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BIRD COMMUNITIES IN TWO TYPES OF ANTHROPOGENIC SUCCESSIONAL VEGETATION IN CENTRAL AMAZONIA[1]

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Abstract. When primary forest in central Amazonia is cut and abandoned, the plant succession is dominated by *Cecropia* spp., whereas when it is cut and burned for pastures, the regrowth vegetation is dominated by *Vismia* spp. The bird communities of these two regrowth forest types were sampled at six sites (9–13 years old) using mist-nets and observations. Bird species richness was similar between the two forest types. *Cecropia* regrowth, however, was richer for strictly forest bird species than was *Vismia* regrowth. Mixed-flock species and ant-following birds were significantly more abundant in the *Cecropia* second growth, whereas nonforest insectivores and omnivores were more common in *Vismia* regrowth. The type of regrowth was found to influence bird species composition in the study sites. These results suggest that the type of human disturbance has an important role in determining the bird communities that occupy early successional areas in central Amazonia.

Key words: Amazon, ant-following birds, Cecropia, *human disturbance, secondary forest birds, tropical birds,* Vismia.

INTRODUCTION

In central Amazonia, bird community studies have been concentrated in primary forest and forest fragments, mostly in conjunction with the Biological Dynamics of Forest Fragments Project (BDFFP), a large-scale experimental project on the effects of fragmentation on forest communities including birds, mammals, and plants (Bierregaard and Lovejoy 1989, Bierregaard et al. 1992, Stouffer and Bierregaard 1995a, 1995b). During the process of establishing the BDFFP study sites on large private farms, extensive areas of primary forest were cleared, and in some cases burned. The process of clearing instigated two major types of regrowth: a *Cecropia*-dominated community that normally regenerates in the absence of fire, and a *Vismia*-dominated community that regenerates where fire was frequently used to manage these grasslands.

This study compared the bird community of these two types of successional forest. We describe general patterns in species richness and abundance considering the following questions: What bird species occur in each type of secondary growth? Is the similarity in bird assemblages affected by the type of regrowth? Are there differences in species richness and abundance of birds among sites? Do bird guilds differ in species composition and abundance in the two types of secondary forest?

METHODS

We selected three sites in *Cecropia*-dominated second growth (hereafter CSG) and three sites in *Vismia*-dominated second growth (hereafter VSG) in study areas of the BDFFP (see Ferreira and Laurance 1997 for map of the study sites). The sites selected have undergone different management practices and differ in age and floristic composition (Table 1). Vegetation in Colosso and Florestal sites was periodically cut and burned until 1985. Because of this intense management and periodic use by cattle, these sites contained large areas of pasture devoid of secondary vegetation. At Dimona, secondary vegetation was not periodically controlled by fire. Some small areas of primary forest, mostly associated with streams, are present in the *Cecropia* site at Dimona. All net lines were separated by at least 1 km, except in Colosso and Florestal where the nets lines were separated by 300 m.

The rainfall in central Amazonia is seasonal, with a dry season from July to October and a

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TABLE 1. Features of study sites of secondary growth types in Amazonia, Brazil. Fire indicates that primary vegetation is burned. Management indicates whether the area is cut, burned, and used by cattle.

Sites	Secondary growth types	Age[a] (in years)	Canopy height (m) (mean ± SD)	Fire	Management
Dimona	*Vismia*	9	7.6 ± 1.6	yes	moderate[b]
Colosso	*Vismia*	13	5.3 ± 3.2	yes	intense[c]
Florestal	*Vismia*	13	5.4 ± 3.0	yes	intense
Dimona	*Cecropia*	12	17.4 ± 3.4	no	no
Porto Alegre	*Cecropia*	10	17.0 ± 3.7	no	no
Cidade Powell	*Cecropia*	10	15.5 ± 3.4	no	no

[a] Years since the last management activities.
[b] Occasional burning.
[c] Annual burning.

wet season from November to June (Stouffer and Bierregaard 1993). The field work described here extended from late March (mid-wet season) to mid October (late dry season) in 1993.

MIST-NET CAPTURES AND OBSERVATIONS

At each site, we used 30 mist-nets (36 mm mesh, 12 × 2 m) arranged in two parallel net-lines, with 15 nets in each line. In each case the net lines were located at two distances from primary forest—50 and 250 m. Two days of field work were expended in each sampling period at each site totaling 72 days of field work. The nets were open from 6:00 to 14:00, and the study sites were visited at monthly intervals. The total sampling effort was 17,280 net-hours equally distributed between types of second growth. Birds were given individually numbered aluminum bands. Compared with the bird list including captures and observations in each study site, nets sampled 55% (range 45–61.5%) and 47% (range 44–52.5%) of the bird species recorded in VSG and CSG, respectively. Relative abundance measurements were based only on net samples.

In addition to the mist-net samples, we used binoculars and a tape recorder to note all species heard or observed in the sites. Tape playback was important for identification of some species. In addition to our previous experience at the sites, tape recording and local lists of birds by other workers at BDFFP study sites (Stotz and Bierregaard 1989, Cohn-Haft et al. 1997) facilitated identifications. Sampling effort dedicated to general observations was similar in each study site and occurred principally between 06:00 and 15:00.

DATA ANALYSIS

Birds observed flying over the study sites (vultures, swallows, and swifts) and nocturnal species were not considered in the comparison between the two types of regrowth. We classified birds as forest and nonforest species as proposed by Cohn-Haft et al. (1997). We used a *G*-test with William's correction for sample size, for testing associations between numbers of captures, species richness, and vegetation types. Only species or groups of species with more than 10 individuals captured were considered in the comparisons between types of secondary growth. The distance of net-lines from primary forest had no effect on total number of species (captured and observed) (Wilcoxon test, $Z = -0.4$, $P > 0.5$), species captured ($Z = 0.1$, $P > 0.5$), and individuals captured ($Z = -1.7$, $P > 0.05$). Thus, unless otherwise indicated, we pooled data from the two net-lines in each study site. In multiple comparisons we adjusted the significance level by Scheffé's correction factor, dividing the significance level assumed ($P < 0.05$) by the number of comparisons.

Because the number of captures differed between sites, the comparison of understory bird species richness was standardized by rarefaction curves. This method generates an expected number of species for a standard sample size (Ludwig and Reynolds 1988). Following recommendations by James and Rathbun (1981), we standardized the sample size by the site with the lowest number of captures.

We performed cluster analysis with Sørensen distance measure and group averaging as weighting procedures to represent the relationships of bird species assemblages in the sites (McCune and Mefford 1995). Each net-line was

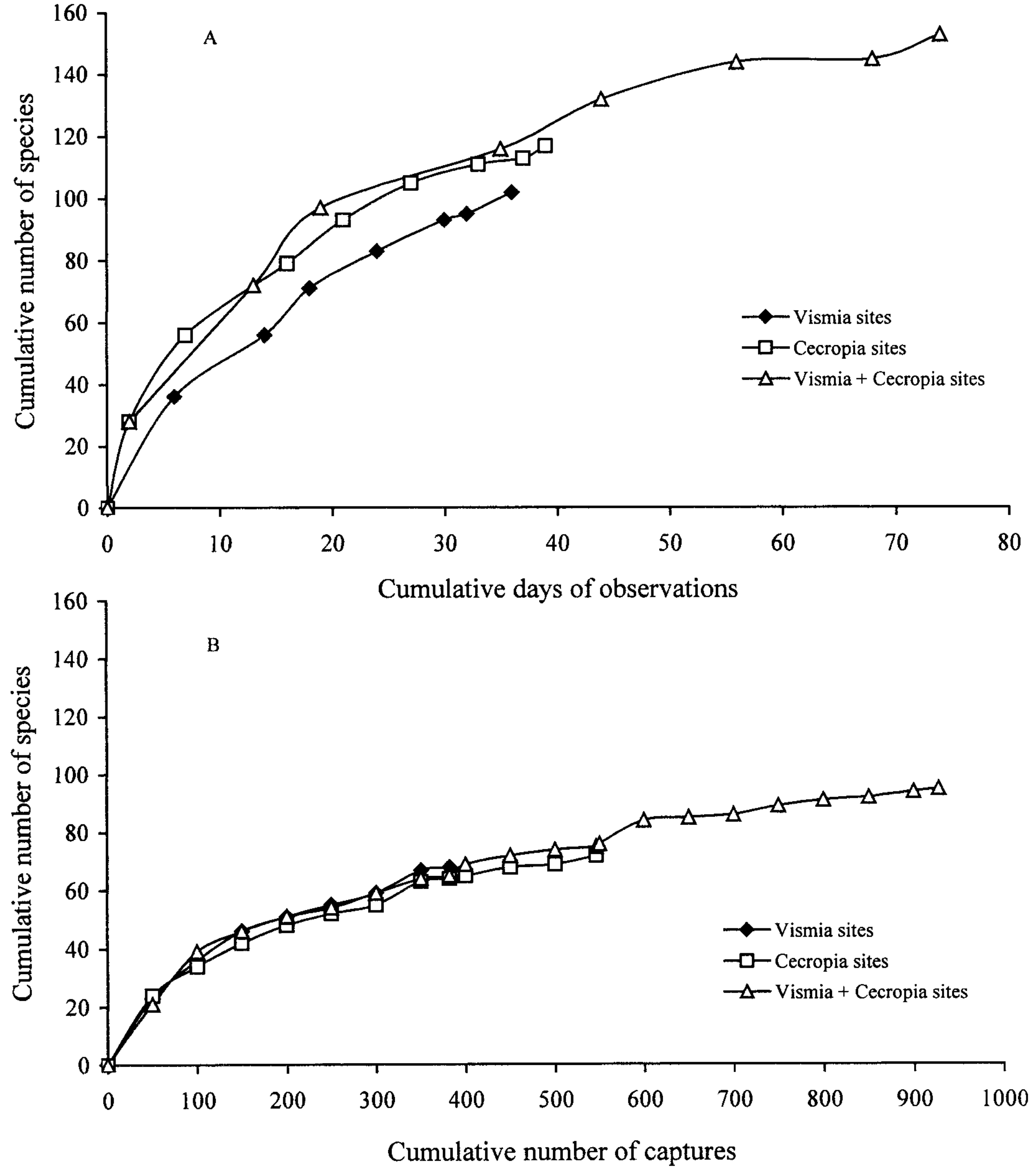

FIGURE 1. Curves of species-sampling effort including observed (A) and captured (B) birds.

considered as a sampling unit for the cluster analyses. Values are reported as means ± SD.

RESULTS

SPECIES RICHNESS AND ABUNDANCE

Combining captures and observations, we recorded 177 bird species on the study sites (check-list available by request from first author). The cumulative curves of observed and captured species (Fig. 1) indicate that sampling was not complete. However, based on previous studies in the area (Bierregaard and Lovejoy 1989), most of the relatively common species in understory were captured.

The total number of species at the *Cecropia* sites was 141, whereas 123 species were en-

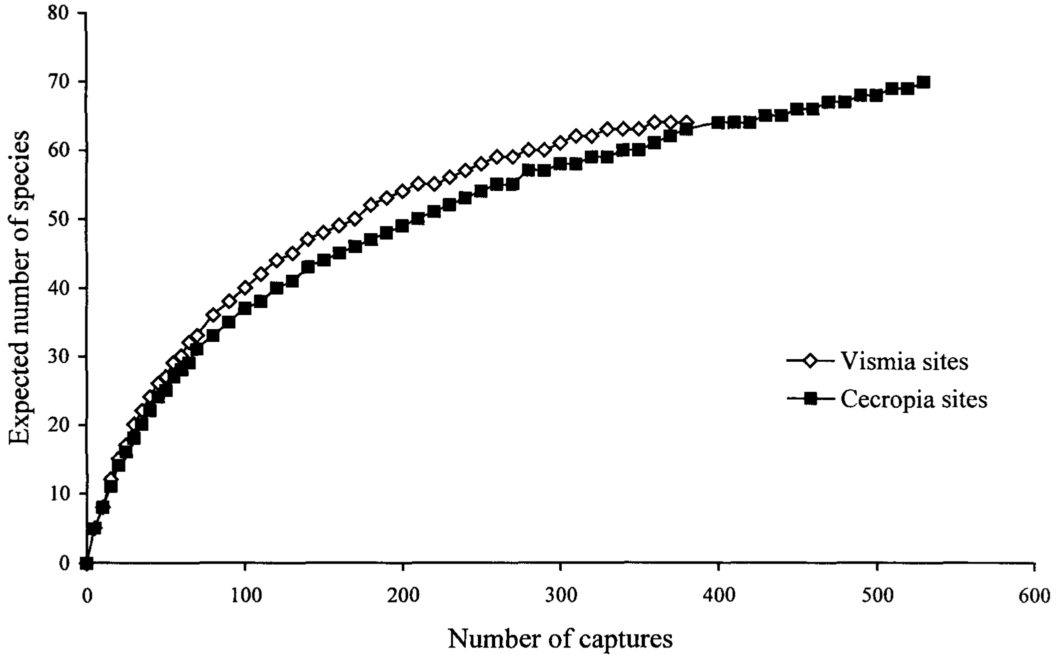

FIGURE 2. Rarefraction curves for the secondary growth bird species. The standard sample size is 380 captures with 63 species from *Cecropia* sites and 64 for *Vismia* sites.

countered on *Vismia* sites. There was no significant difference in species richness of captured birds between VSG (45.5 ± 9.0 species) and CSG (44.6 ± 7.0). When observed species were included in the total species richness calculation, CSG sites are slightly richer than VSG sites (94 ± 5.5 vs. 83 ± 5 species). Rarefaction analysis also showed that the understory of the two types of second growth presents little difference in species richness (Fig. 2). However, CSG is significantly richer in forest bird species than VSG (137 vs. 106 species; G_1 = 4.2, $P < 0.05$). Some forest birds were recorded in only one type of second growth with 54 species restricted to CSG and 22 species restricted to VSG.

We captured 928 individuals (excluding recaptures and same day captures). Ten species contribute with 53.5% of all captures, with the White-plumed Antbird dominating captures in both types of second growth (Table 2; scientific names in Table 2 unless otherwise noted). Significantly more individuals were captured in CSG than in VSG (546 vs. 382) (G_1 = 29.10, $P < 0.01$).

GUILDS

We grouped birds into guilds based on food habits, foraging substrate, habitat, and behavior, and analyzed these guilds in terms of species richness and abundance between secondary forest types (Table 3). The number of species in some bird guilds differed between secondary forest types. Ground insectivores, especially Formicariidae, were more species-rich in CSG (eight vs. four), but the sample sizes were too small for statistical analysis. Some species in this group, such as Thrush-like Antpitta (*Myrmothera campanisona*), Ferruginious-backed Antbird (*Myrmeciza ferruginea*), and Spot-winged Antbird (*Schistocichla leucostigma*), were not recorded in VSG. In contrast, two other species in this guild, Black-throated Antbird (*Myrmeciza atrothorax*) and Ringed Antpipit (*Corythopis torquata*), were recorded only in VSG. The nuclear-species of the mixed-flocks (Cinereous Antshrike *Thamnomanes caesius*) and the three species of specialized ant-followers (Willis and Oniky 1978) were found in the two types of secondary growth. Army ants also were observed in both types of regrowth. Mixed flocks were rarely seen in the study sites. The species listed as understory insectivores represent a heterogeneous group which precludes any generalizations. However, the number of species in the Bucconidade family merits attention. In VSG

TABLE 2. Number of captures of the 10 most commonly captured species in each type of secondary growth. The ranking position for each habitat is listed in parentheses.

Species	CSG	VSG
White-plumed Antbird (*Pithys albifrons*)	82 (1)	48 (1)
Black-headed Antbird (*Percnostola rufifrons*)	44 (2)	12 (6)
Rufous-throated Antbird (*Gymnopithys rufigula*)	40 (3)	11 (7)
White-crowned Manakin (*Pipra pipra*)	30 (4)	37 (2)
Warbling Antbird (*Hypocnemis cantator*)	30 (5)	7 (10)
McConnell's Flycatcher (*Mionectes macconnelli*)	19 (6)	17 (4)
Mouse-Colored Antshrike (*Thamnophilus murinus*)	18 (7)	9 (8)
White-flanked Antwren (*Myrmotherula axillaris*)	18 (8)	8 (9)
Buff-throated Foliage-gleaner (*Automolus ochrolaemus*)	16 (9)	24 (3)
Long-tailed Hermit (*Phaethornis superciliosus*)	13 (10)	14 (5)

TABLE 3. Number of species (observed + captured) and captures in the two types of secondary growth grouped by guilds. The numbers with asterisks (*) are significantly different (G-test, $P < 0.006$, adjusted by Scheffé's correction factor for multiple comparisons).

Guilds[a]	Number of species		Number of captures	
	VSG	CSG	VSG	CSG
Frugivores				
ground	5	5	2	4
understory	13	10	75	62
canopy	11	20	3	1
Insectivores				
ground	4	8	8	18
understory	26	31	129*	201*
canopy	13	12	2	12
open areas	7	2	10	0
bark[b]	5	8	7	12
mixed-flocks[c]	9	11	29*	65*
ant-followers	3	3	65*	128*
Omnivores				
ground	2	3	4	1
understory	1	1	2	4
canopy	7	13	1	1
open areas	7	1	6	0
Nectarivores/insectivores	5	8	24	44
Predators	2	3	2	1
Granivores	3	1	3	1
Piscivores	0	1	0	1

[a] Guild designation follows Karr et al. (1990), Stouffer and Bierregaard (1995b), Powell (1989), and personal observations.
[b] Does not include species that follow mixed flocks and army ants.
[c] Included understory and canopy flocks.

only Black Nunbird (*Monasa atra*), a common forest edge species, was observed. In contrast, five species of this family were recorded in CSG. Open area insectivores/omnivores and granivorous species were almost exclusively found in VSG (17 vs. 4 species, respectively, $G_1 = 8.5$, $P < 0.01$).

Some guilds present differences in relative abundance between the two types of secondary growth (Table 3). Insectivores show the most significant differences in relative abundance between the secondary growth types. In the ant-following guild, only White-chinned Woodcreeper (*Dendrocincla merula*) was equally abundant in the two types of secondary growth. The Cinereous Antshrike, the nuclear-species of the mixed flocks, also was captured in similar frequency among secondary growth types. Ground insectivores that walk rather than fly were rarely captured. Nets do not provide a good indication of the relative abundance of these species. Nevertheless, field observations indicate that these species are more common in CSG. For example, Thrush-like Antpitta is a ground insectivore commonly heard in CSG, but was never detected in VSG sites.

RELATIVE ABUNDANCE OF SPECIES: VSG VS. CSG

Of 33 species for which there were sufficient captures, 8 showed significant differences in abundance between the two types of secondary regrowth, all being more abundant in CSG. These species included five understory insectivores of Thamnophilidae family (Black-headed Antbird, Rufous-throated Antbird, White-plumed Antbird, Warbling Antbird, and White-flanked Antwren), a woodcreeper (Wedge-billed Woodcreeper *Glyphorhynchus spirurus*), a forest wren (Wing-banded Wren *Microcerculus bambla*), and a hummingbird (Fork-tailed Wood-nymph *Thalurania furcata*). The antbird species include two obligate ant-followers (White-plumed Antbird and the Rufous-throated Antbird) and two solitary species commonly found along forest edges: Warbling Antbird and Black-headed Antbird (Willis 1982, Stouffer and Bierregaard 1995b).

Although there was a significant difference in number of captures of White-flanked Antwren between second growth types, the abundance of this species was probably underestimated in VSG sites. This species was frequently observed

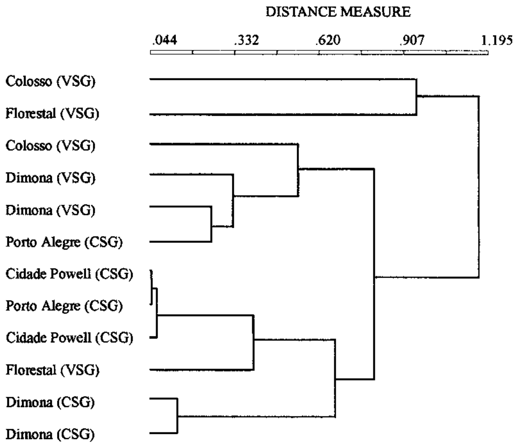

FIGURE 3. Dendrogram of cluster analysis of study sites. Groups of net-lines (sampling units) were grouped by their similarity in bird species composition. The smaller the distance between pairs of sampling units, the more similar they are in species composition.

in familial groups of five individuals foraging in the canopy of VSG where they cannot be sampled by nets. With the exception of White-flanked Antwren, all species cited above also were detected by song and observations in the lowest stratum of the secondary growth, where they should have been well sampled by nets.

AVIFAUNAL SIMILARITY BETWEEN SITES

Three major groups emerged from the cluster analysis and with the exception of two sites (one net-line in Porto Alegre and one in Florestal), all net-lines were grouped by the type of secondary growth (Fig. 3). The first group included two net-lines in very disturbed VSG sites. The remaining VSG and CSG sites were separated by two major groups. This clustering pattern indicates that the structure of bird communities is affected by the type of second growth, despite sites showing no great differences in species richness. Moreover, the sites in VSG were more heterogeneous in species composition than CSG, a result probably associated with the management of the sites.

DISCUSSION

SPECIES RICHNESS AND COMPOSITION

Higher forest bird species richness in CSG was expected based on the greater vegetation complexity of this secondary forest. The canopy in CSG is on average twice as high as in VSG (Table 1). Moreover, a floristic study conducted in the same area showed that CSG was richer in plant species than VSG (Williamson et al. 1998), which may also promote higher bird species richness (Rotenberry 1985). Therefore, plant species diversity and vegetation structure can partially explain the differences in bird abundance and species diversity between the two types of secondary forests.

Apparently, the origin of vegetation succession and consequently the habitat structure in the study sites are influenced by the severity of land management. More severe management, including periodically cutting and burning, results in a more depauperate bird fauna. Alternatively, the secondary forests with lower grazing pressure are colonized by several typical forest bird species.

The age of secondary forests also may explain the differences in bird abundance and composition in the study areas. Studies in secondary forest bird communities in Costa Rica showed that bird species richness and abundance change through time with forest succession (Loiselle and Blake 1994). The age of our sites varied slightly (Table 1), but this can only partially explain the changes in bird community at the secondary forests sites studied.

Some patterns of differential use of secondary forest by bird guilds were expected based on previous reports on the effects of fragmentation and the type of secondary growth around the fragments on the bird community (Stouffer and Bierregaard 1995a, 1995b, Bierregaard and Stouffer 1997). Ant-following birds are very sensitive to habitat disturbance (Canaday 1995). Species of this group are the first to disappear from forest fragments (Bierregaard and Lovejoy 1989). On Barro Colorado Island, the ant-follower birds declined after the island was isolated, and some species became locally extinct, possibly due to their inability to cross the water barrier separating the island from the mainland (Willis 1974).

The mixed-species flocks disintegrate after forest fragmentation (Bierregaard and Lovejoy 1989). Although the flocks as a unit disintegrate, individual species react in different ways to habitat disturbance (Bierregaard and Lovejoy 1989, Stouffer and Bierregaard 1995b, this study). The nuclear-species of flocks (Cinereous Antshrike) is relatively common in both types of secondary forests studied. Conversely, *Myrmotherula* spp.

(excepted *M. axillaris*), common in primary forests mist-net samples (Stouffer and Bierregaard 1995b, Cohn-Haft et al. 1997), are extremely rare in the secondary growth.

Why do species that composed this guild differ in abundance among types of secondary forest? We did not investigate the proximate causes of avoidance or preference for a particular vegetation type, but some hypotheses can be discussed. All species with consistent differences in abundance between secondary forests are insectivores. Hence we expect differences in availability of insects present in the two types of forest.

Another criterion of bird habitat selection are microclimate conditions. Activity patterns of understory birds are influenced by moisture gradients with some species more active in dry and others in moist sites (Karr and Freemark 1983). Although no microclimate data were collected in the study sites, the VSG appears to be hotter, dryer, and brighter than CSG. Birds with higher capture rates in CSG are species typically found in dark and moist understory in forest interior. Physiological tolerance of these species may explain their association with CSG, a habitat that appears more similar in microclimate to the primary forest than is VSG.

CONSERVATION IMPLICATIONS

Large blocks of primary forest in the tropics are cut and burned for agriculture. Due to a variety of circumstances including soil quality, climate, and changes in government policy, these areas are, in most cases, abandoned and occupied by successional vegetation. The history of our study sites follows a similar model of occupation, use, and abandonment. This study suggests that bird communities in secondary forest are affected indirectly by how previous land use history influences vegetation succession. The more severe management practices, especially periodic use of fire, apparently have more negative impact on the bird community, particularly for forest bird species. Less severe land use is preferable over devastation of extensive areas of forest for unsustainable agricultural projects. Research in alternative productive use of secondary forest can diminish the pressure on undisturbed primary forest.

One conservation strategy currently discussed is the use of corridors connecting forest fragments for the maintenance of biological diversity (Saunders and Hobbs 1991). In designing corridors, it is important to consider many ecological factors like dominant tree species and the landscape of the corridor (Lindenmayer and Nix 1993). Our study shows that primary-forest bird species can use the secondary forest, principally that dominated by *Cecropia*. We captured several birds originally banded in forest fragments indicating that some species can move through or utilize secondary forest habitats.

Furthermore, the type of secondary forest affected the use of forest fragments by birds in our study sites. Several species that had disappeared in fragments, returned years later, principally when the surrounding grassland was dominated by *Cecropia* regrowth (Stouffer and Bierregaard 1995b). In contrast, fragments surrounded by *Vismia* remained depauperate in terms of bird species richness (Stouffer and Bierregaard 1995b). Hence, we recommended the use of *Cecropia* species as one of the dominant tree species in the vegetation of wildlife corridors in the Amazon. The *Cecropia* species provide some desired key characteristics for restoring landscape, including sufficient shade to eliminate grasses and weeds, as well as small and medium-sized fruits to attract a wide range of frugivores and potentially seed-dispersing animals (Lamb et al. 1997). *Cecropia* spp. are promising species in management programs designed for landscape restoration.

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