Bird assemblages in secondary forests developing after slash-and-burn agriculture in the Brazilian Amazon

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Abstract: Although indigenous farmers and other traditional peoples have disturbed Amazonian forests for centuries, few studies investigate the effects of these disturbances on biodiversity. This short-term study investigates how bird assemblages are affected by agricultural practices adopted by the residents of a national park in the Brazilian Amazon. Twelve sites in secondary forest (four sites in three age categories) and 12 sites in primary forest were selected for bird sampling. Audio-visual censuses of birds were conducted in small plots (1 ha) of young secondary growth (4–5 y), middle-aged (7–15 y), and old (20–35 y) secondary forests. Each site in secondary forest had a corresponding control site in adjacent primary forest. Young secondary growth had fewer species than old secondary and primary forests. Bird species richness was similar in middle-aged, old secondary and primary forests. Bird communities of young secondary habitat were dominated by species normally found in open habitats, such as agricultural fields and igapó flooded forests. The bird species composition of young secondary growth was more similar to that of middle-aged forest, which in turn was more similar to that of old secondary forests. Bird species composition differed between young secondary growth and old secondary forests and primary forests and between middle-aged secondary and primary forests. Nectarivore/insectivores and frugivore/insectivores of monospecific flocks are significantly associated with secondary forests, especially in initial stages of forest regeneration. In contrast, specialized insectivorous birds that join mixed-flocks show a significant association with primary forest.

Key Words: bird guilds, forest succession, Jaú National Park, secondary forests, traditional agriculture

INTRODUCTION

The effects of human-induced habitat modifications on birds have been studied in several locations in the Amazon region (Barlow *et al.* 2006, Borges & Stouffer 1999, Canaday 1996, Johns 1991, Kattan *et al.* 1992, Silva *et al.* 1996, Thiollay 1999). These studies demonstrate that bird species diversity, abundance and composition are altered in secondary habitats (abandoned pastures and secondary growth), as compared with undisturbed primary forests. Some of these studies have been conducted in fragmented landscapes highly degraded by large-scale agriculture projects (Bierregaard & Lovejoy 1989, Borges & Stouffer 1999, Silva *et al.* 1996). Disturbance of primary vegetation in the Amazon, however, is not exclusively a result of massive government-induced migration of peoples from other

regions (Fearnside 1987). Indigenous farmers and other traditional peoples have disturbed forests in the Amazon for centuries (Liu & Colinvaux 1988). Some anthropologists even say that the Amazon is far from pristine or untouched due to the strong cultural component in the ecological processes affecting complex landscapes (Balée 1992, Heckenberger *et al.* 2003).

Indigenous peoples and Amazonian *caboclos* (a generic term applied to rural peoples in the Brazilian Amazon), have developed complex systems of land use that certainly affect biological communities (Moran 1989, 1990). However, few studies have addressed how the low-intensity disturbance carried out by traditional farmers affects biodiversity. For example, sites managed for agriculture and abandoned for more than 10 y in Colombia show few differences in species richness and abundance of understorey birds when compared with sites in primary forest (Andrade & Rubio-Torgler 1994). Similar results were found in vegetation mosaics managed by the Kekchi-Maia people in Belize (Kricher & Davis 1992). These studies suggest that slash-and-burn agriculture

has a less pronounced effect on bird communities than large-scale disturbance such as pasture implementation. Studies about the effects of traditional land use on biodiversity are critical to evaluate the sustainability of these agriculture practices (Andrade & Rubio-Torgler 1994).

In this short-term study I investigate the effects on bird communities of the agriculture practices adopted by the peoples living in the Jaú National Park (JNP), Brazilian Amazon. Since these agricultural practices are widely adopted in the Amazon basin, this study allows a general understanding of how bird communities are affected by this type of land use. It is expected that a lower species richness and a distinctive bird species composition in secondary compared with primary forests will be found (Johns 1991). Also the local bird assemblages will change across the successional gradient provided by the recovery of vegetation after disturbance. This change in bird assemblages is probably associated with ecological and behavioural traits of birds since the response to habitat disturbance varies within guilds (Borges & Stouffer 1999, Stouffer & Bierregaard 1995a, b).

METHODS

Study area

Jaú National Park (JNP) is one of the largest conservation units in the Brazilian Amazon encompassing 2 272 000 ha situated on the western bank of the Rio Negro (1°54′S, 61°27′W). The rainfall in JNP is very seasonal with a wet season extending from January to July and a dry season from August to December. JNP is characterized by several forests and non-forest vegetation including terra firme forests, forests seasonally inundated by black waters or igapó, white sand woodland and other minor vegetation types such as secondary forests and vegetation growing in hydromorphic soils. The avifauna of these vegetation types has been extensively studied and approximately 470 bird species are recorded in JNP (Borges & Carvalhaes 2000, Borges *et al.* 2001, Borges, unpubl. data).

The study took place in March, April, June and July 2003 in two small villages in the eastern portion of the JNP (Figure 1). These villages are occupied by 10–12
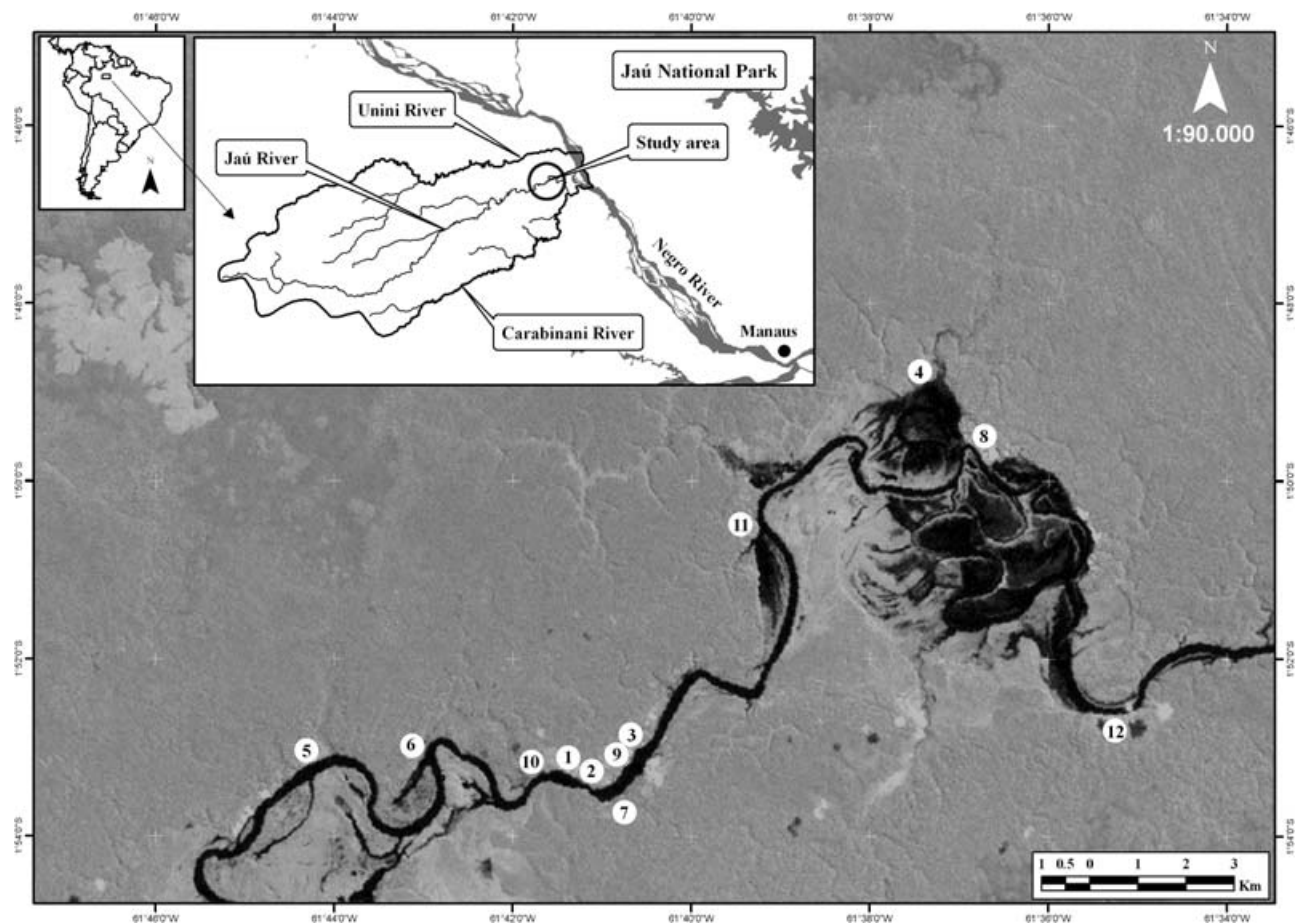

Figure 1. Approximate locations of study sites in the eastern region of the Jaú National Park, Brazilian Amazon. Only the secondary forest sites are shown. The sites numbered 1–4 are young secondary growth, numbers 5–8 are middle-aged secondary forests, and 9–12 are old secondary forests.

families distributed along 40 km of the Jaú river. The residents of JNP slash and burn primary or secondary vegetation then cultivate and abandon the agricultural sites over variable periods of time (Borges *et al.* 2004). The agricultural fields generally occupy 1 ha and are used for 2–3 y (Borges *et al.* 2004). They are generally located 100–500 m away from houses, in places that are not affected by the seasonal flooding of rivers. The landscape around the villages is composed of large tracts of primary or less-disturbed terra firme forest, igapó flooded forest, secondary forest in different successional stages and agricultural fields. The agriculture practices adopted in the study region are described in more detail elsewhere (Borges *et al.* 2004).

Site description

The sampling sites were established in three age-categories of secondary forest, based on interviews with local farmers: young secondary growth, middle-aged and old secondary forests. In each secondary forest type four 1-ha plots were established to sample birds and each plot had a corresponding control plot of the same size in adjacent near-undisturbed or primary forest. The 12 experimental and 12 control sites were always 200–300 m distant from each other.

The vegetation structure and landscape matrix in and around each of the secondary forest sites were highly variable, in part because of previous agriculture management (Table 1). Young secondary vegetation is defined as 4–5 y post-abandonment. Two of these study sites (1 and 2) were cultivated more than once and had open and lower canopy than the other sites in the same age category (Table 1). Site 1 was located near to (∼100 m)

Table 1. Vegetation structure and landscape characteristics of the study sites in the Jaú National Park, Brazilian Amazon. Canopy height was estimated at five points per site and canopy openness was estimated by 10 readings per site using a spherical densiometer. Values are mean ± SE. Abbreviations IG: igapó forest, AF: agriculture field, TF: terra firme forest.

Forest category	Sites	Canopy height (m)	Canopy openness (%)	Surrounding vegetation
Young	1	6.20 ± 0.37	40 ± 1.25	IG, AF, TF
	2	4.20 ± 0.62	56 ± 7.60	IG, TF
	3	14.2 ± 0.86	28 ± 1.81	IG, TF
	4	15.0 ± 0.54	35 ± 2.17	TF
Middle-aged	5	16.4 ± 0.67	31 ± 1.46	IG, AF, TF
	6	13.8 ± 0.37	38 ± 2.87	IG, TF
	7	18.8 ± 0.86	29 ± 1.46	IG, TF
	8	21.4 ± 1.07	29 ± 0.99	IG, AF, TF
Old	9	21.2 ± 1.35	26 ± 1.36	IG, TF
	10	19.6 ± 1.20	29 ± 1.17	IG, TF
	11	18.0 ± 0.70	32 ± 1.82	TF, AF
	12	18.2 ± 0.80	31 ± 1.17	TF

an active field. Pioneer plant species common in this successional stage include *Vismia* spp. and several species of Melastomataceae, such as *Miconia* spp. and *Clidemia* spp. The understorey of these sites is very dense and almost impenetrable.

Middle-aged secondary forest had a taller canopy (Table 1) and more open understorey than young secondary growth. The canopy in this forest was very open, and in this way similar to sites in young secondary growth (Table 1). *Cecropia* spp. dominated the canopy and *Heliconia* spp. appeared frequently in the understorey. Shrubs of Rubiaceae, especially from the genera *Psycothria* and *Palicourea*, were also very abundant in the understorey. The four middle-aged secondary sites ranged from 7 to 15 y after abandonment and two of them were in the neighbourhood of active fields (Table 1).

Old-aged forests had a taller and more closed canopy than middle-aged secondary vegetation (Table 1). The floristic composition was more diverse than other secondary forest stages, although large individuals of *Cecropia* spp. were still observed. In this category, sites ranged from 20–35 y post-abandonment and one site was adjacent to an active field.

The control plots in primary forest were the most variable in terms of vegetation structure with canopy height ranging from 22.5–35 m. The mean canopy height was greater than secondary forests and the understorey was denser, more shady and dominated by several palm species.

Bird censuses

Quantitative data on bird abundance and species diversity were obtained by counting individuals along two 100-m trails bisecting the 1-ha plots. The trails cut through relatively uniform patches of primary or secondary forests. The size of the sampling unit roughly coincides with the size of the agricultural fields. The small size of study plots did not permit the use of more traditional methods of counting birds, such as point counts. The census consisted of counting all individual birds seen or heard inside the plots. Birds observed along the border of the plots or in adjacent habitats were ignored. Each plot was sampled for birds once, between 06h00 and 10h00, the time of day with the highest bird activity. The sequence of sampling the sites followed no specific protocol and was constrained by logistic considerations. However, each pair of secondary and primary forest plots was sampled on sequential mornings.

During the census, the observer moved slowly along the trails, identifying and counting all individuals detected. A species was considered to be represented by more than one individual only if multiple individuals were simultaneously seen and/or heard. Small plot

size permitted monitoring the movements of most individuals, diminishing the probability of counting the same individual more than once. However, some fast-moving species, such as hummingbirds, manakins and some woodcreepers (e.g. *Glyphorynchus spirurus*) were likely underestimated. While this technique did not completely avoid the problem of double counting, it provided minimum estimates of the number of individuals present in the plots during the census.

The vegetation structure of the study sites may affect bird detection probabilities. The lower and more open canopy of the secondary forests makes the direct observation of birds easier than in the primary forests affecting among-site comparisons. However, only a small proportion of species (14%) and individuals (4%) were detected by sight alone. Given most species were detected by sound and the small plot sizes used, detection biased by the vegetation structure was likely marginal.

Data analyses

Differences in the number of species and individuals between secondary forests and the control sites were tested by a Kruskall–Wallis analysis of variance. Although the sampling effort applied in each site was identical, the number of individual birds recorded varied widely among sites. Rarefaction analysis, which uses repeated subsampling to estimate the number of species expected in a standard sample (Gotelli & Colwell 2001, Sanders 1968), was used to compare the number of species among sites. Rarefaction analysis has long been used in ornithological studies (Blake & Loiselle 2001, James & Rathbun 1981) and is known to avoid pitfalls when comparing species richness among samples (Gotelli & Colwell 2001). The average number of expected species and confidence intervals (95%) were calculated using the software ECOSIM 7.0. Non-overlapping confidence intervals around the mean number of expected species was interpreted as a statistical difference between groups (Blake & Loiselle 2001).

A non-metric multidimensional scaling (NMDS) using Sørensen's index as a similarity distance was performed to illustrate species similarity among sites. For this analysis, a matrix of the number of individuals of each species detected in each site was created. Two matrices were analysed: one with all species and another containing only species with at least five individuals detected. The patterns of site distribution in multidimensional space were similar in these two analyses and only the result from the analysis with all species is presented.

The hypothesis of no differences between groups of secondary and primary forest sites was tested through a multi-response permutation procedure (MRPP) using ranked Sørensen as distance measure. In MRPP are estimated a P value for evaluating if the observed difference between groups is due chance and a chance-corrected within-group agreement (A), a statistic that describes within-group homogeneity compared to random expectation (McCune & Grace 2002). The software PC-ORD was used to make NMDS and MRPP analysis following the general recommendations of McCune & Grace (2002).

Each bird species recorded in secondary forests was assigned to a probable source habitat: (1) primary terra firme forest, (2) igapó flooded forest, and (3) open habitats, such as agricultural fields. These are based on ornithological observations in JNP over the last 10 y and previous analyses of avian habitat use in the region (Borges & Carvalhaes 2000, Borges *et al.* 2001).

Birds were also assigned to the following guilds based on principal food items and social behaviour: (1) carnivores, (2) frugivores of monospecific flocks, (3) frugivore/insectivores of monospecific flocks, (4) frugivores of multispecies flocks, (5) solitary frugivores, (6) solitary frugivore/insectivores, (7) mixed-flocking insectivores, (8) insectivores of monospecific flocks, (9) army ant-following insectivores, (10) solitary insectivores, (11) nectarivore/insectivores, (12) omnivores of monospecific flocks and (13) solitary omnivores. Each species was assigned to a guild based on information from the literature (Karr *et al.* 1990, Powell 1989, Remsen *et al.* 1986, 1993; Willis & Oniki 1978) and field observations.

Bird species or guilds that had significant association with specific habitats or forest categories were identified through an indicator species analysis (Dufrêne & Legendre 1997). In this analysis relative abundance and relative frequency are used to calculate an indicator value (IndVal) that ranges from zero (no indication) to 100 (perfect indication) for a given species (or guild) across groups of sites or habitats (Dufrêne & Legendre 1997). Two approaches were adopted in the analysis. First, two general groups of habitats were defined: secondary and primary forests. Second, the a priori habitat categorization (young secondary growth, middle-aged and old secondary forests) was used to identify species (or guilds) that can be indicators of habitats in a more refined way. The Monte Carlo test (1000 runs) was used to evaluate the statistical significance of the indicator value measured for each species or guild. Tests were performed using PC-ORD software on species with at least five individuals recorded.

RESULTS

Bird species richness and abundance

During the study 1168 individuals of 150 bird species were recorded; 116 species in secondary and 110 in primary forests (the species checklist is available on

Table 2. Summary of species richness (number of species) and abundance (number of individuals) of birds in secondary forests and corresponding control sites in primary forests in the Jaú National Park, Brazilian Amazon.

Forest category	Sites	Species richness	Control site species richness	Number of individuals	Control site number of individuals
Young	1	19	35	28	47
	2	24	40	34	61
	3	30	40	37	52
	4	46	35	66	44
Middle-age	5	40	49	62	64
	6	51	38	74	51
	7	28	26	37	34
	8	42	39	53	49
Old	9	30	39	37	48
	10	21	35	26	43
	11	30	42	39	76
	12	33	41	48	58

request from the author). Species richness and abundance of birds were highly variable among sites (Table 2). Considering all species there are no differences in species richness (H = 7.38; df = 5; P = 0.193) and abundance (H = 6.34; df = 5; P = 0.274) among group of sites. Excluding no terra firme forest species, the young secondary growth sites have significantly lower number of species (H = 15.0; df = 5; P = 0.01) and individuals (H = 11.8; df = 5; P = 0.04) than primary forest sites.

Comparisons standardized by sample size show that only young secondary growth had lower species richness than corresponding control sites and old secondary forest (Figure 2). Pooling the sites in two forest categories (primary and secondary) the species richness was significantly higher in secondary forests (mean expected species = 116, CI(95%) = 113–119, standard 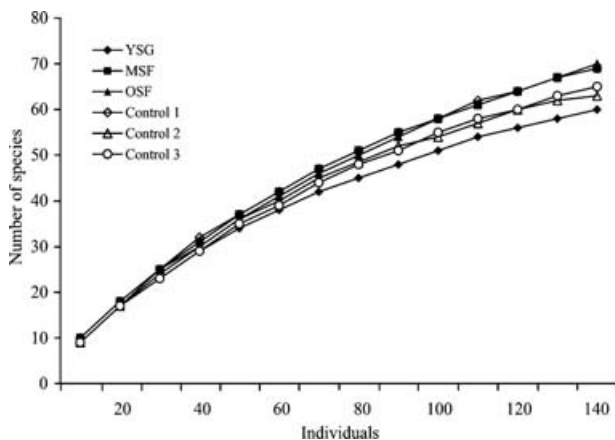sample size = 500 individuals) than in primary forests (mean expected species = 108, CI(95%) = 103–112). Excluding species recorded in secondary forests that came from habitats other than primary terra firme forest, the pattern is reversed and primary forests have significantly more species (mean expected species = 89, CI(95%) = 84–95, standard sample size = 350 individuals) than secondary forests (mean expected species = 80, CI(95%) = 78–82).

Bird species composition

Sites in young secondary growth and primary forest were the furthest apart along a relatively well-defined gradient of species compositions based on forest type (Figure 3). Sites in middle-aged secondary forest occupy intermediary positions and sites in old secondary forests group with primary forest (Figure 3). Sites in primary forests formed a distinct and relatively homogeneous group. On the other hand, the sites in young secondary growth and old secondary forest were heterogeneous in species composition (Figure 3). Sites 1 and 2, with the least successional development, had more negative scores along the primary axis compared with the other two sites of young secondary growth. These two sites were also somewhat distinct in bird species richness and vegetation structure.

The MRPP results show that the bird species composition differed between young secondary growth and old secondary (A = 0.34; P = 0.007) and primary forests (A = 0.35; P = 0.000001) and between middle-aged secondary forests and primary forests (A = 0.27; P = 0.00001). In contrast, no significant differences in species composition were found between young secondary growth and middle-aged secondary forests (A = 0.26;
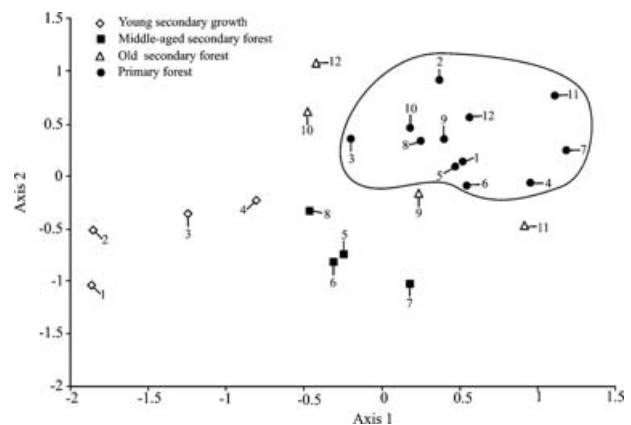

Figure 2. Species rarefraction curves in young secondary growth (YSG), middle-aged secondary forest (MSF), old secondary forests (OSF) and primary forests (controls 1, 2, 3) in the Jaú National Park, Brazilian Amazon.

Figure 3. Ordination of sampling sites based on a non-metric multidimensional scale (NMDS), using data on bird abundance in the Jaú National Park, Brazilian Amazon. The sites are numbered as in Figure 1. The numbers shown in the primary forest sites (encircled) represent the corresponding secondary forest site. The first NMDS axis represents 61% of the variation in the original dataset and the second axis represents 22%.

P = 0.015; P adjusted by a Bonferroni procedure), middle-aged and old secondary forests (A = 0.26; P = 0.011; P adjusted by a Bonferroni procedure) and old and primary forests (A = 0.04; P = 0.14).

Sources of avifauna

The usual source habitats of birds recorded in secondary vegetation in JNP are primary terra firme forest, igapó flooded forest, and open habitats such as agricultural fields and open igapó. The contribution of primary terra firme forest or other habitats to the species richness and abundance of birds invading secondary forests is significantly associated to the age categories (G test, $G = 392$, df = 9, P < 0.01). A large proportion of the species and individuals found in young secondary growth arrives from open habitats and igapó flooded forests (Figure 4).
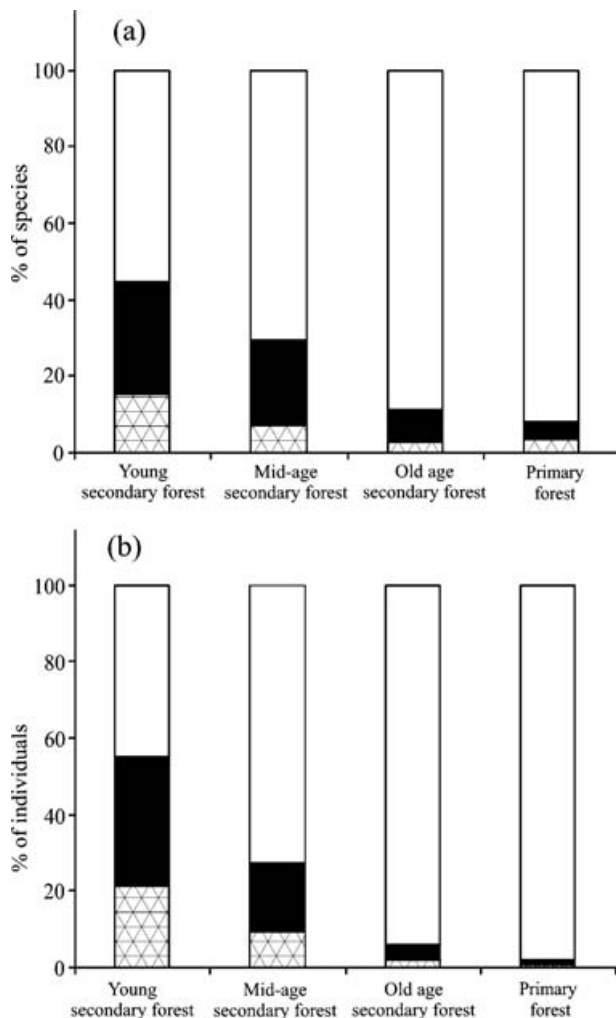

Figure 4. Proportion of species and individual birds recorded in primary and secondary forest sites, categorized by source habitat: terra firme forest (white bars), igapó flooded forest (black bars) and open habitats (crossed lines) in the Jaú National Park, Brazilian Amazon.

Table 3. Bird species significantly associated with secondary or primary forests in the Jaú National Park, Brazilian Amazon, identified by indicator species analysis (Dufrêne & Legendre 1997). Indicator values (IndVal) are expressed as percentages and P values are calculated using a Monte Carlo procedure.

Bird species	IndVal (observed)	IndVal (randomized)	P
Secondary forest			
Patagioenas cayennensis	58.3	24.4	0.004
Phaethornis ruber	69.4	33.8	0.001
Cercomacra tyrannina	66.7	27	0.001
Tolmomyias poliocephalus	58.3	24.3	0.005
Cyclarhis gujanensis	51.9	26.3	0.018
Thryothorus coraya	53.8	26.1	0.012
Thraupis episcopus	45.5	24.1	0.042
Ramphocelus carbo	63.6	29.5	0.006
Cyanocompsa cyanoides	53.3	29.8	0.037
Primary forest			
Galbula dea	59.3	28.5	0.014
Herpsilochmus dorsimaculatus	55.3	36.8	0.048
Terenura spodioptila	41.7	19.4	0.039
Hylophylax naevius	68.6	34.8	0.003
Xiphorhynchus ocellatus	66.2	42.4	0.014
Automolus infuscatus	41.7	19.5	0.042
Myiopagis caniceps	60	28.3	0.010
Lipaugus vociferans	81.5	37.3	0.001
Tyranneutes stolzmanni	66.2	42	0.011
Schiffornis turdina	50	21.4	0.017
Hylophilus ochraceiceps	75	28.8	0.001
Turdus albicollis	41.7	19.4	0.038

The contribution of these source habitats to the species richness and abundance of middle-aged and old stands of secondary forests is substantially diminished (Figure 4). Birds typical of open habitats (e.g. *Ramphocelus carbo* and *Columbina passerina*) and igapó flooded forest (*Cercomacra tyrannina* and *Patagioenas cayennensis*) were more abundant in young secondary growth and middle-aged secondary forests than in old secondary and primary forests.

Species and guilds as habitat indicators

In a general categorization, 12 bird species were significantly associated with primary and nine significantly associated with secondary forests (IndVal > 40%, P < 0.05; Table 3).

Grouping the sites by age category, three species (*Leptotila* sp., *Cercomacra tyrannina* and *Ramphocelus carbo*) emerged as being significantly associated with young secondary growth and two with middle-aged secondary forest (*Hypocnemis cantator* and *Terenotriccus erythrurus*). No species was identified as an indicator of old secondary forest.

From 13 ecological guilds, only mixed-flock insectivores showed a significant association with primary forest (IndVal = 67.9%, P = 0.003). Frugivore/insectivores of monospecific flocks (IndVal = 70.5%, P = 0.002) and the

nectarivore/insectivores (IndVal = 76.4%, P = 0.004), mainly hummingbird species, were identified as indicator guilds of secondary forest. Bird species of these two guilds were especially abundant in the young and middle-aged secondary vegetation.

DISCUSSION

Secondary succession and bird communities

Despite the limited sampling effort, the results of this preliminary assessment of effects of agriculture practices in bird assemblages can be generally compared with other studies in the tropics. Bird species diversity in JNP increases with secondary forest age and only early successional forests have a notably lower diversity such as has been documented in Africa and India (Blankespoor 1991, Bowman *et al.* 1990, Raman *et al.* 1998). In JNP, the bird species richness in middle-aged and old secondary forests becomes more similar to primary forests as happened in landscape managed by the Kekchi-Mayan Indians in Belize and habitats managed for agriculture in Colombia (Andrade & Rubio-Torgler 1994, Kricher & Davis 1992). In addition to time since abandonment of farms, how secondary sites are managed apparently influenced bird community structure (Borges & Stouffer 1999). The two sites repeatedly cultivated had a distinct bird species composition and lower species richness compared with fields cultivated once (Table 2).

Birds from open habitats or igapó flooded forests provide the additional species richness in secondary vegetation as has been observed in other parts of the Amazon (Andrade & Rubio-Torgler 1994, Johns 1991, Remsen & Parker 1983, Terborgh & Weske 1969). Similarly, non-forest birds that colonize 1–5-y-old secondary growth also are an important component of species diversity in agriculture systems in India (Raman *et al.* 1998).

In JNP, Belize, Africa and India bird species composition was more similar among sites in the same phase of succession providing evidence for a relatively well-defined temporal gradient of avian community structure in secondary forests (Blankespoor 1991, Kricher & Davis 1992, Raman *et al.* 1998). Similarity between species composition in secondary and primary forest sites increases with the age of secondary forest stands (Raman *et al.* 1998). Compared with later phases of succession, young secondary growth is remarkably distinct in vegetation structure, bird species composition and richness (Andrade & Rubio-Torgler 1994, Blankespoor 1991). Plant species composition and vegetation structure likely explained a good part of the bird colonization processes in the secondary growth (Bowman *et al.* 1990, Raman *et al.* 1998). Additionally, features of the landscape surrounding the sites may have

had an influence on the bird assemblages that occupied secondary forest sites in JNP.

The avian community in secondary and primary forests in India, became rapidly more similar during the first 25 y of abandonment and, after this time, avifaunal recovery diminished dramatically (Raman *et al.* 1998). A study of bird population dynamics in young secondary growth in Costa Rica also documented major changes in bird communities over a relatively short period of 4 y (Loiselle & Blake 1994). These results suggest a fast and incomplete recovery of bird species richness and composition in the initial of secondary succession followed by a deceleration phase as observed in studies of tropical plant succession (Steininger 2000, Uhl *et al.* 1981).

Bird ecological groups

The process of altering vegetation to implement agricultural fields does not affect all ecological groups of birds similarly. Open-habitat birds, such as frugivore/insectivores that form monospecific flocks, are favoured in initial phases of succession (Blankespoor 1991, Johns 1991, Raman *et al.* 1998). It is possible that secondary forests offer a higher abundance of food resources for these generalist species.

Nectarivore/insectivores were significantly more abundant in young secondary growth and middle-aged secondary than in primary forests in JNP as shown in indicator analysis. In contrast, primary forests in India had more nectarivore/insectivores than secondary forests and in Colombia the abundance of this guild did not differ within forest type (Andrade & Rubio-Torgler 1994, Raman *et al.* 1998). In India, this guild is represented by bird families not found in South America, such as Irenidae and Dicruridae (Raman *et al.* 1998), suggesting that species in the same guild in different continents react in different ways to habitat disturbance.

The abundance of nectarivore/insectivores, especially the hummingbirds, is probably related to the availability of food resources. The abundance of flowering and fruiting understorey plants in the study sites was four times higher in secondary than primary forests (Borges, unpublished data), and hummingbirds were observed feeding in several of those plants. Understorey hummingbirds respond favourably to habitat disturbance and their abundance increases in fragmented landscapes and along edges (Restrepo & Gómez 1998, Stouffer & Bierregaard 1995a).

Insectivores with specialized social behaviours, such as birds that follow army ants and mixed-flocks, seem to avoid secondary forests, especially in the initial phases of succession. Individuals of these guilds were more frequently observed in primary and old secondary forests. Ant-followers were also more abundant in undisturbed forest than in second growth in Colombia (Andrade

& Rubio-Torgler 1994). Mixed-flocks and ant-following birds are very sensitive to forest fragmentation and secondary succession in highly degraded landscapes of the Central Amazon (Bierregaard & Lovejoy 1989, Borges & Stouffer 1999, Stouffer & Bierregaard 1995b). The results of the present study add to the evidence that understorey insectivorous birds with specialized behaviours are highly sensitive to habitat disturbance in Amazon, even on a small scale (Barlow *et al.* 2006, Bierregaard & Lovejoy 1989, Borges & Stouffer 1999, Canaday 1996, Stouffer & Bierregaard 1995b).

Birds characteristic of primary forests, such as ground insectivores and large-bodied frugivores were rarely recorded in the censuses. The ground insectivores of the Formicariidae are very sensitive to habitat disturbance (Canaday 1996, Canaday & Rivadeneyra 2001, Stratford & Stouffer 2001). Large frugivores (trumpeters and currasows) were also absent from the censuses. These species require large territories (Terborgh *et al.* 1990) and the size of the study plots may have been too small to allow their detection. Additionally, hunting probably affects the abundance of these species, especially currasows, guans and trumpeters, which are hunted for food by residents of JNP (Pezzuti *et al.* 2004, Silva & Strahl 1991).

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