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The value of forest strips for understorey birds in an Amazonian plantation landscape

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ABSTRACT

Remnant forest strips are frequently proposed as valuable conservation tools in fragmented tropical landscapes, yet we currently lack evidence to evaluate their potential conservation value for native biota. We examined the potential value for understorey forest birds of 30-year-old riparian and terra firme (unflooded) primary forest strips within a large silvicultural landscape in the north-east Brazilian Amazon, where the matrix is dominated by Eucalyptus plantations. We conducted mist-netting in eight forest strips connected to continuous forest (four of each forest type), with a total of 24 replicate sampling sites located near to (<1 km), far from (2.5-9 km), and within undisturbed forest controls (i.e. 16 samples within the strips, and 8 in controls). Bird communities in both strip types changed with increasing distance along forest remnants into the plantation matrix. Matrix-embedded samples were characterised by a higher representation of birds typical of secondary growth forest but not those typical of the Eucalyptus-dominated matrix. While the long-term viability of the bird populations in these remnants remains unclear, our data demonstrate that forest strips can provide important habitat for many bird species that are otherwise rarely found outside primary forest. Forest strips therefore provide an important tool to enhance biodiversity conservation in plantation landscapes. The relative practical ease with which these areas can be selected and maintained means that the protection of forest strips as part of a wider conservation strategy is likely to have particular appeal to policy makers and landscape managers working in the human-dominated tropics.

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1. Introduction

Deforestation rates remain high throughout the tropics, with Brazilian Amazonia recently experiencing the highest absolute rates in the world (INPE, 2006). The two main consequences of deforestation, which are often mistaken as synonymous, are habitat loss and habitat fragmentation (Schmiegelow and Mönkkönen, 2002; Fahrig, 2003; Lindenmayer and Fischer, 2007). Habitat loss is undoubtedly the greatest

threat currently facing the future of tropical forest species, leading to calls to prioritise the protection of large tracts of remaining pristine habitat (e.g. Peres, 2005). However, beyond a certain level of habitat loss many faunal groups also respond negatively to fragmentation (Didham et al., 1996; Malcolm, 1997; Laurance et al., 2002; Lees and Peres, 2006; Peres and Michalski, 2006), and as the area of land already affected by deforestation increases, the 'megareserve' approach will require complementary conservation efforts in the intervening

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human-dominated 'countryside' (Barlow et al., 2007a; Daily et al., 2001; Hughes et al., 2002; Lindenmayer and Franklin, 2002; Sekercioglu et al., 2002; Sekercioglu et al., 2007).

Deforested areas in the tropics are usually characterised by high levels of fragmentation (e.g. Lees and Peres, 2006), and conservation efforts have focused on enhancing the representation of native biota both within remnant areas of forest and the intervening landscape matrix. One persistently popular conservation strategy in human-dominated landscapes has been the use of 'wildlife corridors' (Diamond, 1975; Wilson and Willis, 1975), which are generally defined as strips or areas of habitat specifically connecting two or more larger habitat blocks (Fahrig and Merriam, 1985; Beier and Noss, 1998) and differing from the land-use type on either side (Lindenmayer and Franklin, 2002). Another common feature of many agricultural production and plantation landscapes is the existence of forest strips (also termed 'linear forest remnants': Lima and Gascon, 1999; Laurance and Laurance, 1999), which are thin remnants of forest often extending from continuous primary forest into the matrix but which, unlike 'corridors', do not necessarily directly connect habitat patches (Bennett, 2003; Taylor et al., 2006). These forest strips are particularly common features of degraded Amazonian landscapes. For example, the Brazilian Forest Code legally requires landowners to set aside 30-200 m wide forest strips alongside streams and rivers, depending on the width of the watercourse (Código Florestal, 2001). Terra firme (unflooded) forest strips are less common than these riparian remnants, but nevertheless are often used to separate large agricultural and silvicultural blocks to help prevent soil erosion and the spread of pests, disease and fire (e.g. Zanuncio et al., 1998).

While forest strips are therefore usually maintained to protect water sources or production interests, a number of studies have suggested that they can also be a potentially valuable conservation asset (Sodhi et al., 1999; Haddad et al., 2003), by providing areas of habitat in their own right (Lima and Gascon, 1999; Lees and Peres, 2008). It is important to note that while remnant forest strips do not necessarily provide physical linkages they can still confer a level of "functional connectivity" (i.e. as perceived by organisms themselves, Taylor et al., 2006) by increasing the representation and facilitating the movement of species (Castellón and Sieving, 2006) as well as the persistence of key plant–animal interactions (Tewksbury et al., 2002) across the landscape.

Despite their potential benefits for biodiversity and relatively common existence (together with the approval, or at least widespread tolerance of them by large landowners), we have a very poor understanding of the potential conservation value of forest strips in production landscapes (Hobbs, 1992; Harrison and Bruna, 1999; Haddad and Tewksbury, 2006). Specifically, there is a distinct lack of knowledge regarding the relative importance of strip type (i.e. terra firme or riparian forest), strip length, together with correlated changes in forest structure and degradation status (MacDonald, 2003; but see Lees and Peres, 2008), and whether narrow forest remnants suffer the same "ecological implosion" as small forest fragments (Lindenmayer et al., 1997; Laurance et al., 1997; Gascon et al., 2000). Finally, there is a marked research bias towards temperate zones (Wiens, 2006) and a resulting deficit of studies from tropical forest regions.

The purpose of this study was to address the critical lack of knowledge regarding the potential value of forest strips in the tropics by examining 30-year-old terra firme and riparian forest strips in the north-east Brazilian Amazon. In particular, we examine the effects of forest strip type and length (with any corresponding variations in local and landscape habitat structure) on the potential conservation value of these remnants. To do this we examined patterns of abundance and occupancy of bird species already identified as characteristic of continuous primary forest (very rarely found in planted or regenerating forest). Birds were selected as the focal taxon because of their well-documented ecology (e.g. Stotz et al., 1996), and because they have been shown to be particularly cost-effective to survey in tropical forests (Gardner et al., 2008). Furthermore, our knowledge of the surrounding matrix habitats in the Jari landscape and their relative value for native forest birds (Barlow et al., 2007b) offers a very rare opportunity to compare the avifauna sampled in forest strips with that which is known to occur in neighbouring continuous forest. Specifically, we test the a priori hypotheses that (1) bird species richness and community structure in remnant forest strips will be clearly distinct from bird assemblages in continuous primary forest, (2) bird species richness and community structure will become more similar to the matrix avifauna with increasing distance from adjoining areas of continuous forest (Stratford and Stouffer, 1999; Laurance et al., 2006a, b).

2. Methods

2.1. Study sites

Sampling was conducted in the 1.7 Mha landholding of Jarí Celulose S.A., located on the border between the states of Amapá and Pará in north-eastern Brazilian Amazonia (0°53′S, 52°36′W). Average annual rainfall is 2115 mm, and the mean daily air temperature is 26 °C (Coutinho and Pires, 1996). About 10% of the primary forest in this landholding was converted to exotic tree plantations between 1969 and 1990. At the time of study the landscape consisted of fastgrowing Eucalyptus plantations on 5-7 year rotations, large tracts of regenerating secondary forest (14-19 years old), and vast expanses of relatively undisturbed primary forest (Fig. 1). We examined remnant forest strips that extended from areas of primary forest into the matrix of plantations and fallow land (secondary forest) both on unflooded land (terra firme forest strips) and along perennial streams (riparian forest strips). All of the remnant strips were part of an extensive and continuous region of undisturbed primary forest when the area was initially cleared approximately 30 years ago. These remnant strips have since been exposed to little further disturbance other than selective logging of a few commercially valuable species from some sites during the initial land clearance.

We selected eight forest strips in total, with four on *terra* firme and four along perennial streams. Two sampling treatments were conducted in each strip: 'near' sites were always located where the remnant became substantially wider and connected with the neighbouring continuous forest, and 'far' sites were located a minimum of 2.5 km along remnants the strip into the matrix. Control sites were located within an area

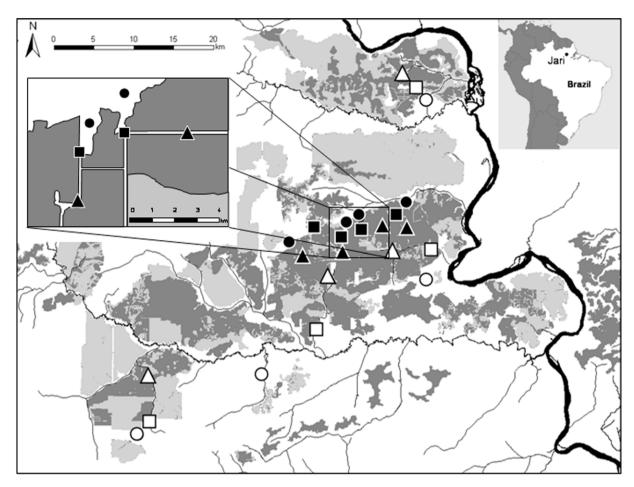


Fig. 1 – Map of study area showing the 24 sampling sites and areas of plantation (dark grey), secondary forest (light grey) and primary forest (white). Symbols show continuous forest (circles), 'near' sites (squares) and 'far' sites (triangles) in terra firme (black) and riparian (white) forest strips. Inset shows detail of the three sample treatments in forest strips.

of continuous primary forest that was adjacent to each of the strips. We therefore sampled a total of 24 sites in a fully replicated block-design, with four replicates for each sampling treatment (near, far and control) for both terra firme and riparian strips. Unfortunately, the landscape configuration limits our ability to compare directly between riparian and terra firme strips because of some important differences: remnants were generally wider (terra firme mean width = 115 m [range 95–150]; riparian mean width = 213 m [125–300]) and 'far' sites within riparian remnants were typically further from continuous forest (terra firme mean distance = 3.4 km [2.5–4.0]; riparian mean distance = 7.0 km [range 6.0–9.0]). Furthermore, riparian sites were considerably more dispersed geographically than the terra firme sites (Fig. 1). Site characteristics are summarised in Table 1.

2.2. Avifaunal sampling

We used understorey mist-netting to examine the avifauna at each of the 24 sites. Although this sampling technique can occasionally capture some canopy species, to avoid misinterpretation we refer to all captures as the understorey bird community. All sampling was undertaken between 19 January and 29 April 2006, during the transition between the dry and wet

seasons, thus providing a snap-shot of the distribution of these birds across our study areas. The order of sampling in the different sites was stratified to minimise the potential influence of seasonality, by alternating both between the two types of forest strip and the three distance treatments (distance from continuous forest). We erected 24 mist nets (12 \times 2.5 m; mesh size 36 mm) end to end along a cleared transect at each of the 24 sampling sites, creating a net-line of approximately 320 m once large treefalls had been avoided. Nets were opened from 0630 h to 1230 h for three consecutive days at each site, with extra net-hours added to account for the closure of nets during periods of persistent heavy rain, giving a standard effort of 432 net-hours per site and a total effort of 10,368 net-hours. Nets were checked hourly, and all captures were identified to species, and weighed, measured and sexed whenever possible. All birds were marked by a small notch cut in their 3rd outermost primary feather (or 3rd outermost tail feather in hummingbirds) enabling recaptures to be excluded from this analysis.

Although mist nets are generally less efficient than point-counts (Thiollay, 1994; Blake and Loiselle, 2001; Barlow et al., 2007b) and resulted in relatively small sample sizes in this study, they are also free of observer bias, and provide a useful standardised technique for comparing understorey avifaunal

* p < 0.05. ** p < 0.01. ARTICLE IN PRESS

Variable	Unit			Т	erra fii	rme							Ripar	rian				tests l and r	se Mann–W petween te iparian rer ies in pare	rra firme nnants
		Mean control	SE	Mean near	SE	Mean far	SE	χ^2	р	Mean control	SE	Mean near	SE	Mean far	SE	χ^2	р	Controls	Nears	Fars
Primary forest within 1 km	%	58.3	2.6	15.8	6.5	3.7	0.8	8.8	0.01*	88.6	1.4	43.1	8.9	14.7	3.3	9.8	0.01**	0.0* (0.03)	2.0 (0.11)	0.0* (0.03)
Distance from primary forest	km	0.0	0.0	0.6	0.3	3.4	0.3	9.5	0.01**	0.0	0.0	0.6	0.3	7.0	0.7	9.5	0.01**	8.0 (1.00)	8.0 (1.00)	0.0* (0.03
Distance from remnant edge	m	_	-	45.1	3.4	45.5	3.8	0.0	1.00	-	_	66.6	45.0	72.3	43.0	0.5	0.47	_	5.0 (0.44)	6.0 (0.69)
Linear remnant width	m	-	-	113.8	13.0	116.3	7.7	0.3	0.56	-	-	250.0	20.4	175.0	42.1	1.8	0.19	_	0.0* (0.03)	2.0 (0.11)
Canopy openness	%	6.7	0.7	8.8	1.9	8.6	0.3	3.1	0.21	5.8	1.1	7.6	1.2	7.4	0.6	2.3	0.31	5.0 (0.49)	6.0 (0.69)	2.5 (0.11)
Understorey density	n	8.2	0.7	6.3	1.6	5.3	1.6	1.9	0.39	5.4	0.5	6.7	1.0	7.3	1.3	1.0	0.61	0.0* (0.03)	7.0 (0.89)	4.0 (0.34)
Live tree basal area		6.7	0.6	5.5	0.4	3.4	1.2	4.3	0.12	7.3	1.0	8.0	0.8	7.2	0.9	0.5	0.79	7.0 (0.89)	0.0* (0.03)	2.0 (0.11)
Dead tree basal area		0.6	0.2	0.4	0.2	0.6	0.3	0.2	0.93	1.0	0.3	0.9	0.7	0.5	0.1	1.9	0.39	4.0 (0.34)	8.0 (1.00)	8.0 (1.00)
Live palm basal area		0.1	0.0	0.1	0.0	0.2	0.1	2.5	0.29	0.2	0.1	0.5	0.3	0.5	0.2	0.5	0.79	6.0 (0.69)	3.0 (0.20)	4.0 (0.34)
Dead palm basal area		0.0	0.0	0.0	0.0	0.0	0.0	2.0	0.37	0.0	0.0	0.0	0.0	0.0	0.0	2.6	0.27	4.0 (0.34)	6.0 (0.69)	8.0 (1.00)
Live liana basal area		0.6	0.2	0.4	0.2	0.8	0.3	1.2	0.55	1.0	0.3	0.9	0.7	0.5	0.1	1.9	0.39	4.0 (0.34)	8.0 (1.00)	4.0 (0.34)
Dead liana basal area		0.0	0.0	0.0	0.0	0.0	0.0	3.8	0.15	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.92	7.0 (0.89)	8.0 (1.00)	6.0 (0.69)
Pioneer basal area		0.1	0.1	0.4	0.2	0.6	0.2	2.7	0.26	0.1	0.1	0.4	0.1	0.2	0.1	2.4	0.30	5.5 (0.49)	8.0 (1.00)	5.0 (0.49)
Water-loving basal area		0.1	0.1	0.0	0.0	0.0	0.0	2.0	0.37	0.3	0.1	1.0	0.5	0.4	0.2	2.9	0.24	3.0 (0.20)	0.0* (0.03)	0.0* (0.03

communities composed of many non-vocal and secretive species (Karr, 1981; Stouffer and Bierregaard, 1995; Barlow and Peres, 2004; Barlow et al. 2007b). Capture rates may not accurately represent relative species abundances (Remsen and Good, 1996), but our estimates are supported by the strong positive correlation between the abundance of species surveyed independently by mist nets and point-counts in the same region (Barlow et al., 2007b). Nevertheless, particular caution should be applied to estimates of species richness, as mist nets tend to be more effective in more disturbed habitats, where birds fly closer to the ground (Blake and Loiselle, 2001; Barlow et al., 2007b).

2.3. Vegetation sampling

Trees and lianas were sampled in each of the 24 avifaunal sampling sites, using a standard procedure described by Barlow et al. (2002). Trees were included in a sample if more than 50% of their trunk was within 5 m of the centre of the transect. We measured all dead and live standing trees ≥10 cm DBH and lianas ≥ 5 cm in a 10×1000 m plot established at each site, recording whether species were palms, early pioneers (mainly Cecropia spp. and Vismia spp.) and/or typical of water-logged soils (e.g. Iriartea exorrhiza and Mauritia spp.). We calculated basal area excluding the largest tree from each sample to remove the potential bias from the stochastic presence of single large trees in relatively small forest plots (although results using all the data remained quantitatively very similar). Canopy cover and understorey density were measured at each mist-netting location, using a spherical densitometer and 2.5 m graded pole, respectively, following Barlow et al. (2002).

2.4. Land-cover analysis

A geographic information system (GIS) was used to quantify the land-use composition surrounding each sampling site. Site locations were recorded using a handheld GPS receiver (Garmin eTrex) and a semi-supervised land-cover classification, with ground-truthing based on our intimate knowledge of the landscape, was developed from a combination of land-use data provided by Jari Celulose S.A and a 2003 Landsat 7 (30-m pixel) image. Buffers of 1 km were created around the central point of each avifaunal sampling site before performing an intersect overlay with land-use layers containing data on major land-cover types (old and young plantation forest, old and young secondary forest, closed-canopy primary forest, open canopy forest, flooded areas, natural savannahs and human settlements) to provide a buffer measure of connectivity (Moilanen and Hanski, 2006).

2.5. Data analysis

We combined capture data from the standard 432 net-hours conducted at each sampling site. Because of the consistent differences in the widths and distance treatments in terra firme and riparian strips we avoided direct comparisons of the two habitat types, and analysed them separately when assessing the importance of distance from continuous forest. Patterns of species richness in the three sampling treatments (near,

far and control) for each forest remnant type (terra firme and riparian) were compared using sample-based rarefaction curves produced in EstimateS 7.5 (Colwell, 2005). The structure and composition of communities were examined with nonmetric multi-dimensional scaling (MDS) ordinations using Bray-Curtis similarity matrices based on square-root transformed and standardised abundance data, and presence/absence data. Differences between sampling treatments were assessed using analyses of similarities (ANOSIM), the identity of species contributing the most to any differences was determined by an analysis of percentage similarities (SIMPER), and the influence of environmental parameters on community structure was assessed using the BIOENV procedure. All community analyses were conducted using Primer (v.5) (Clarke and Warwick, 2001).

Species were assigned to dietary and foraging guilds following Terborgh et al. (1990), with additional information from Ridgley and Tudor (1989, 1994) and Hilty (2002), and categorised according to their degree of habitat specialisation and sensitivity to disturbance (Stotz et al., 1996). In addition, both mist-net and point-count data from an independent study (Barlow et al., 2007b) were examined using Indicator Species Analysis in PC-ORD (McCune and Mefford, 1999). This analysis uses the IndVal procedure (Dufrene and Legendre, 1997; McGeoch and Chown, 1998) to identify species that are characteristic of continuous primary forest and the matrix habitats (secondary forest and Eucalyptus plantations). This method combines measures of both habitat specificity (through patterns of abundance) and habitat fidelity (through patterns of presence-absence), producing a percentage indicator value (IndVal) for each species - i.e. to be characteristic of a certain land-use type a species has to be found reliably and almost exclusively within that land-use. Dufrene and Legendre, (1997) random reallocation procedure of sites within site groups was used to test the significance of the IndVal measure for each species.

Data from Barlow et al. (2007b) were also used to compare bird communities from forest strips to those found in the wider landscape mosaic at Jari but, in this case, the point-count data were omitted to ensure a common methodology and level of sampling effort. Our approach to assessing patterns of potential conservation value was limited by knowledge of the viability of populations sampled within the strips. Recording the presence of a bird species, even in large numbers, within a forest strip masks the fact that it may suffer from a depleted level of fitness or breeding success. Nevertheless, in the absence of more detailed population or physiological data, patterns of occupancy and abundance provide a valuable proxy of the potential these areas have for the persistence of native species in an otherwise hostile landscape. Moreover, we are interested in documenting broad patterns of avifaunal diversity and abundance between different forest strips and the surrounding matrix, and not in generating specific conclusions about the suitability of these areas for individual species.

3. Results

3.1. Habitat and landscape structure

Local vegetation structure was broadly similar in terra firme and riparian forest strips (Table 1), although riparian

remnants had a significantly higher basal area of tree species that are associated with water-logged soils, and a higher tree basal area in 'near' sites than in the 'near' sites of terra firme remnants. In addition 'Far' sites within riparian remnants had more primary forest within a 1-km buffer than those in terra firme remnants (Table 1).

Within each type of forest strip, there were no significant differences in vegetation structure between continuous primary forest and the strips (Table 1). Unsurprisingly, measures of the wider landscape composition varied with length along the strips. Almost the entire matrix adjacent to all the strips was under *Eucalyptus* plantation, and 1-km buffers around 'far' sites in both *terra firme* and riparian remnant strips retained a significantly lower percentage of primary forest cover than 'near' sites (Table 1).

3.2. Avifaunal sampling

We captured a total of 1910 birds from 117 species. Site-level captures ranged from 32 to 117 individuals, and the number of species observed per site ranged from 14 to 44. Similar numbers of bird individuals (967 and 943) and species (93 and 89) were captured in terra firme and riparian forest types, respectively (see Appendix). The species richness of terra firme strips was significantly lower than that recorded in continuous terra firme forest controls, while riparian strips and riparian forest sites embedded within continuous forest displayed similar levels of bird species richness (Fig. 2). The two types of forest strip (terra firme and riparian) hosted distinct bird communities when analysed using both abundance (ANOSIM: R = 0.31, p < 0.003) and presence/absence data (R = 0.33, p = 0.001), and these differences were independent of sampling location (Near: R = 0.75, p = 0.029; Far: R = 0.542, p = 0.029; Control: R = 0.427, p = 0.029).

There was no statistically significant difference between the species richness of 'near' and 'far' sites, for both *terra firme* and riparian remnants (Fig. 2). However, an influence of strip length on community structure and composition was detected for both remnant types; in each case only 'far' sites had communities significantly distinct from those of continuous primary forest (Fig. 3, Table 2). SIMPER analysis showed that terra firme 'far' sites were most evidently distinct from terra firme forest controls due to higher abundances of species such as Pectoral Sparrow (Arremon taciturnus), Reddish Hermit (Phaethornis ruber), and Guianan Slaty Antshrike (Thamnophilus punctatus), and lower abundances of White-crowned Manakin (Dixiphia pipra). By contrast, riparian 'far' sites had higher abundances of White-bearded Manakin (Manacus manacus), Wedge-billed Woodcreeper (Glyphorynchus spirurus), and Rufous-breasted Hermit (Glaucis hirsuta), and lower abundances of Dusky-throated Antshrike (Thamnomanes ardesiacus) than riparian forest controls (see S1–2 in Supplementary material).

3.3. Potential value of forest strips for native forest birds

The pattern of bird abundance between treatments and according to different species classes was similar whether we considered categories based on the disturbance-sensitivity classes of Stotz et al. (1996), or groups of species that were identified as characteristic of specific forest types in the Jari landscape by the IndVal procedure (Barlow et al. 2007b). There was a large overlap in these two independent classification methods (Table 3). For example, 17 of the 24 species identified as characteristic of primary forest were classed by Stotz et al. (1996) as being highly disturbance-sensitive. Similarly, 16 of the 17 species found to be characteristic of secondary forest are categorised as species of medium or low sensitivity to disturbance and all five species found to be characteristic of Eucalyptus plantations are species of low sensitivity (see Table 3 for details).

In comparison to continuous primary forest, highly disturbance-sensitive birds (as classified by Stotz et al., 1996) were found in significantly lower abundances in terra firme remnants, but not in riparian remnants (Fig. 4). However, all samples from forest strips supported fewer birds that are characteristic of primary forest (as identified by the IndVal procedure) than the primary forest controls, while demonstrating a higher abundance of species that are characteristic of

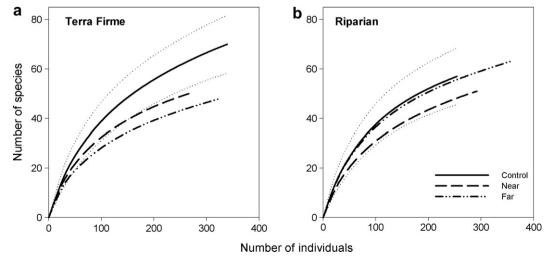


Fig. 2 – Sample-based species rarefaction curves (rescaled by number of individuals) for the three sample treatments in (a) terra firme, and (b) riparian forest strips. Dotted lines indicate 95% confidence intervals for continuous primary forest.

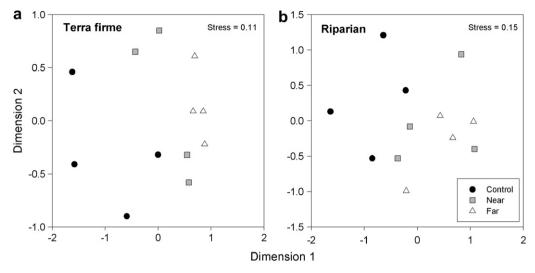


Fig. 3 – Multi-dimensional scaling plot (based on abundance data) of the bird communities for the three sample treatments in (a) terra firme and (b) riparian forest strips.

Table 2 – ANOSIM : forest strip	results showing	the change in co	nmunity structure	with increased d	istance into the ma	atrix along the
Pair-wise tests	Terra firme (global R = 0.		Riparian 1 (global R = 0.1			nant types 197, p = 0.008)
	R	р	R	р	R	р
Control × near	0.365	0.114	0.24	0.057	0.174	0.067
Control × far	0.771	0.029*	0.552	0.029*	0.506	0.002*
Near × far	0.125	0.257	0.042	0.457	0.075	0.845

secondary forest (Fig. 4). Although Eucalyptus plantations dominated the matrix, species characteristic of this forest type were recorded at low abundances in all sample sites and none of the strip samples supported these species in significantly greater numbers than continuous primary forest, irrespective of how far the remnants extended into the matrix (Table 3, Fig. 4). Consequently the assemblages of birds found in the remnants much more closely reflect samples from continuous forest than samples from the adjoining matrix. This result is further supported by the ordination plot combining all sampling sites from this study with those from our earlier work in the wider landscape (Barlow et al. 2007b) (Fig. 5). These results therefore support our first but not our second hypothesis, by demonstrating that bird communities sampled in remnant forest strips are distinct from those sampled in continuous forest communities, but as a result of becoming increasingly similar (with increased distance into the matrix) to communities sampled in secondary forest sites rather than samples from the surrounding matrix of Eucalyptus plantations.

Of the 13 foraging and dietary guilds captured, only three exhibited significantly depleted abundances in the forest strips. Terra firme strips supported fewer arboreal dead-leaf insectivores ($\chi^2 = 7.55$, p = 0.023) and fewer arboreal frugivores ($\chi^2 = 7.20$, p = 0.027) than sites in continuous *terra* firme forest. In addition, ant-following insectivores were virtually absent from all forest strips, being recorded only twice outside contin-

uous forest (both in 'near' riparian sites). Examining individual species responses demonstrates differences in the extent to which different species utilise the forest strips, with some taxa being commonly found outside continuous forest, including Plain-brown Woodcreeper (Dendrocincla fuliginosa), Bluecrowned Motmot (Momotus momota), and Long-tailed Hermit (Phaethornis superciliousus), while others were largely limited to control sites, including White-plumed Antbird (Pithys albifrons) and White-necked Thrush (Turdus albicollis) (Table 3).

4. Discussion

4.1. Use of riparian and terra firme forest strips by forest birds

The importance of vegetation structure in determining patterns of species diversity and abundance is well established (MacArthur et al., 1966; Henein and Merriam, 1990), yet the role of forest type in determining the use of remnant strips by native forest biota has received little attention. Riparian forests are well documented as areas of high species richness (Naiman and Décamps, 1997; Bennett, 2003) partly due to the additional presence of aquatic species and also the diversity of habitats they contain. As far as bird species are concerned they may also offer particular benefits due to the presence of water-loving plant species such as açaí (Euterpe oleracea),

Table 3 – Abundance in forest strips of species identified by the IndVal procedure (Dufrene and Legendre 1997) as characteristic of primary, secondary and plantation forest

Species	Guild ^a	Sens ^b		Number of individuals captured							
				Terra firme		Riparian					
			Control	Near	Far	Control	Near	Far			
Species characteristic of primary f	orest										
Pithys albifrons	IAF	High	6			8	2				
Gymnopithys rufigula	IAF	Med	2			6					
Hylophilus muscicapinus	IAG	High	1								
Myrmotherula menetriesii	IAG	High	2			3	1	1			
Hylophylax poecilinota	IAG	Med	2	1		5	1	7			
Dendrocincla fuliginosa	IAS	High	2	3	6	8	2	5			
Lipaugus vociferans	IAS	High	2								
Thamnomanes ardesiacus	IAS	High	10	3		12	10	4			
Thamnophilus murinus	IAS	High	2			2					
Tolmomyias assimilis	IAS	High	1								
Momotus momota	IAS	Med		2	4	1		5			
Tolmomyias poliocephalus	IAS	Med	1								
Xiphorhynchus pardalotus	IBS	High	2	1		7	3	3			
Glyphorynchus spirurus	IBS	Med	30	36	37	38	33	45			
Formicarius colma	ITG	High				2		1			
Sclerurus rufigularis	ITG	High	2			5	3				
Formicarius analis	ITG	Med									
Dixiphia pipra	FA	High	20	5	1	13	6	7			
Pipra erythrocephala	FA	High	10	10	2	4	4	10			
Ramphastos vitellinus	FA	High	1			1	2				
Schiffornis turdinus	FA	High	4			1					
Geotrygon montana	GT	Med	9	2	1	4		1			
Phaethornis bourcieri	NA	High				5					
Phaethornis superciliosus	NA	High	36	22	26	29	32	27			
Turdus albicollis	OA	Med	7			6		3			
Total			152	85	77	160	99	119			
0 ' 1 ' ' ' ' 1											
Species characteristic of secondary	-	Ŧ	•	40	_						
Cercomacra tyrannina	IAG	Low	9	10	5						
Thamnophilus punctatus	IAG	Low	3	4	20		2	2			
Thryothorus coraya	IAG	Low	10	9	12		3	8			
Lophotriccus galeatus	IAS	Med	1		1			0			
Automolus ochrolaemus	IDL	Med	1		1			3			
Percnostola rufifrons	ITG	High	11	21	23	8	8	12			
Myrmeciza atrothorax	ITG	Low		_		1	7	7			
Myrmoborus leucophrys	ITG	Med		1	13			1			
Manacus manacus	FA	Low	9	9	20	4	29	33			
Machaeropterus pyrocephalus	FA	Med						1			
Cryptrellus erythropus	GT	Low					1				
Phaethornis ruber	NA	Med	6	9	29	4	11	8			
Saltator maximus	OA	Low			3		1	1			
Arremon taciturnus	OA	Med	2	24	30	1		10			
Cyanocompsa cyanoides	OA	Med	7	7	5	5	5	6			
Mionectes oleagineus	OA	Med	14	9	7	9	13	14			
Turdus fumigatus	OA	Med					3	2			
Myrmothera campanisoma	ITG	High									
Taraba major	IAG	Low									
Total			73	103	169	32	83	108			
Species characteristic of eucalyptu	s plantations										
Tolmomyias flaviventris	IAS	Low			2						
Volatinia jacarina	GT	Low		1							
Amazilia fimbriata	NA	Low	2	3	3	1	3	4			
Coereba flaveola	NA	Low		2	2		1				
Glaucis hirsuta	NA	Low	8	4	10	7	38	21			
Anthracothorax nigricollis	NA	Low									
Camptostoma obsoletum	IAG	Low									
Cyclarhis gujanensis	IAG	Low									

Table 3 – (continued)											
Species	Guild ^a	Sens ^b		Nu	Number of individuals captured						
				Terra firme			Riparian				
			Control	Near	Far	Control	Near	Far			
Troglodytes aedon	IAG	Low									
Myiopagis gaimardii	IAG	Med									
Polytmus theresiae	NA	Med									
Total			10	10	17	8	42	25			

a IAF = insectivore ant-following, IAG = insectivore arboreal gleaning, IAS = insectivore arboreal sallying, IBS = insectivore bark-searching, IDL – insectivore dead leaf, ITG = insectivore terrestrial gleaning, FA = frugivore arboreal, GT = gramnivore terrestrial, NA = nectivore arboreal, OA = omnivore arboreal.

b Stotz et al. (1996). Disturbance-sensitivity classes: high, medium (med) and low.

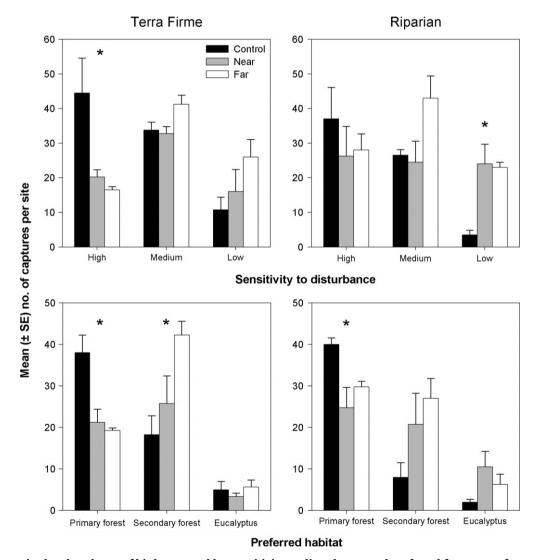


Fig. 4 – Changes in the abundance of birds grouped by sensitivity to disturbance and preferred forest type for terra firme and riparian forest strips. Significance was calculated using Kruskal–Wallis tests: * = <0.05, ** = <0.01.

which are important resources for frugivorous birds (Moegenburg and Levey, 2003).

Due to potentially confounding landscape factors, we are unable to provide a direct comparison of the suitability of riparian and terra firme forest strips for forest birds in our study region. Nevertheless, we are able to demonstrate that the two types of remnant forest strip hosted distinct bird communities, both of which closely reflected samples from

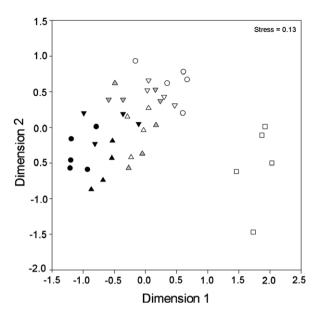


Fig. 5 – Multi-dimensional scaling plot (based on abundance data) of the bird communities in forest strips in relation to bird communities from the surrounding landscape.

Triangles represent sites in 'near' (grey), 'far' (white) and primary continuous forest control sites (black) for terra firme (downward pointing triangles) and riparian (upward pointing triangles) forest strips. Additional symbols show continuous primary (black circles), secondary (white circles) and plantation forest sites (white squares) from Barlow et al. (2007b).

continuous primary forest, implying that these two types of forest strip may provide a complementary service for the conservation of these species in plantation landscapes (see also Baker et al., 2006).

4.2. Forest strip length and the influence of the matrix

Increases in the length of forest strips and isolation from neighbouring continuous forest has been associated with declines in the richness and abundance of primary forest birds in both connected (Lees and Peres, 2008) and unconnected or poorly connected remnants (Ferraz et al., 2003; Stouffer and Bierregaard, 1995; Stratford and Stouffer, 1999; Antongiovanni and Metzger, 2005). A negative effect of forest strip length on the abundance of forest interior species has been found for other vertebrate groups too (e.g. arboreal marsupials; Lindenmayer et al., 1993), suggesting that this effect may be general. There is also increasing evidence to show that disturbancesensitive species (e.g. the ant-follower guild) may only enter short distances into silvicultural habitats or cross small forest gaps (Roberts et al., 2000; Laurance et al., 2004; Laurance and Gomez, 2005; Barlow et al., 2007b). In demonstrating a loss of disturbance-sensitive species and species characteristic of primary forest, with increasing distance from continuous forest, our results further strengthen these findings and add support to the management recommendation for minimising the length of forest strips (connected or unconnected) when attempting to design more functionally connected landscapes (Wilson and Lindenmayer, 1995).

Working on patterns of bird diversity in Australian pine plantations, Tubelis et al. (2007) recently invoked the "peninsular effect" – a biogeographic phenomenon that results in a decrease in species richness from the base to the tip of a peninsular – to help explain local scale changes in the number of bird species occupying small "peninsulars" of native Eucalyptus forest. The results of our study for terra firme strips are qualitatively similar to that found by Tubelis et al. (2007), suggesting that this phenomenon may be widespread in human-dominated forest landscapes, although the underlying mechanism to explain the process occurring in our study remains unclear.

One explanation for this decline in disturbance-sensitive and primary forest characteristic species (and the associated increase in species characteristic of secondary forest) with increasing strip length could be changes in local vegetation structure and condition (Laurance et al., 2006a). Similar replacements of bird communities have been found following habitat degradation by fire and selective logging (Barlow and Peres, 2004; Barlow et al., 2006) that are, in turn, strongly related to changes in local habitat structure (e.g. Mason, 1996; Barlow et al., 2002; Barlow and Peres, 2004). However, our data do not give support to this explanation, as the "secondarisation" of the bird community appears to have occurred independently of changes in our measured forest structure variables. For example, variables identified from previous studies as important in structuring Amazonian avifauna, such as live tree basal area, understorey density and canopy cover (e.g. Barlow and Peres, 2004) did not differ significantly with strip length (although our sample sizes were low, very few of these comparisons even approached significance, see Table 1), and therefore are unlikely to explain the observed differences in bird communities sampled in 'near' and 'far' strip sites. Furthermore, the BIOENV analysis conducted in this study showed that these variables were also very poorly correlated with changes in bird community structure (see S3 in Supplementary material).

The lack of any observed changes in sampled bird communities in association with changes in vegetation variables, as reported for small forest fragments elsewhere in Amazonia (Laurance et al., 2002, 2006a,b), could be due to buffering of the strips by the surrounding landscape matrix. Matrix habitats consisting of secondary forest have been shown to be important in mitigating against the loss of forest species in isolated Amazonian fragments (Antongiovanni and Metzger, 2005; Stouffer et al., 2006). The matrix in Jari, however, is principally composed of Eucalyptus plantations, and while some forest species were lost in the 'far' sites, we also found very limited evidence of a shift towards a bird community characteristic of Eucalyptus. For example, only five of the 12 species that were known to be characteristic of Eucalyptus plantations were ever recorded in the forest strips, and only two species were recorded frequently (Table 3). These were both species of hummingbird (the Rufous-breasted Hermit, Glaucis hirsuta; and the Glitteringthroated Emerald, Amazilia fimbriata), which are wide-ranging and known to persist in a variety of habitats (Stouffer and Bierregaard, 1995). This shows that disturbance caused by increased isolation from continuous primary forest within an inhospitable matrix can have the effect of filtering out some primary forest species while creating opportunities for species typical of secondary forest, but that the Eucalyptus plantation matrix itself does not act as a source of species recruitment (c.f. Gascon et al., 1999). Because the matrix in most landscapes throughout Amazonia is dominated by pasture or arable land (e.g. Lees and Peres, 2006) it is critical to consider the type of dominant economic land-use when assessing the consequences of isolation on fragmented biota (Stouffer et al., 2006).

4.3. Classifying species of conservation concern

Our analyses allow a novel comparison of the relative merits of two different methods for classifying bird species of potential conservation concern. The general agreement between both methods used (Table 3) provides support for the current widespread use of the Stotz et al. (1996) sensitivity classes in neotropical bird studies that are concerned with understanding the consequences of landscape change to native biota. However, the IndVal procedure (Dufrene and Legendre, 1997) also provides useful additional information showing, in this case, that the greater abundance of disturbance-tolerant birds in linear remnants is due to a greater abundance within species characteristic of secondary forests, and not of Eucalyptus plantations. Specific differences between the two classifications highlight species, such as Percnostola rufirons, that may require reclassification from high to medium disturbancesensitivity.

4.4. Conservation management implications

There is a growing interest in identifying the management options that are available to improve the biodiversity value of tree plantations (Hartley, 2002; Lindenmayer and Hobbs, 2004). This challenge is amplified by the fact that Eucalyptus plantations, the most prevalent type of tropical timber plantations (Evans and Turnbull, 2004) approximate an 'inhospitable sea' (sensu Daily, 2001) for tropical primary forest birds, with virtually no overlap in species composition between the two forest types (Barlow et al., 2007b). Our study, although preliminary, demonstrates that remnant forest strips can provide a valuable refuge for many primary forest birds that would otherwise be absent from the plantation landscape. Both terra firme and riparian forest strips in our study area support more species, and contain bird communities more similar to those of continuous primary forest, than either of the two land-uses that dominate the landscape matrix (secondary re-growth or Eucalyptus plantations), although certain groups of species and guilds were notably depleted (e.g. the ant-following insectivores).

The decrease in the numbers of birds characteristic of primary forest with increased strip length highlights the value of value of maintaining a network of relatively short primary forest strips to enhance the biodiversity and functional connectivity of highly modified plantation landscapes. It is important to note that our results are limited to the consideration of forest strips that are connected to neighbouring areas

of primary forest, and work elsewhere in Amazonia suggests that isolated strips often harbour fewer species (Lees and Peres, 2008). Furthermore, without comparable data from multiple landscapes, it is unclear the extent to which our findings are peculiar to the Jari landscape, as many other heavily-modified landscapes are not adjacent to such large areas of primary forest.

We do not advocate that forest strips are promoted as alternatives to other management options, such as the maintenance and buffering of larger forest fragments with smaller edge: area ratios, for enhancing the diversity of forest birds in plantation landscapes However, because forest strips can be incorporated into the plantation management plan with little conflict with landowners (due to legal compliance, and the utility of strips as demarcation lines and defences against the spread of fire, pests and disease), they can serve to complement the maintenance of large areas of undisturbed forest, and offer a practical approach to help minimise the impact of large-scale plantation forestry on forest biodiversity.

Riparian forest strips within private landholdings often receive some level of protection, both through federal laws (e.g. Brazilian Forest Code: Código Florestal, 2001) and forestry certification schemes (e.g. Forest Stewardship Council guidelines: www.fsc.org), but there are few specific guidelines in place concerning their design, spatial configuration and degradation status, all of which affect their relative value for conservation (Lees and Peres, 2008). Our results show that protected riparian forest strips, connected to larger patches of adjacent forest, contain large numbers of forest bird species even 30 years after their creation. Ensuring their potential value for conservation requires enforcement to prevent degradation by hunting, selective logging or fire (Peres and Michalski, 2006; Barlow et al., 2006). A novel finding of our study is that extending the protection afforded to riparian forest strips within production areas to encompass remnant strips of terra firme forest that harbour a complementary set of species, can help maximise the conservation value of degraded tropical forest landscapes.

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Appendix

Species list and abundances of understorey birds from terra firme and riparian forest remnants within the Jari landscape, northern Brazilian Amazonia

Species	Guilda	Sens ^b	Ind ^c		Numbe	er of indi	viduals cap	tured in		Total
				·	Terra Firn	ne		Ripariar	ı	
				Control	Near	Far	Control	Near	Far	
Accipitridae										
Harpagus bidentatus	RaD	Med					1			1
Leucopternis albicollis	RaD	High						1		1
Bucconidae										
Bucco capensis	IAS	High			1	1				2
Bucco tamatia	IAS	Med				1				1
Malacoptila fusca	IAS	High		5						5
Monasa atra	IAS	Med			2				6	8
Capitonidae										
Capito niger	OA	Med		2						2
Cardinalinae										
Cyanocompsa cyanoides	OA	Med	SF	7	7	5	5	5	6	35
Saltator grossus	OA	Med					1			1
Saltator maximus	OA	Low	SF			3		1	1	5
Alcedinidae										
Chloroceryle aenea	Aqu	Med					2	2	6	10
Chloroceryle inda	Aqu	Med							1	1
Columbidae										
Claravis pretiosa	GT	Low						1		1
Geotrygon montana	GT	Med	PF	9	2	1	4	-	1	17
Leptotila rufaxilla	GT	Med		1	3	3	-		4	11
Conopophagidae										
Conopophaga aurita	ITG	High		2						2
		8								
Cuculidae	TAC	T 0						1	1	2
Piaya minuta	IAG	Low						1	1	2
Dendrocolaptidae	140	771.1.		0			4			0
Deconychura stictolaema	IAS	High		2	•		1	•	_	3
Dendrocincla fuliginosa	IAS	High	PF	2	3	6	8	2	5	26
Dendrocolaptes certhia	IAS	High	DE	00	1	0.7	1	3	2	7
Glyphorynchus spirurus	IBS	Med	PF	30	36	37	38	33	45	219
Hylexetastes perrotii	IBS	High		2					4	2
Sittasomus griseicapillus	IBS	Med		4				0	1	1
Xiphorhynchus guttatus	IBS	Med		1	1	1		2	4	5
Xiphorhynchus obsoletus	IBS	Med	DE	0	4		7	_	1	1
Xiphorhynchus pardalotus Xiphorhynchus picus	IBS IBS	High Low	PF	2	1 1		7	3	3	16 1
		_3			_					_
Emberizinae	0.4	l L - J	CF	2	2.4	20	1		10	<i>C</i> 7
Arremon taciturnus	OA	Med	SF	2	24	30	1	_	10	67
Oryzoborus angolensis Volatinia jacarina	GT GT	Low Low	EUC	1	4 1	4		5	5	19 1
Falconidae										
Micrastur gilvicollis	RaD	Ligh		1						1
Micrastar gitotcoms	KaD	High		1						1

Appendix - continued

Species	Guild ^a	Sens ^b	Ind ^c			Total				
					Terra Firm	ie		Riparian	1	
				Control	Near	Far	Control	Near	Far	
Formicariidae										
Formicarius colma	ITG	High	PF				2		1	3
Furnariidae										
Automolus ochrolaemus	IDL	Med	SF	1		1			3	5
Cranioleuca gutturata	IDL	High						1		1
Philydor erythrocercus	IDL	High		1			1			2
Philydor pyrrhodes	IDL	High					1			1
Sclerurus mexicanus	ITG	High					5	1	1	7
Sclerurus rufigularis	ITG	High	PF	2	0	2	5	3	4	10
Xenops minutus	IBS	Med		2	2	3		1	1	9
Galbulidae		1								_
Galbula albirostris	IAS	High					1			1
Momotidae										
Momotus momota	IAS	Med	PF		2	4	1		5	12
Parulinae										
Basileuterus rivularis	ITS	Med		3		1	5	3	5	17
Granatellus pelzelni	IAS	Med							1	1
Pipridae										
Dixiphia pipra	FA	High	PF	20	5	1	13	6	7	52
Lepidothrix serena	FA	High	CE	2					4	2
Machaeropterus pyrocephalus	FA	Med	SF	0	0	20	4	20	1	1
Manacus manacus Pipra aureola	FA FA	Low Med	SF	9	9	20	4	29	33 2	10 2
Pipra aureola Pipra erythrocephala	FA	High	PF	10	10	2	4	4	10	40
	171	IIIgii	11	10	10	2	7	-	10	10
Ramphastidae Ramphastos vitellinus	FA	High	PF	1			1	2		4
Thamnophilidae										
Cercomacra tyrannina	IAG	Low	SF	9	10	5				24
Frederickena viridis	IAG	High	01	2	10	3	3			5
Gymnopithys rufigula	IAF	Med	PF	2			6			8
Hylophylax naevia	IAG	High					1			1
Hylophylax poecilinota	IAG	Med	PF	2	1		5	1	7	16
Hypocnemis cantator	IAG	Med		14	7	6	2	7	7	43
Microrhopias quixensis	IAG	Med			2	1				3
Myrmeciza atrothorax	ITG	Low	SF				1	7	7	15
Myrmeciza ferruginea	ITS	High		5	1					6
Myrmoborus leucophrys	ITG	Med	SF		1	13			1	15
Myrmotherula axillaris	IAG	Med		7	9	11	1	4	10	42
Myrmotherula guttata	IAG	High		3	4		1	1	1	6
Myrmotherula gutturalis Myrmotherula longipennis	IDL IAG	High		7 3	1			4	5	17 6
Myrmotherula menetriesii	IAG	High High	PF	2			3	3 1	1	7
Percnostola rufifrons	ITG	High	SF	11	21	23	8	8	12	83
Pithys albifrons	IAF	High	PF	6	21	23	8	2	12	16
Schistocichla leucostigma	ITG	High		3			2	7	11	23
Sclateria naevia	ITG	Med				1	_		2	3
Thamnomanes ardesiacus	IAS	High	PF	10	3		12	10	4	39
Thamnomanes caesius	IAS	High		12	4	1	4	9	8	38
Thamnophilus murinus	IAS	High	PF	2			2			4
Thamnophilus punctatus	IAG	Low	SF	3	4	20		2	2	31
Thraupinae										
Coereba flaveola	NA	Low	EUC		2	2		1		5
Lanio fulvus	IAS	High		1			2			3
Ramphocelus carbo	OA	Low			2	8		4	4	18
Tachyphonus rufus	OA	Low				2				2
Tachyphonus surinamus	OA	Med		6			1		4	11

Appendix - continued

Species	Guild ^a	Sens ^b	Ind ^c	Number of individuals captured in							
				Terra Firme				Riparian	1		
				Control	Near	Far	Control	Near	Far		
Tinamidae											
Cryptrellus erythropus	GT	Low	SF					1		1	
Trochilidae											
Amazilia fimbriata	NA	Low	EUC	2	3	3	1	3	4	16	
Campylopterus largipennis	NA	Med		2	5		4	3	1	15	
Chlorestes notatus	NA	Low			7	1			4	12	
Florisuga mellivora	NA	Low			3					3	
Glaucis hirsuta	NA	Low	EUC	8	4	10	7	38	21	88	
Heliothyrax aurita	NA	Med		2	1					3	
Hylocharis cyanus	NA	Low			2	1	1			4	
Hylocharis sapphrina	NA	Med			1					1	
Phaethornis bourcieri	NA	High	PF				5			5	
Phaethornis ruber	NA	Med	SF	6	9	29	4	11	8	67	
Phaethornis superciliosus	NA	High	PF	36	22	26	29	32	27	172	
Thalurania furcata	NA	Med		6	4	1	9	7	9	36	
Threnetes niger	NA	Med		1	•	-	,	,		1	
•	1421	ivicu		1						-	
Troglodytidae											
Thryothorus coraya	IAG	Low	SF	10	9	12		3	8	42	
Thryothorus leucotis	IAG	Low		1	3	9			2	15	
Turdinae											
Turdus albicollis	OA	Med	PF	7			6		3	16	
Turdus fumigatus	OA	Med	SF					3	2	5	
Tyrannidae											
Lipaugus vociferans	IAS	High	PF	2						2	
Schiffornis turdinus	FA	High	PF	4			1			5	
Attila spadiceus	IAS	Med				1			1	2	
Laniocera hypopyrra	OA	High			1					1	
Lophotriccus galeatus	IAS	Med	SF	1		1				2	
Mionectes oleagineus	OA	Med	SF	14	9	7	9	13	14	66	
Myiobius barbatus	IAS	High		6	1		2	1	2	12	
Onychorhynchus coronatus	IAS	High		3	6	6	5		8	28	
Pachyramphus polychopterus	IAS	Low				1				1	
Platyrinchus coronatus	IAS	High					2		3	5	
Platyrinchus saturatus	IAS	High		5			5			10	
Ramphotrigon megacephala	IAS	Med		1	1	4		1	3	10	
Rhynchocyclus olivaceous	IAS	High		1			3	1	1	6	
Terenotriccus erythrurus	IAS	Med		4					1	5	
Tolmomyias assimilis	IAS	High	PF	1						1	
Tolmomyias flaviventris	IAS	Low	EUC			2				2	
Tolmomyias poliocephalus	IAS	Med	PF	1						1	
Tolmomyias sulphurescens	IAS	Med		1	2	3				6	
Vireonidae											
Hylophilus muscicapinus	IAG	High	PF	1						1	
Hylophilus ochraceiceps	IAG	Med	11	1			1	2		3	
Vireo olivaceous	IAG	Low				1	1	2		3 1	
Ollowecoup	110	HO W								1	
Total				356	276	335	268	299	376	191	

a IAF = insectivore ant-following, IAG = insectivore arboreal gleaning, IAS = insectivore arboreal sallying, IBS = insectivore bark-searching, IDL – insectivore dead leaf, ITG = insectivore terrestrial gleaning, FA = frugivore arboreal, GT = gramnivore terrestrial, NA = nectivore arboreal, OA = omnivore arboreal.

b Stotz et al. (1996). Disturbance-sensitivity classes: high, medium (med) and low.

c Species identified by the IndVal procedure as significant indicators of primary forest (PF), secondary forest (SF), or Eucalyptus plantation (EUC).

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.biocon.2008.06.017.

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