among studies carried out in many different temperate and tropical regions, indicating an effect of distance from streams itself. Protection of riparian habitats is one of the most widely used conservation strategies, and Brazilian environmental legislation mandates the protection of a 30 m wide strip of riparian vegetation on either side of small streams. We show that the protected strip should be much wider and recommend strategies to place other forms of land protection contiguous with riparian areas so that Brazilian environmental legislation better fulfills its role of protecting biodiversity associated with riparian habitats.

Key words: biodiversity conservation; Brazil; buffer strips; community structure; ecological boundaries; environmental gradients; environmental legislation; Neotropical birds; riparian corridors; species distributions; tropical forest.

INTRODUCTION

Habitat specificity at the species level (Tuomisto et al. 1995, Jankowski et al. 2009) may generate distinct species assemblages within a given community due to environmental heterogeneity (Keller et al. 2009). However, this phenomenon is not universal among taxonomic groups (Aguiar et al. 2006), being stronger in some (Drucker et al. 2008) and weaker in others (Kinupp and Magnusson 2005).

Birds typically show high habitat specificity, as shown in the classic study of their distribution in vertical vegetation strata (MacArthur and MacArthur 1961). Habitat selection in birds may be determined by vegetation type (Rotenberry and Wiens 1980) or, within the same vegetation type, by plant species composition (Lee and Rotenberry 2005), treefall gap characteristics (Banks-Leite and Cintra 2008), and dynamics (Schemske and Brokaw 1981). Moreover, bird species distributions may vary in relation to distance from streams (Willis 1977, Cohn-Haft et al. 1997, Woinarski et al. 2000, Cintra and Cancelli 2008).

Ecologists typically recognize two habitat types along the gradient of increasing distance from streams: riparian and non-riparian, each with its own characteristics and dynamics (Naiman et al. 1993). Many studies of the conservation value of riparian habitats have documented differences between the species composition and abundance of birds in riparian and non-riparian habitats defined a priori (e.g., Bub et al. 2004, Palmer and Bennett 2006, Lehmkuhl et al. 2007). Since the width of riparian habitats as defined by environmental legislation is typically arbitrary, and varies between jurisdictions (Lee et al. 2004), making that legislation more effective requires studies to determine the width of riparian habitats (Metzger 2010). Here we estimated, a posteriori, how wide the riparian habitat is that is used by birds in relation to distance from streams.

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The Brazilian Forest Code (law 4.771/1965; *available online*)[5] designates riparian zones as Permanent Protection Areas (hereafter referred to by the Portuguese acronym APP). The width of the strip in which riparian vegetation must be protected is defined according to the width of the stream at its highest level, in marginal strips, varying from 30 m on each side for streams less than 10 m wide to 500 m for streams wider than 600 m. However, in an Amazonian forest, Drucker et al. (2008) showed that the understory herb assemblage associated with riparian habitats extends much farther than 30 m for small streams. Also, 30 m may not be sufficient to account for edge effects (Brosofske et al. 1997) and ecosystem processes, such as above- and belowground water flow.

The Brazilian Forest Code mandates that all rural landholdings located in forest areas in the country's Amazon region must maintain at least 80% forest cover. A strong political movement has been pressing the government to reduce this to 50%, and proposals have been made to reduce the width of APPs for small streams (Lewinsohn 2010; also BIOTA-FAPESP [Programa de Pesquisas em Caracterização, Conservação e Uso Sustentável da Biodiversidade do Estado de São Paulo] and ABECO [Associação Brasileira de Ciência Ecológica e Conservação], information *available online*).[6] If the width of the riparian habitat used by riparian-associated species is greater than 30 m around small streams, then the spatial arrangement of the forest cover that rural landholders must maintain might determine the effectiveness of APPs. For example, maintaining 50% forest cover that is contiguous to APPs could be more efficient than maintaining 80% of forest cover that is not contiguous to APPs, since the latter arrangement would strand populations of riparian species in narrow, isolated strips of forest extending 30 m to each side of streams.

In this study, we examined the distribution of understory birds in a terra firme forest in central Amazonia in relation to both distance from streams and edaphic and topographic variables (clay content and slope), which are known to be related to plant species composition (Costa et al. 2005, Kinupp and Magnusson 2005, Poulsen et al. 2006, Bohlman et al. 2008, Drucker et al. 2008). The community composition of understory birds indicates that the riparian habitat extends much farther than the strip protected by Brazilian environmental legislation.

MATERIALS AND METHODS

Study area

This study was carried out in Reserva Ducke, a central Amazonian forest reserve administered by the Instituto Nacional de Pesquisas da Amazônia (INPA), in Manaus, Amazonas State, Brazil (02°55′–03°01′ S, 59°53′–59°59′ W; Fig. 1). The reserve protects 10 000 ha of well-drained relatively undisturbed terra firme forest that is not subject to long-term floods (Ribeiro et al. 1999). The understory is dominated by sessile palms and shaded by a closed canopy approximately 30–37 m high, in which occasional emergent trees reach 40–45 m (Ribeiro et al. 1999).

Topography at the site is a mosaic of plateaus and valley bottoms, the latter with riparian habitats (Ribeiro et al. 1999) along streams that typically measure <10 m wide. The elevational difference between the highest (105 m) and lowest (43 m) plot we sampled in the reserve is 63 m. The clay content of soils varies with elevation, such that soils in higher areas contain more clay (Chauvel et al. 1987). The strong correlation between clay content and elevation ($r_S = 0.916$, $P < 0.001$) means that elevation is an effective proxy for clay content (Costa et al. 2005, Costa and Magnusson 2010). Distance from streams is positively correlated with clay content ($r_S = 0.764$, $P < 0.001$), but not with slope ($r_S = -0.055$, $P = 0.773$). The rainy season at the site typically extends from November to May, and the dry season from July to October (Marques Filho et al. 1981). Between April 1965 and November 1980, mean annual temperature was 26°C, and mean annual precipitation was 2362 mm (Marques Filho et al. 1981).

Bird species composition in Reserva Ducke is well known. Avifaunal studies conducted during the last 40 years were summarized by Cintra (2008). Since the first bird species list (Willis 1977), nearly 50 species have been added by Cohn-Haft et al. (1997), Naka (2004), Banks-Leite and Cintra (2008), and Cintra and Naka (2012), for a total of >340 species recorded in the reserve and its surroundings.

Sampling design

As Site 1 of Brazil's Long-term Ecological Research Program (PELD), Reserva Ducke contains a standard RAPELD (a system that combines RAP [Rapid Assessment Program] and PELD [Pesquisas Ecológicas de Longa Duração], which is the Brazilian acronym for LTER [Long-Term Ecological Research Program]) sampling grid (Magnusson et al. 2005, Costa and Magnusson 2010) established by the Research Program in Biodiversity (PPBio). This 25-km^2 grid is composed of six north–south trails and six east–west trails, each measuring 5 km long and spaced from adjacent trails at 1-km intervals. These trails provide access to 45 plots (Fig. 1). The plots measure 250 m long and have widths that depend on the taxonomic group being studied (Costa and Magnusson 2010). Mist nets are placed only along the center line, but terrestrial herbs are recorded in 2 m wide plots, while trees with diameter at breast height greater than 30 cm are recorded in 40 m wide plots. Thirty of these 45 plots are evenly spaced on the grid at 1-km intervals and 15 are close (3.7 ± 1.2 m [mean ±

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[5] http://www.planalto.gov.br/ccivil_03/leis/L4771.htm

[6] http://www.abecol.org.br/wordpress/wp-content/uploads/extra-pdf/biota-fapesp_e_abeco-sintese-cfb_e_biodiversidade.pdf

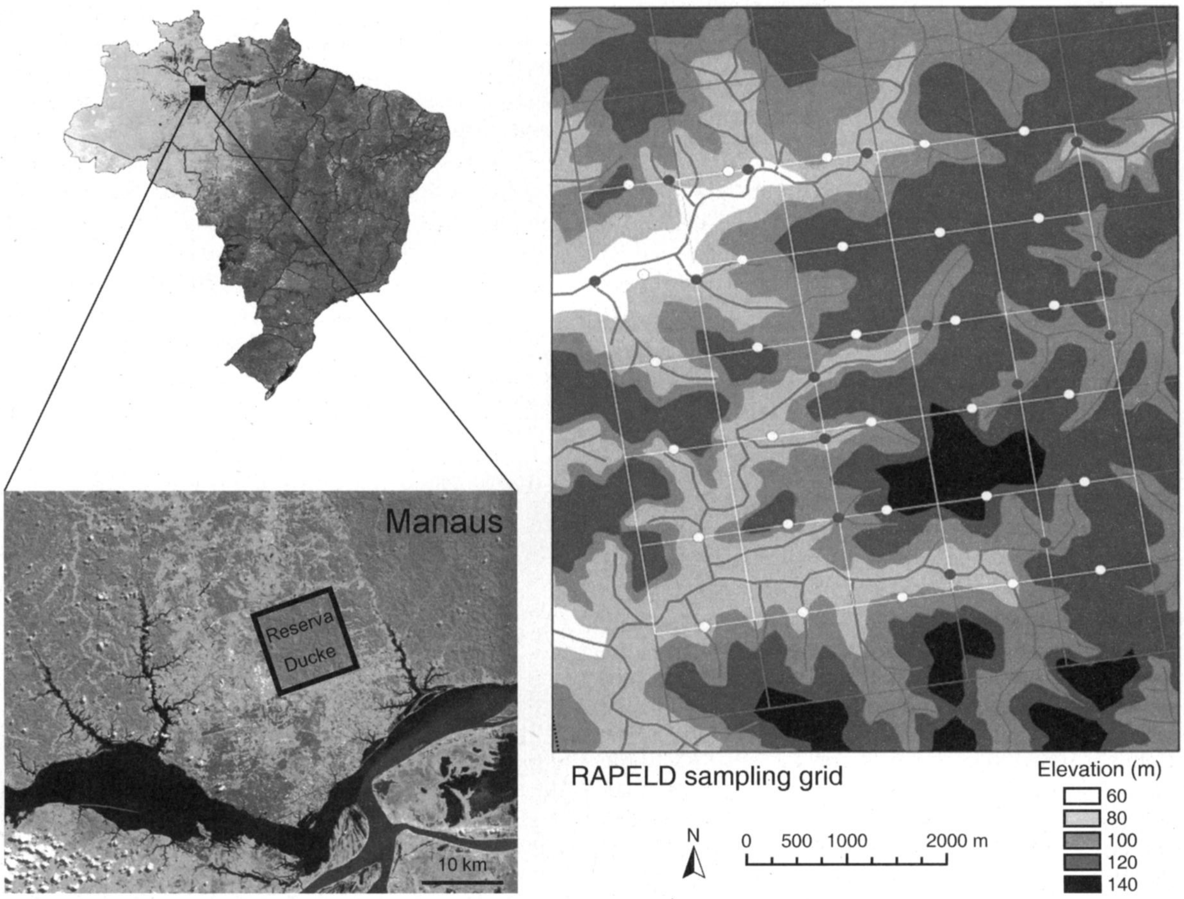

FIG. 1. Localization of Reserva Ducke, Manaus, Amazonas State, Brazil. Topography and streams in the study area, showing the trails and plots of the RAPELD sampling grid (see *Materials and methods: Sampling design* for further clarification). White dots indicate the location of the evenly spaced plots, and gray dots indicate riparian plots. The figure is modified from Ribeiro et al. (1999), de Miranda et al. (2005), and Instituto Nacional de Pesquisas Espaciais (www.cbers.inpe.br).

SD]) to stream margins and thus classified as riparian. The stream reaches (12 different streams) beside these 15 riparian plots were 1.32 m to 4.14 m wide (2.28 ± 0.77 m). Plots are not rectangular, but follow landscape features. The evenly spaced plots follow elevational contours in order to minimize edaphic variation within each plot, while the riparian plots follow the stream margin (Costa and Magnusson 2010).

Data collection

We sampled birds in three discrete periods in 2009: 10 January to 25 May, 12 July to 7 September, and 19 September to 19 November. We sampled each of the 45 plots once in each sampling period. We used 16 9-m mist nets arranged in pairs along the 250-m length of each plot, such that each pair was separated from adjacent pairs by 10 m. As sampling effort is usually measured as net-hours (i.e., one 12-m mist net open for one hour; Keyes and Grue 1982), we converted our sampling effort with 9-m mist nets to those units. In the first sampling period, we used eight mist nets with 50-mm mesh and eight mist nets with 70-mm mesh. In the later sampling periods, all mist nets had 32-mm mesh. Variation in mesh sizes increases the range of species that can be captured efficiently by the mist nets (Heimerdinger and Leberman 1966, Piratelli 2003), but as all mesh sizes were used in all plots, within-plot variation in mesh sizes does not affect our conclusions about differences among plots.

Mist nets were left open from 06:00 to 12:00 and revised hourly. Captured birds were identified using the field guide of Restall et al. (2007) and were banded with standard CEMAVE (Centro Nacional de Pesquisa para Conservação das Aves Silvestres) bands (ICMBio/SNA permission number 3052 [Chico Mendes Institute for Biodiversity Conservation/Sistema Nacional de Anilhamento]). Since the use of mist nets captures mainly understory birds and occasionally birds that walk on the ground or that fly above net level (Karr 1981), we considered all individuals captured as understory birds to avoid misinterpretation. Birds that could not be identified in the field were photographed or collected (IBAMA/SISBIO permission number 17229-1 [Instituto Brasileiro do Meio Ambiente e dos Recursos Naturais

Renováveis/Sistema de Autorização e Informação em Biodiversidade]) and later identified by specialists. All collected birds were deposited in the INPA Bird Collection.

For plots whose starting point was <30 m from the nearest stream ($n = 17$), the distance between the plot and the stream was measured at six points spaced at 50-m intervals along the central line of each plot with a measuring tape, and the mean distance was used in analyses. For the other plots ($n = 28$), the linear distance between the geographic coordinates of the plot center and the nearest stream was used. The distance between plots and streams varied from 1.34 m to 579 m (141.64 ± 165.89 m). A soil sample was collected to a depth of 5 cm at each of the same six points per plots. These samples were mixed to form a composite sample for each plot, 500 g of which was analyzed for clay content in the INPA Soil and Plant Thematic Laboratory. Slope was measured with a clinometer along a 3-m line perpendicular to the central line (1.5 m to each side) at each of the same six points per plots. The mean of the six values for each plot was used in analyses.

Data on distance from streams were obtained for all 45 plots, while data on clay content and slope were available only for the 30 evenly spaced plots. Distance from streams was measured in previous studies and the data provided by R. de Fraga and J. Schietti. Clay content and slope data, as well as information on the collection methods and the researchers involved, are on the PPBio website.[7]

Data analysis

Dissimilarity in species composition between plots was calculated with both abundance data (referred to hereafter as quantitative composition) and presence–absence data (qualitative composition). Patterns in quantitative data are typically driven by common species, which tend to show large differences in abundances between plots. Qualitative data give more weight to rare species, because common species occur in most plots and contribute little to between-plot differences.

We used nonmetric multidimensional scaling (NMDS) to reduce the dimensionality of species composition data to one axis of a multivariate ordination, in order to describe the major patterns in understory bird community (McCune and Grace 2002). The ordinations with quantitative data were based on the Bray-Curtis distance measure. Abundance of each species in each plot was standardized by converting it to relative abundance prior to analysis. Abundance of a given species in a given plot was calculated as the total number of individuals captured in the three sampling periods, excluding recaptures of banded birds in the plot where they were originally captured. The ordinations with qualitative data were based on Sørensen's index.

We tested the effect of distance from streams on species quantitative and qualitative composition, represented by NMDS scores. To identify discontinuities in community attributes with increasing distance from streams, we used piecewise regression, an objective technique useful for estimating ecological thresholds (Toms and Lesperance 2003). Piecewise regression identifies the two lines that best characterize variance in the data. The intersection point of the two lines was considered an indicator of the size of the riparian habitat recognized by understory birds. Piecewise regression has been used to identify ecological thresholds in many biological groups, such as vegetation (Toms and Lesperance 2003, Cancino 2005), corals (Zvuloni et al. 2008), and mayflies (Sonderegger et al. 2009). The piecewise regression was undertaken with the statistical package SiZer version 0.1-3 (*available online*)[8] in the program R version 2.12.0 (R Development Core Team 2010), which uses a nonparametric method to approximate the response function and its derivatives and then examines how those functions change across the range of the explanatory variable. SiZer makes fewer assumptions than conventional threshold models and explores a full range of smoothing functions (Sonderegger et al. 2009).

We used direct gradient analysis (McCune and Grace 2002) to illustrate in a compound graph (developed in the program R by C. S. Dambros) the distribution of species in relation to distance from streams. Analysis of similarity (ANOSIM; McCune and Grace 2002) was employed to test whether there was a difference in species quantitative and qualitative composition between riparian and non-riparian plots.

RESULTS

The understory bird community

During 9720 net-hours in 45 plots, we captured 1499 birds belonging to 98 species and 29 families. During 6480 net-hours in the 30 evenly spaced plots, we captured 916 birds belonging to 80 species and 25 families. The number of species captured in each plot varied from 10 to 28 (18.31 ± 3.85 [mean ± SD]) and the number of individuals captured varied from 15 to 58 (32.62 ± 9.71). The 20 most-captured species ($n \geq 23$) accounted for 72% of all captures. Twenty-five species were captured only once (Table 1). Single captures may not represent the habitat association of the species. Therefore, we also analyzed the data without these species. However, their inclusion did not change the conclusions, and the 95% confidence intervals overlapped for all analyses, so we present only the data for analyses of all captured species.

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[7] http://ppbio.inpa.gov.br

[8] http://CRAN.R-project.org/package=SiZer

TABLE 1. The number of understory bird species recorded in Reserva Ducke, Manaus, Amazonas State, Brazil, in riparian ($n = 26$) and non-riparian plots ($n = 19$).

	Riparian		Non-riparian	
Species, by family	Plots	Individuals	Plots	Individuals
Accipitridae				
Leucopternis melanops	1	1	0	0
Alcedinidae				
Chloroceryle aenea	7	7	0	0
Chloroceryle inda	5	5	0	0
Bucconidae				
Bucco capensis	1	1	0	0
Bucco tamatiá	2	2	2	2
Malacoptila fusca	0	0	1	1
Monasa atra	1	1	0	0
Caprimulgidae				
Hydropsalis nigrescens	1	1	0	0
Cardinalidae				
Cyanoloxia cyanoides	13	20	3	3
Columbidae				
Geotrygon montana	14	20	5	8
Dendrocolaptidae				
Campylorhamphus procurvoides	0	0	1	1
Certhiasomus stictolaemus	8	10	7	8
Deconychura longicauda	1	1	8	12
Dendrocincla fuliginosa	15	21	10	22
Dendrocincla merula	12	21	13	20
Dendrocolaptes certhia	3	3	2	2
Dendrocolaptes picumnus	0	0	1	1
Glyphorynchus spirurus	22	67	18	46
Hylexetastes perrotii	4	5	3	4
Sittasomus griseicapillus	0	0	1	1
Xiphorhynchus pardalotus	19	39	14	25
Emberizidae				
Arremon taciturnus	1	2	0	0
Formicariidae				
Formicarius colma	9	11	9	13
Furnariidae				
Automolus infuscatus	5	7	1	1
Philydor erythrocercum	2	2	0	0
Philydor pyrrhodes	3	3	1	1
Xenops minutus	2	4	1	1
Galbulidae				
Galbula albirostris	3	7	5	9
Jacamerops aureus	1	1	0	0
Grallariidae				
Grallaria varia	1	1	0	0
Myrmothera campanisona	0	0	1	1
Icteridae				
Cacicus haemorrhous	2	3	0	0
Momotidae				
Momotus momota	9	10	6	7
Picidae				
Celeus elegans	3	3	0	0
Pipridae				
Corapipo gutturalis	2	2	0	0
Dixiphia pipra	18	36	15	26
Lepidothrix serena	7	10	5	5
Manacus manacus	1	1	1	1
Pipra erythrocephala	1	1	4	5
Tyranneutes virescens	0	0	1	1
Polioptilidae				
Microbates collaris	0	0	2	2
Rhynchocyclidae				
Corythopis torquatus	1	1	0	0
Hemitriccus zosterops	0	0	1	1
Lophotriccus vitiosus	1	1	0	0
Mionectes macconnelli	21	61	12	25
Mionectes oleagineus	2	2	1	1
Tolmomyias assimilis	0	0	1	1

TABLE 1. Continued.

	Riparian		Non-riparian	
Species, by family	Plots	Individuals	Plots	Individuals
Scleruridae				
Sclerurus caudacutus	0	0	1	1
Sclerurus mexicanus	4	5	2	2
Sclerurus rufigularis	5	6	4	5
Strigidae				
Glaucidium hardyi	2	2	3	3
Thamnophilidae				
Epinecrophylla gutturalis	1	1	5	7
Frederickena viridis	4	7	5	6
Gymnopithys rufigula	18	43	10	22
Hypocnemis cantator	14	32	1	1
Myrmeciza ferruginea	0	0	1	2
Myrmornis torquata	1	1	0	0
Myrmotherula axillaris	2	2	0	0
Myrmotherula guttata	2	5	0	0
Myrmotherula longipennis	0	0	3	5
Myrmotherula menetriesii	1	1	3	4
Percnostola rufifrons	9	16	5	14
Pithys albifrons	26	132	16	60
Schistocichla leucostigma	16	25	0	0
Thamnomanes ardesiacus	9	21	7	17
Thamnomanes caesius	8	9	6	7
Thamnophilus murinus	3	5	5	10
Willisornis poecilinotus	8	13	3	4
Thraupidae				
Lanio fulvus	0	0	6	7
Lanio cristatus	0	0	1	1
Lanio surinamus	8	12	12	19
Tityridae				
Myiobius barbatus	1	1	1	1
Onychorhynchus coronatus	9	13	1	1
Schiffornis turdina	5	7	4	4
Terenotriccus erythrurus	0	0	1	1
Trochilidae				
Amazilia versicolor	1	1	0	0
Campylopterus largipennis	10	12	4	5
Florisuga mellivora	11	16	1	1
Glaucis hirsutus	2	2	0	0
Heliothryx auritus	1	1	0	0
Phaethornis bourcieri	20	35	7	10
Phaethornis ruber	2	2	0	0
Phaethornis superciliosus	22	61	10	11
Thalurania furcata	17	34	7	7
Topaza pella	2	2	0	0
Troglodytidae				
Microcerculus bambla	2	3	3	3
Pheugopedius coraya	2	4	3	3
Trogonidae				
Trogon rufus	2	2	1	1
Turdidae				
Turdus albicollis	13	16	10	12
Tyrannidae				
Attila spadiceus	7	10	3	4
Neopipo cinnamomea	1	1	0	0
Platyrinchus coronatus	5	7	0	0
Platyrinchus platyrhynchos	0	0	1	1
Platyrinchus saturatus	3	4	0	0
Ramphotrigon ruficauda	1	1	0	0
Rhytipterna simplex	2	2	0	0
Vireonidae				
Hylophilus muscicapinus	0	0	1	2
Hylophilus ochraceiceps	3	4	2	5

Note: Species names follow Comitê Brasileiro de Registros Ornitológicos (CBRO; www.cbro.org.br).

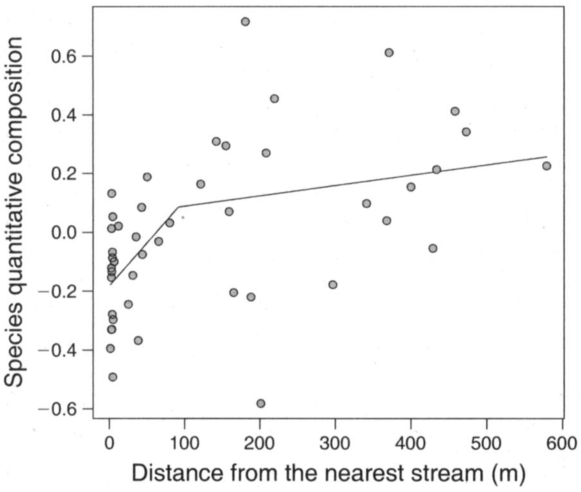

FIG. 2. Effect of distance from streams on the quantitative composition of understory birds in Reserva Ducke, Manaus, Amazonas State, Brazil. Quantitative composition is represented by a nonmetric multidimensional scaling (NMDS) axis derived from Bray-Curtis distances of site-standardized data from mist-net captures. Lines represent piecewise regressions ($R^2 = 0.27$, $P < 0.001$), carried out in the statistical package SiZer version 0.1-3 in the R program version 2.12.0 (see *Materials and methods: Data analysis* for more information).

The effects of environmental variables on the distribution of understory birds

In the ordination of quantitative data from the 45 plots, one NMDS axis explained 40% of the variation in the matrix of original distances between plots. The quantitative composition of birds, represented by the NMDS axis, showed turnover throughout the gradient of increasing distance from streams (Fig. 2), and piecewise regression indicated that the main effect of distance from streams on the relative abundance of species extended ~90 m (95% CI = 49.7–494.9) from streams ($R^2 = 0.27$, df = 42, $P < 0.001$).

In the ordination of qualitative data from the 45 plots, one NMDS axis explained 36% of the variation in the matrix of original distances between plots. The qualitative composition of birds, represented by the NMDS axis, showed turnover throughout the gradient of increasing distance from streams (Fig. 3), and piecewise regression indicated that the main effect of distance from streams on the presence-absence of species extended ~140 m (95% CI = 50.5–417.8) from streams ($R^2 = 0.343$, df = 42, $P < 0.001$).

Based on the distance from streams at which qualitative composition showed a distinct turnover, we considered riparian plots to be those within 140 m of streams and non-riparian plots to be all others. Using this criterion, 26 of the 45 plots were in riparian habitat and 19 in non-riparian habitat (Fig. 4). More species were captured in riparian plots ($n = 81$) than in non-riparian plots ($t = 2.77$, df = 43, $P = 0.008$; $n = 69$). More species ($n = 52$) were captured in both riparian and non-riparian plots than exclusively in riparian or non-riparian plots ($t = 29.019$, df = 68.26, $P < 0.001$; $n = 46$). The number of species captured exclusively in riparian plots ($n = 29$) was greater than the number of species captured exclusively in non-riparian plots ($t = 3.679$, df = 37.99, $P < 0.001$; $n = 17$). The number of individuals captured was also greater in riparian plots ($n = 973$) than in non-riparian plots ($t = 3.893$, df = 43, $P < 0.001$; $n = 526$). Both quantitative (ANOSIM $R = 0.263$, $P = 0.001$) and qualitative (ANOSIM $R = 0.291$, $P = 0.001$) species compositions differed between riparian and non-riparian plots. The mean Sørensen's index between plots within habitat categories was 0.551 ± 0.094 and between plots in different habitats was 0.601 ± 0.098.

In the ordination of quantitative data from the 30 evenly spaced plots, in which clay content and slope were measured, one NMDS axis explained 45% of the variation in the matrix of original distances between plots. Variation in scores on the NMDS axis was related to clay content ($R^2 = 0.165$, df = 28, $P = 0.015$; Fig. 5), but was independent of slope ($R^2 = -0.023$, df = 28, $P = 0.556$).

In the ordination of qualitative data from the 30 evenly spaced plots, one NMDS axis explained 35% of the variation in the matrix of original distances between plots. Neither clay content ($R^2 = -0.016$, df = 28, $P = 0.473$) nor slope ($R^2 = -0.019$, df = 28, $P = 0.511$) were related to variation in scores on the NMDS axis.

DISCUSSION

The understory bird assemblage in sites closer to streams was different and had more habitat-restricted

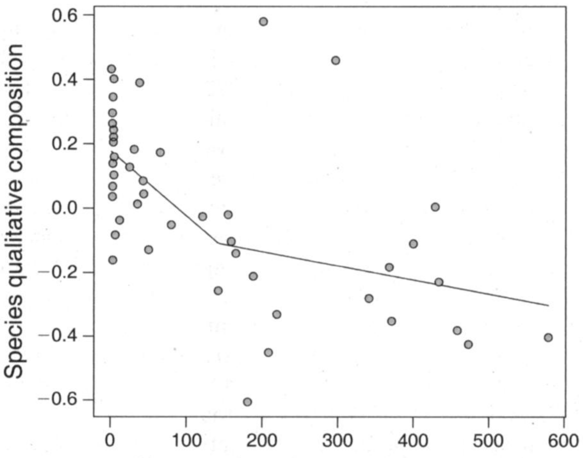

FIG. 3. Effect of distance from streams on the qualitative composition of understory birds in Reserva Ducke, Manaus, Amazonas State, Brazil. Qualitative composition is represented by a NMDS axis derived from Sørensen's index for presence–absence data from mist-net captures. Lines represent piecewise regressions ($R^2 = 0.343$, $P < 0.001$), carried out in the statistical package SiZer version 0.1-3 in the R program version 2.12.0 (see *Materials and methods: Data analysis* for more information).

species than that farther from streams (Fig. 4). More bird species and more individual birds were captured at sites closer to streams. The average magnitude of dissimilarities between riparian and non-riparian plots was only moderate (0.601 ± 0.098 on the Sørensen scale), because there was a cline in similarities with distance from streams, rather than abrupt differences. Both quantitative and qualitative compositions of riparian bird assemblages were statistically distinct from those farther from streams. These patterns are similar to those documented for bird assemblages in riparian and non-riparian habitats throughout the world (Woinarski et al. 2000, Catterall et al. 2001, Bub et al. 2004, Palmer and Bennett 2006, Anjos et al. 2007, Lehmkuhl et al. 2007, Chan et al. 2008), and confirm that riparian habitats play an important role in maintaining regional biodiversity (Naiman et al. 1993). However, many riparian corridors in deforested areas may be too narrow to sustain wildlife in Amazonia (Lees and Peres 2008).

Previous studies comparing bird assemblages in riparian and non-riparian habitats used arbitrarily defined thresholds between these habitat types. Riparian habitats have been defined as anywhere from the stream bank to 100 m from the stream, while non-riparian habitats have been proposed at between 100 and 750 m from streams (Catterall et al. 2001, Bub et al. 2004, Palmer and Bennett 2006, Anjos et al. 2007, Lehmkuhl et al. 2007, Chan et al. 2008). Although all of these studies report differences between sites that are very close to streams and sites that are distant from them, a rigorous comparison of riparian and non-riparian habitats is difficult without a standard definition of the size of the riparian zone.

The distribution of species along a given environmental gradient may reflect changes in factors correlated with that gradient (Whittaker 1972). In our study, the distribution of understory birds along the gradient of increasing distance from streams was related to soil clay content, but not to slope. In Reserva Ducke, distance from streams is positively correlated with clay content, but not with slope. Earlier studies in Reserva Ducke have shown that plant species composition is related to clay content (Costa et al. 2005, Costa et al. 2008). However, the effect of clay content could be due to its correlation with distance from streams, since distance from streams (Drucker et al. 2008) and soil moisture (Catterall et al. 2001) were also found to be related to plant species composition. Vegetation is an important determinant of bird species composition (Rotenberry 1985, Fleishman et al. 2003, Lee and Rotenberry 2005). A relationship between bird species composition and clay content documented in a tropical savanna in Australia, for example, was more likely driven by changes in vegetation structure than soil characteristics (Woinarski et al. 1999). Likewise, in a subtropical eucalypt forest in Australia, where plant species composition was independent of clay content, bird species composition was independent of clay content as well (Catterall et al. 2001).

Bird species may respond differently to the gradient of distance from streams. Some species, such as *Schistocichla leucostigma* (Willis 1977), are more associated with streams, while others, such as *Willisornis poecilinotus* (Cintra and Cancelli 2008), are more often found away from streams. Moreover, the distributions of many species, such as *Dendrocincla fuliginosa* and *D. merula* (Cintra et al. 2006), are independent of distance from streams. A segregation of species along the gradient of distance from streams may result from selection for different resources (Jankowski et al. 2009) or interspecific aggression (Robinson and Terborgh 1995), but we do not have data to distinguish between those hypotheses.

At the community level, distributional patterns of birds with regard to distance from streams are similar in studies carried out in temperate (Bub et al. 2004, Lehmkuhl et al. 2007) and tropical regions (Palmer and Bennett 2006, Chan et al. 2008). This indicates that distance from streams itself may exercise an effect on bird species distributions, rather than specific local effects, such as changes in vegetation structure or soil. Areas close to streams have more insects, and consequently, attract more insectivorous birds (Iwata et al. 2003, Chan et al. 2008). In addition, species, such as kingfishers (*Chloroceryle aenea* and *C. inda*), depend on streams for the fish they eat. However, it is difficult to untangle the effects of distance from streams from the effects of environmental variables correlated with that gradient (e.g., Catterall et al. 2001). Studies carried out in discretely defined habitats complicate the interpretation of the individual effects of correlated variables, while studies carried out with continuous habitats variables allow for more detailed interpretations, since correlated variables may vary in different ways along a given environmental gradient. Since measures to protect riparian habitats are based on distance from streams, more studies are needed to clarify the effects of distance from streams per se on bird community structure.

Implications for conservation

Understanding how biological communities vary at increasing distances from streams is vital for designing effective conservation strategies because preserving strips of riparian vegetation is one of the most commonly used conservation strategies (Marczak et al. 2010). However, it is difficult to establish a single riparian strip that protects all species associated with riparian habitats because the optimal width may vary among streams and taxonomic groups (Spackman and Hughes 1995).

In Brazil, the strips of riparian vegetation protected by law vary with stream size. For streams <10 m wide, mandated strips are 30 m wide on either side of the stream. The Brazilian Forest Code (law 4.771/1965; see footnote 5) has established Permanent Protection Areas

(APPs) in order to "protect hydrological resources and the surrounding landscape, as well as geological stability, biodiversity, and the gene flow of plants and animals, in addition to preserving soils and assuring the well-being of human populations." Studies carried out in Reserva Ducke, where streams are typically <10 m wide, have shown that this 30-m definition is too small to protect understory herbs (Drucker et al. 2008), snakes (de Fraga et al. 2011), and understory birds (this study) associated with riparian habitats.

The most efficient width of a riparian strip for protecting riparian-associated species depends on stream size (Lock and Naiman 1998, Woinarski et al. 2000), adjacent vegetation (Peak and Thompson 2006), and edge effects that influence populations in riparian habitats (Marczak et al. 2010). In addition, we have shown that the specific community attribute used to determine the width of riparian habitats affects estimates of that width. Since common species tend to occur widely, and are thus poor indicators of specific assemblages (Strong and Bock 1990), qualitative composition may be a more useful attribute for quantifying the distances to which riparian-associated species assemblages extend.

Given that edge effects may extend 60 m into riparian habitats in temperate regions (Brosofske et al. 1997), and given that the effect of distance from streams on species qualitative composition extended for 140 m in our study, we hypothesize that at least 200 m on each side of streams are needed to protect understory birds associated with riparian habitats in Reserva Ducke. Some edge effects may extend much further into Amazonian forest fragments (Laurance et al. 2002), and a previous Amazonian study in a deforested area showed that riparian strips <400 m wide tend to degrade and have depauperate bird and mammal faunas (Lees and Peres 2008). The riparian strips studied by Lees and Peres (2008) were subject to many disturbances, including fires and cattle trampling, and it is difficult to distinguish the effects of strip width from area and matrix effects. However, our study indicates that, even in the best-case scenario, with no deleterious matrix effects, the bird community recognizes a riparian zone that is ~280 m wide (140 m each side of the stream) for streams <10 m wide. That is nearly five times the current width of APPs for small streams as defined by the Brazilian Forest Code.

Not all taxa respond the same way to deforestation. Lima and Gascon (1999) found little effect of isolation in riparian strips 140–190 m wide for frogs and small mammals in a study site only 80 km from Reserva Ducke. Also, our data are for only a single site and the critical width of the riparian zone probably depends on soil characteristics, topography, and climate. Nevertheless, the large critical width we estimated (~400 m) is the same as that suggested for birds in the State of Mato Grosso by Lees and Peres (2008), an area with different vegetation and climate that is on the southern edge of the Amazon rainforest. In the absence of other information, it appears that riparian strips of at least hundreds of meters are needed on each side of streams to conserve Amazonian riparian bird assemblages.

Since 2009, the Brazilian Parliament, which has two Houses (Chamber of Deputies and Federal Senate), has been considering modifications of the Brazilian Forest Code (Lewinsohn 2010, Metzger et al. 2010) that would reduce the width of the legally protected strips for small streams <5 m wide to 15 m (BIOTA-FAPESP and ABECO; see footnote 6). Such a modification might give short-term economic benefits to landholders, but was not based on science and may lead to irreversible loss of biodiversity (Michalski et al. 2010). The Brazilian Forest Code was passed by the Chamber of Deputies in May 2011 and is now being considered by the Senate. The Brazilian scientific community, represented by the Brazilian Society for the Progress of Science (SBPC) and the Brazilian Academy of Sciences (ABC), has participated in these discussions, and published a background document to support the debate (SBPC and ABC 2011). The proposal sent to the Senate (Projeto de Lei da Câmara [PLC] 30/2011; *available online*)[9] maintains a minimum width of 30 m on each side of small streams in agricultural areas, but an amendment presented by a Senator reduces the protected riparian habitats to 15 m in urban areas. Moreover, the proposal in the Senate uses the edge of the regular stream channel, instead of the stream width at highest level, to determine the width of APPs. This modification reduces the APPs of streams wider than 10 m only during high water from 50 m to 30 m on each side of streams.

The fight to maintain 30 m as the width of legally protected riparian strips around small streams indicates that it would not be politically feasible to increase their width in the near future, and our data indicate that 30 m is too narrow for many bird species. Therefore, we

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[9] http://legis.senado.gov.br/mate-pdf/91478.pdf

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Fig. 4. Occurrence of understory bird species in relation to distance from streams in 45 plots in Reserva Ducke, Manaus, Amazonas State, Brazil. The vertical line indicates the distance estimated by piecewise regression to which streams influence species qualitative composition. Squares indicate presence in the plot of the species listed to the right of the graph. Plots are ordered from left to right by distance from the nearest stream, and the bars at the bottom indicate the relative distance of each plot from the nearest stream, which varied from 1.34 m to 579 m.


Platyrinchus platyrhynchos
Microbates collaris
Sittasomus griseicapillus
Sclerurus caudacutus
Hylophilus muscicapinus
Myrmotherula longipennis
Lanio fulvus
Tolmomyias assimilis
Terenotriccus erythrurus
Hemitriccus zosterops
Myiobius barbatus
Deconychura longicauda
Glaucidium hardyi
Epinecrophylla gutturalis
Myrmotherula menetriesii
Galbula albirostris
Campylorhamphus procurvoides
Frederickena viridus
Lanio cristatus
Formicarius colma
Tyranneutes virescens
Dendrocolaptes certhia
Myrmothera campanisona
Dendrocincla merula
Lanio surinamus
Thamnomanes caesius
Pipra erythrocephala
Thamnomanes ardesiacus
Thamnophilus murinus
Dendrocolaptes picumnus
Bucco tamatia
Hylophilus ochraceiceps
Microcerculus bambla
Turdus albicollis
Dixiphia pipra
Malacoptila fusca
Glyphorynchus spirurus
Lepidothrix serena
Xenops minutus
Schiffornis turdina
Myrmeciza ferruginea
Momotus momota
Dendrocincla fuliginosa
Xiphorhynchus pardalotus
Pithys albifrons
Manacus manacus
Pheugopedius coraya
Mionectes macconnelli
Certhiasomus stictolaemus
Phaethornis superciliosus
Gymnopithys rufigula
Sclerurus rufigularis
Geotrygon montana
Hylexetastes perrotii
Percnostola rufifrons
Thalurania furcata
Mionectes oleagineus
Philydor pyrrhodes
Attila spadiceus
Phaethornis bourcieri
Trogon rufus
Sclerurus mexicanus
Cyanoloxia cyanoides
Campylopterus largipennis
Willisornis poecilinotus
Neopipo cinnamomea
Hypocnemis cantator
Automolus infuscatus
Onychorhynchus coronatus
Jacamerops aureus
Celeus elegans
Florisuga mellivora
Rhytipterna simplex
Schistocichla leucostigma
Myrmotherula guttata
Phaethornis ruber
Cacicus haemorrhous
Chloroceryle inda
Chloroceryle aenea
Platyrinchus coronatus
Grallaria varia
Amazilia versicolor
Bucco capensis
Monasa atra
Corythopis torquatus
Myrmotherula axillaris
Topaza pella
Glaucis hirsutus
Philydor erythrocercum
Myrmornis torquata
Lophotriccus vitiosus
Leucopternis melanops
Ramphotrigon ruficauda
Hydropsalis nigrescens
Platyrinchus saturatus
Corapipo gutturalis
Heliothryx auritus
Arremon taciturnus
Presence–absence
580 m
0 m
Plot, by distance from the nearest stream

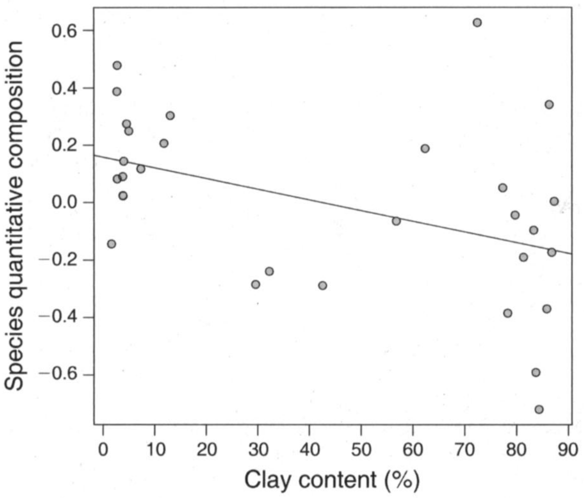

FIG. 5. Relationship between clay content and quantitative composition of understory birds in Reserva Ducke, Manaus, Amazonas State, Brazil. Quantitative composition is represented by a NMDS axis derived from Bray-Curtis distances of site-standardized data from mist-net captures (R^2 = 0.165, P = 0.015).

recommend that, where feasible, other legally required protected areas within a property are placed contiguous to APPs in riparian habitats. This is important because the species richness in riparian strips depends on distances from sources, as well as strip width (Hawes et al. 2008, Lees and Peres 2008). Protected areas contiguous with APPs would increase the width of natural vegetation around streams and the riparian strips would act as corridors between other protected areas (Lima and Gascon 1999). Inclusion of such a requirement in the Brazilian Forest Code is probably not feasible, but federal, state, and municipal governments, and agricultural extension agencies could encourage the practice by providing subsidies or tax incentives to landholders who maintain such configurations. Some such initiatives have already been implemented in the State of Santa Catarina in Southern Brazil (FATMA [Fundação do Meio Ambiente]; information *available online*),[10] and could be implemented in Amazonia.

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