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Influence of matrix habitats on the occurrence of insectivorous bird species in Amazonian forest fragments

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Abstract

The influence of matrix habitats on the occurrence of seven understory insectivorous bird species in forest fragments was examined at the Biological Dynamics of Forest Fragments Project, Manaus, Amazonia. Playback techniques were used to detect individuals in the continuous primary forest, fragments of 1, 10 and 100 ha, and in two matrix habitats of secondary forest dominated by *Vismia* spp. and *Cecropia* spp. Sampling points in secondary forest areas were distributed at 50, 250 and 500 m from the continuous forest. Using *G*-tests of frequency distribution, species occurrences were compared in the following ways: (a) continuous forest vs. fragments; (b) continuous forest vs. second growth forest; (c) in second growth at different distances from continuous forest. Species were divided into three categories according to their sensitivity to the fragmentation process. Highly sensitive species (*Cyphorhinus arada*, *Hylophilus ochraceiceps* and *Thamnomanes ardesiacus*) did not occur in small fragments or in matrix habitats. Moderately sensitive species (*Formicarius colma* and *T. caesius*) occurred in small fragments and utilized infrequently matrix habitats. Positively affected species (*Percnostola rufifrons* and *Hypocnemis cantator*) were frequently detected in small fragments and all matrix habitats. Distances from the continuous forest did not influence the frequency of species occurrences in the secondary forest areas. Species were more frequent in small fragments surrounded by *Cecropia* spp. than by *Vismia* spp. Our results support the idea that the maintenance of species in small fragments may depend on their ability to use the matrix, and that increasing the permeability of the matrix may be an option to lessen the effects of forest fragmentation.
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1. Introduction

Studies on habitat fragmentation commonly emphasize the extent of the habitat patch (Galli et al., 1976; Hovel and Lipcius, 2001), the degree of isolation of patches (Andrén, 1994; Dunning et al., 1995; Davies et al., 2000), and the connectivity provided by corridors (Laurance and Laurance, 1999; Lima and Gascon, 1999; Haddad, 2000; Sieving et al., 2000). However, it is increasingly evident that the inter-habitat matrix also affects fragmented populations and communities (Laurance, 1991; Stouffer and Bierregaard, 1995; Gascon et al., 1999; Estades and Temple, 1999; Ricketts, 2001).

The matrix is defined as the portion of the landscape that has, at some point in time, undergone intense anthropogenic perturbation, such as slashing and burning of the original vegetation (Jonsen et al., 2001; Ricketts, 2001; Gobeil and Villard, 2002; Ray et al., 2002; Lindenmayer and Franklin, 2002; Joly et al., 2001; Perfecto and Vandermeer, 2002). The matrix is often a heterogeneous area, composed of several different types of

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land use and land cover (Davies et al., 2001; Lindenmayer and Franklin, 2002).

The importance of the matrix in species' responses to fragmentation varies depending on the structural features of the matrix and the biological characteristics of the species. Depending on its structure and composition, the matrix can offer food resources and even breeding areas of inferior quality but passable for use as territory (see, for example, Gates and Gysel, 1978). Because some species are able to exploit a matrix, or at least tolerate its effects, populations may remain stable or even increase in abundance throughout a fragmentation process (Pearson, 1993; Jokimäki and Huhta, 1996). Species that are the most vulnerable to habitat fragmentation are those that do not tolerate changes in the structure of their habitat and that rarely use the inter-habitat matrix (Bierregaard and Stouffer, 1997; Warburton, 1997). In extreme cases, there is a "phobia" to the presence of new elements in a landscape, such as road clearings, which can inhibit movements (Develey and Stouffer, 2001; Laurance et al., 2004). For birds inhabiting forest patches, the inability of some species to use the matrix is the main factor cited for population declines and extinctions (Diamond et al., 1987; Opdam et al., 1995; Gascon et al., 1999).

Many forest bird species sensitive to fragmentation prefer to colonize portions of the matrix that are structurally similar to the primary forest (Terborgh and Weske, 1969; Johns, 1991; Gascon et al., 1999; Stouffer and Borges, 2001), have been used less intensively by humans, are in more advanced stages of regeneration (Farley et al., 1994; Silva et al., 1996), or are closer to forested areas (Tubelis et al., 2004). Alternatively, the more open areas of the matrix are usually occupied by species associated with clearings and forest edges (Borges and Stouffer, 1999). These species may migrate during the breeding season (Haas, 1995; Machtans et al., 1996) or have generalist habits that allow them to exploit structurally diverse habitats (Keith, 1983; Askins et al., 1990; Andrén, 1992).

Previous studies at the *Biological Dynamics of Forest Fragments Project* (hereafter called *Forest Fragments Project*, Laurance et al., 2002) in central Amazonia demonstrated that the reestablishment of bird communities in forest fragments depends on the type of surrounding matrix habitat (Stouffer and Bierregaard, 1995; Bierregaard and Stouffer, 1997). At the beginning of the Forest Fragments Project, isolated fragments were surrounded by a completely open, grassland matrix. However, many years have passed since such fragments were isolated and matrix characteristics are now different. This change in context may have impacted the survival capacity of some bird species in those fragments. Thus, this study addresses the influence of the inter-habitat matrix in the occurrence of seven understory insectivorous bird species inhabiting these forest fragments. We compare species' occurrences in four situations: (i) between continuous forest and fragments; (ii) between the continuous forest and areas of secondary growth; (iii) between fragments surrounded by *Vismia* spp. and those surrounded by *Cecropia* spp.; (iv) in secondary growth at increasing distances from continuous forest.

2. Methods

2.1. Study area

This study was conducted at the Forest Fragments Project region, located approximately 80 km north of Manaus, Brazil (60°00′ W, 2°20′ S). The local soil is acidic and poor in nutrients (Laurance et al., 1999). The annual precipitation ranges from 1900 to 2500 mm, with the dry season from June to October. The primary forest in the region has a canopy height of 30–37 m, with emergents reaching 55 m. Tree diversity is extremely high, with approximately 280 species per hectare (Oliveira and Mori, 1999).

The areas of the Forest Fragments Project include three large cattle ranches (Dimona, Porto Alegre and Esteio, Fig. 1 and Table 1), which, subsidized by the government, began the process of deforestation in the early 1980s. The Forest Fragments Project has 23 primary forest reserves, 12 in continuous forest, and 11 fragments surrounded by the deforested areas of the ranches (Table 1).

At the Forest Fragments Project the inter-habitat matrix is quite heterogeneous. Clearcuts and pastures created between 1970 and 1985 were gradually abandoned, giving way to a matrix composed of three basic units: pasture; secondary vegetation dominated by *Vismia* spp.; and secondary vegetation dominated by *Cecropia* spp. The second growth areas characterized by the presence of pioneers of the genus *Vismia* (principally *V. guianensis, V. japurensis*, and *V. cayennensis*) dominate the matrix in the areas that were used most intensely, i.e. subject to slashing and burning. Whereas areas that were used less intensively, i.e. were cleared but never burned, were dominated by the genus *Cecropia* (principally *C. sciadophylla* and *C. purpurascens*).

2.2. Sampling design

We studied six different landscape elements: continuous forest (two sites, reserves 1301 and 1501 – Fig. 2); second-growth forest dominated by *Cecropia* spp. (three sites); second-growth forest dominated by *Vismia* spp. (three sites); and three sizes of forest fragments (five-1 ha, four-10 ha, and two-100 ha). Secondary-growth vegetation dominated by *Vismia* spp. surrounds six of the forest fragments and *Cecropia* spp.-dominated second-growth surrounds the other five (Table 1).

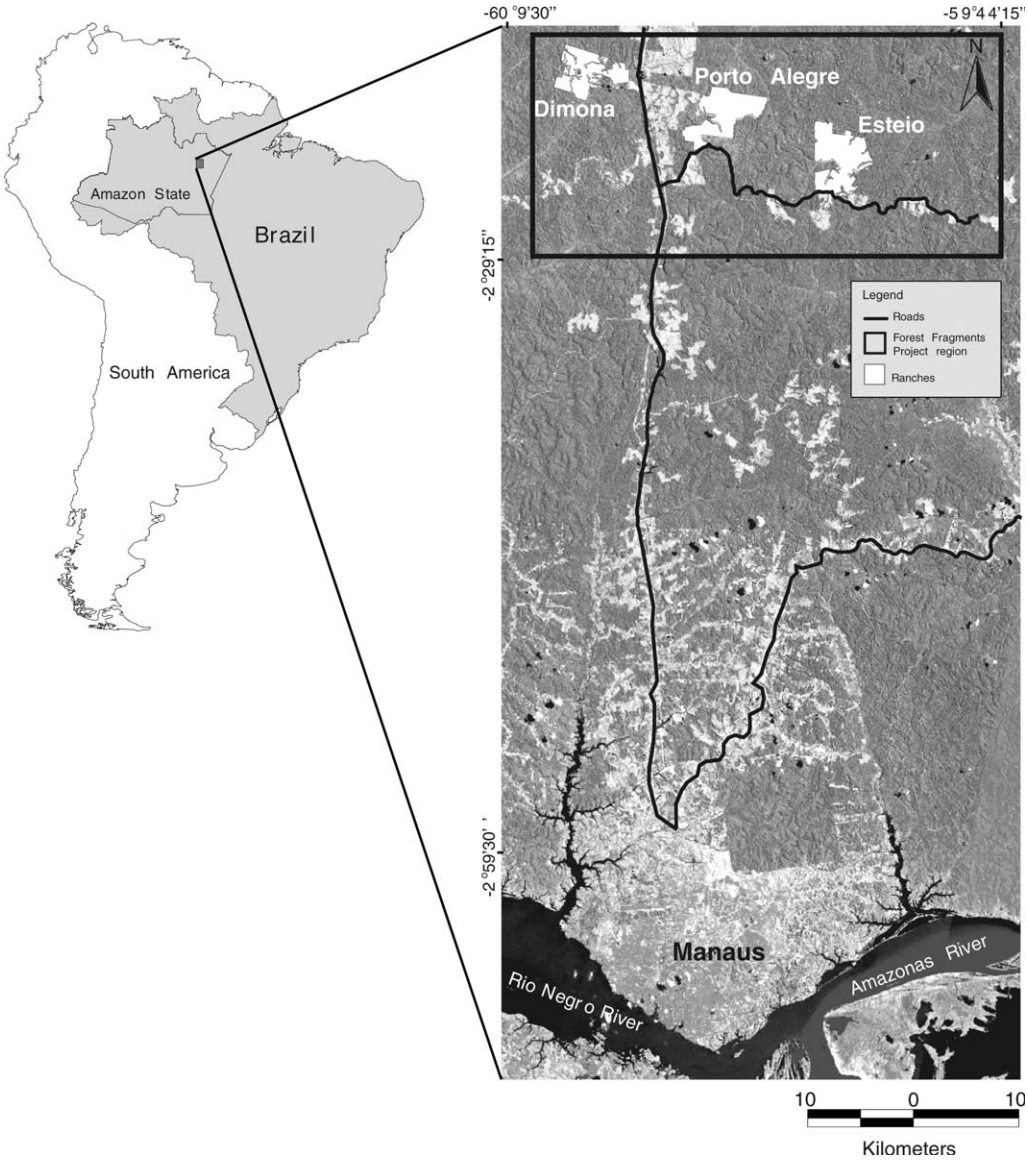

Fig. 1. Location of Dimona, Porto Alegre and Esteio Ranches, north Manaus, Brazil (Forest Fragments Project region). The Landsat satellite image is from 1997. Disturbed areas (pastures, second growth areas and Manaus city) appear in white while forests appear in dark/gray.

Table 1
Main characteristics of the forest fragments in which playback surveys were conducted (adapted from Bierregaard and Stouffer, 1997)

Fragment code	Ranch	Size (ha)	Distance (m)	Year of Isolation	Vegetation in the adjacent matrix
1104	Esteio	1	120	1980	*Vismia* spp./pasture
1112	Esteio	1	300	1983	*Cecropia* spp.
3114	Porto Alegre	1	210	1983	*Cecropia* spp.
2107	Dimona	1	270	1984	Pasture/*Vismia* spp.
2108	Dimona	1	480	1984	Pasture/*Vismia* spp.
1202	Esteio	10	540	1980	*Vismia* spp./pasture
1207	Esteio	10	60	1983	*Cecropia* spp.
3209	Porto Alegre	10	780	1983	*Cecropia* spp.
2206	Dimona	10	180	1984	Pasture/*Vismia* spp.
3304	Porto Alegre	100	1800[a]	1983	*Cecropia* spp.
2303	Dimona	100	150	1990	*Vismia* spp./*Cecropia* spp.

Distance: approximate distance between the fragment and the nearest area of continuous forest.
[a] The north face of fragment is connected to continuous forest by a corridor of primary forest.

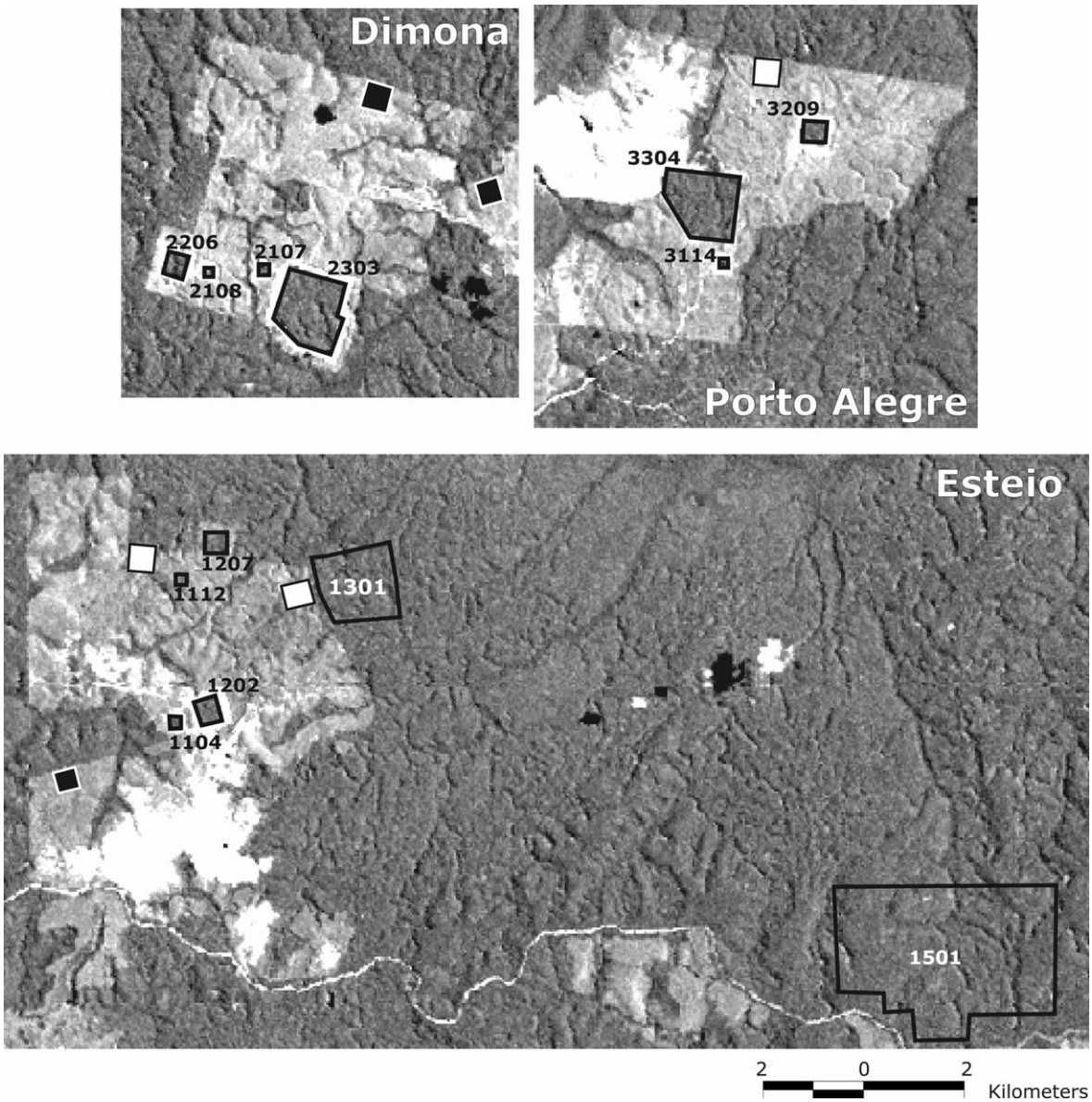

Fig. 2. Landsat satellite image from 1997 showing the Forest Fragments Project's ranches. The deforested areas are shown in light gray and white, and the primary forest areas are in dark gray. White polygons: areas sampled in the second growth of *Cecropia* spp. Black polygons: areas sampled in the second growth of *Vismia* spp. The studied fragments are indicated by their codes (see Table 1). Continuous forest was sampled in areas 1501 and 1301.

We sampled bird species' occurrence using sampling points distributed at least 200 m apart across study sites. Numbers of sampling points within each site varied, based on the size of the study site. We sampled the five-1 ha fragments using one central point each ($N = 5$); the four-10 ha fragments using three points each ($N = 12$); the two-100 ha fragments using nine points each ($N = 18$); and the two continuous forest sites using 24 points ($N = 24$). All points, except those in the 1-ha fragments, were located at least 100 m away from the forest edges. The points in the 1-ha fragments were located at 50 m away from the edges.

Three areas of secondary vegetation dominated by *Vismia* spp. and three dominated by *Cecropia* spp. were sampled in areas adjacent to continuous primary forest (Fig. 2). According to the historical description of the Forest Fragments Project areas and a multi-temporal analysis of Landsat Thematic Mapper (TM) images these secondary growth areas had been cleared more than nine years ago. A detailed presentation of the areas' structure can be found in Mesquita et al. (2001). We sampled each second growth study site using three trails, each one with sampling points at 50, 250, and 500 m from the continuous primary forest. One study site dominated by *Vismia* spp. was not large enough to accom-

modate the sampling point at 500 m, and therefore only the points located 50 and 250 m from the continuous forest were sampled. We sampled a total of 27 points in secondary growth areas dominated by *Cecropia* spp. and 26 points in mature second growth areas dominated by *Vismia* spp.

2.3. Selection of the species

We decided to focus on seven bird species based on previous mist net and playback studies in the Forest Fragment Reserves. First, we wanted to select common species, so that their absence during censuses would be more likely to be due to landscape effects, rather than overall rarity. The selected species were among the 35 most-captured during mist net study in the reserves (Stouffer and Bierregaard, 1995). Second, we selected species that are known to respond to playback, in order to have greater confidence in the registration of occurrences. Galeotti and Pavan (1993) found these species to be territorial and respond well to playback.

Although the seven species selected are all understory insectivores, their foraging strategies vary (Stouffer and Bierregaard, 1995): *Cyphorhinus arada* (Troglodytidae) and *Formicarius colma* (Formicariidae) forage close to the ground (terrestrial species); *Hypocnemis cantator* (Thamnophilidae) and *Percnostola rufifrons* (Thamnophilidae) are arboreal, solitary species specialized in using forest gaps; *Hylophilus ochraceiceps* (Vireonidae), *Thamnomanes ardesiacus* (Thamnophilidae) and *T. caesius* (Thamnophilidae) forage in mixed flocks guided by *T. caesius*.

2.4. The playback technique

The sampling was carried out from July through September 1999 by one of the authors (MA). The occurrence of species was determined with a playback technique that consisted of reproducing the pre-recorded vocalizations of a given species, obtained in the study area, using an amplifier (Parker, 1991; Catchpole and Slater, 1995). The volume of the broadcast was set to stimulate birds in a radius of about 75 m.

At each sampling point, the vocalization of each species was played continuously for 1 min, followed by a 20-s listening interval. This process was repeated four times for each species, until all seven species' vocalizations had been played, resulting in a 40-min playback session at each sampling point. We randomized the sequence of species' vocalizations during each playback session. A species was registered as being present at a sampling point if it was visually or vocally detected at any time during the 40-min playback session. Once the sequence of species in each point was determined randomly, the given chances to each species to answer its playback were the same. We use playback session as the sampling unit.

In the secondary growth areas, each trail was sampled on different days, and in the fragments and areas of continuous forest, three listening points were sampled per day. The sampling was carried out each day in the morning, beginning at 6:00 a.m., with the order of the trails, the points, and the species determined randomly.

2.5. Data analysis

We calculated the frequency of occurrence of each species by dividing the number of samples in which a given species was recorded by the total number of samples conducted in each landscape element (1, 10 and 100 ha fragments, continuous forest, *Vismia* spp. regrowth, and *Cecropia* spp. regrowth). We combined data from different sites within each landscape element because of low number of sites replication (for example, only two replicates of 100-ha fragments). The number of samples per landscape element varied from 5 for 1-ha fragments to 27 in the case of *Cecropia* spp. matrix (Table 2). Even if each point was only observed once, representing so a snap shot in time, we considered that the large number of sampling point replicates for most landscape elements allowed to represent correctly the pattern of occurrences of the species. Using *G*-tests (Zar, 1999), differences between expected and observed values of the frequency of occurrence of each species were compared among: (a) continuous primary forest and fragments of 1, 10, and 100 ha; (b) continuous primary forest and second growth areas dominated by *Cecropia* spp. or *Vismia* spp.; (c) fragments surrounded by *Cecropia* spp. and fragments surrounded by *Vismia* spp.; (d) second growth at three different sampling distances from continuous forest, considering second growth dominated by *Cecropia* spp., dominated by *Vismia* spp., or pooling data from both types of second growth. When we compared species' occurrence in fragments surrounded by *Cecropia* spp. and *Vismia* spp., we also excluded fragments of 100 ha in order to prevent the effect of the matrix being masked by the effect of fragment size. *G*-tests were considered significant at $P < 0.05$ and significant comparisons were subjected to a posteriori tests.

3. Results

The seven understory bird species showed distinct patterns of occurrences in the six landscape elements (Table 2). *H. cantator* and *P. rufifrons* were very common in all landscape elements. Although *F. colma* and *T. caesius* occurred in all environments, their frequencies of occurrence were low, especially in the two types of matrix regrowth and in the small fragments. *H. ochraceiceps* and *T. ardesiacus* were not registered in 1-ha

Table 2
Frequency of occurrence of the seven understory bird species in the different landscape elements (Forest Fragments Project region, north Manaus)

Landscape element	*C. arada*	*H. ochraceiceps*	*T. ardesiacus*	*F. colma*	*T. caesius*	*H. cantator*	*P. rufifrons*	*N*
Cecropia spp. matrix	0.00	0.04	0.04	0.04	0.26	0.78	0.81	27
Vismia spp. matrix	0.00	0.04	0.00	0.11	0.15	0.77	0.58	26
1-ha Fragments	0.00	0.00	0.00	0.20	0.40	0.60	0.80	5
10-ha Fragments	0.00	0.00	0.08	0.33	0.42	0.58	0.67	12
100-ha Fragments	0.17	0.28	0.33	0.61	0.50	0.67	0.61	18
Continuous forest	0.12	0.25	0.46	0.46	0.37	0.42	0.29	24
Total number of occurrences	6	13	19	31	36	73	67	

N: total number of sampling points per landscape element.

fragments and were very rare in 10-ha fragments and second growth areas. Finally, *C. arada* was absent in fragments of 1 and 10 ha and in both *Cecropia* spp. and *Vismia* spp. dominated regrowth.

3.1. Effect of fragment size

In the comparisons between continuous forest and fragments of 1, 10, and 100 ha, the frequencies of occurrence of *P. rufifrons*, *H. ochraceiceps* and *T. ardesiacus* showed significant differences (Table 3). *P. rufifrons* occurred significantly more frequently in fragments of 100, 10 and 1 ha than in areas of continuous primary forest. There were no significant differences in the occurrence of *H. ochraceiceps* and *T. ardesiacus* between continuous forest and 100 ha fragments, but the occurrence of these species was significantly lower in 10 ha fragments than in continuous areas. Although no *H. ochraceiceps* individuals were reported in the 1-ha fragments, its frequency of occurrence did not differ significantly between these fragments and areas of continuous forest. *T. ardesiacus* was significantly less frequent in 1-ha fragments than in continuous areas.

The occurrence of *H. cantator*, *F. colma* and *T. caesius*, did not differ between continuous forest and fragments of 1, 10, and 100 ha (Table 3). *C. arada* only occurred in fragments of 100 ha and in continuous forest, but even in these areas it was recorded infrequently (Table 3). Due to its scarcity, its frequency of occurrence could not be compared among fragments of different size (Table 3).

3.2. Effect of matrix type

For *H. cantator*, *P. rufifrons*, *F. colma*, *T. ardesiacus*, *H. ochraceiceps* and *C. arada* there were significant differences in the frequencies of occurrence in continuous primary forest areas compared with the two types of second growth forest (Table 4). *H. cantator* and *P. rufifrons* were more frequent in *Cecropia* spp. regrowth and *Vismia* spp. regrowth than in the areas of continuous forest. However, *F. colma*, *T. ardesiacus*, *H. ochraceiceps* and *C. arada* were significantly more frequent in the continuous areas than in these two types of second growth forest. We detected *T. ardesiacus* only once in secondary growth of *Cecropia* spp., while *H. ochraceiceps* was detected only once in each of the types of secondary growth. *C. arada* was never reported in second growth areas (Table 2).

Frequencies of occurrence for *T. caesius* were not significantly different between secondary growth areas dominated by *Cecropia* spp. or *Vismia* spp. and areas of continuous forest (Table 4).

3.3. Effect of the matrix on the occurrences in fragments

When all fragments were considered, *C. arada* and *H. ochraceiceps* were significantly more frequent in the fragments surrounded by *Vismia* spp. than in those surrounded by *Cecropia* spp. (Table 5). No significant differences in occurrence were observed for the other species (Table 5).

Table 3
G-test results for comparison of seven bird species occurrences among continuous primary forest ($N = 24$) and fragments of 1 ha ($N = 5$), 10 ha ($N = 12$), and 100 ha ($N = 18$) (Forest Fragments Project region, north Manaus)

Species	CF vs. F100 vs. F10 vs. F1 (df = 3)	CF vs. F100 (df = 1)	CF vs. F10 (df = 1)	CF vs. F1 (df = 1)
P. rufifrons	$G = 8.4$; $P = 0.037$	$G = 4.6$; $P = 0.031$	$G = 4.6$; $P = 0.031$	$G = 4.5$; $P = 0.034$
H. cantator	NS	–	–	–
T. caesius	NS	–	–	–
F. colma	NS	–	–	–
H. ochraceiceps	$G = 8.5$; $P = 0.037$	NS	$G = 5.4$; $P = 0.020$	NS
T. ardesiacus	$G = 9.7$; $P = 0.021$	NS	$G = 5.8$; $P = 0.016$	$G = 5.4$; $P = 0.020$
C. arada	NS	–	–	–

NS: Not significant, –: no test performed. F1, F10 and F100: fragments of 1, 10 and 100 ha, respectively; CF: continuous forest.

Table 4
G-test results for comparisons of seven bird species occurrences among continuous primary forest ($N = 24$) and second growth areas dominated by *Cecropia* spp. ($N = 27$) and *Vismia* spp. ($N = 26$) (Forest Fragments Project region, north Manaus)

Species	CF vs. *Cecropia* spp. vs. *Vismia* spp. (df = 2)	CF vs. *Cecropia* spp. (df = 1)	CF vs. *Vismia* spp. (df = 1)
P. rufifrons	$G = 14.9$; $P = 0.001$	$G = 14.9$; $P<0.001$	$G = 4.2$; $P = 0.041$
H. cantator	$G = 9.2$; $P = 0.010$	$G = 7.1$; $P = 0.008$	$G = 6.6$; $P = 0.010$
T. caesius	NS	–	–
F. colma	$G = 15.7$; $P<0.001$	$G = 14.0$; $P<0.001$	$G = 7.6$; $P = 0.006$
H. ochraceiceps	$G = 7.3$; $P = 0.025$	$G = 5.2$; $P = 0.022$	$G = 5.0$; $P = 0.010$
T. ardesiacus	$G = 25.0$; $P<0.001$	$G = 14.0$; $P<0.001$	$G = 19.6$; $P<0.001$
C. arada	$G = 7.2$; $P = 0.026$	$G = 4.7$; $P = 0.030$	$G = 4.6$; $P = 0.032$

NS: Not significant, –: no test performed. CF: continuous forest; *Cecropia* spp.: second growth areas dominated by *Cecropia* spp.; *Vismia* spp.: second growth areas dominated by *Vismia* spp.

Table 5
G-test results for comparison of seven bird species occurrences between fragments surrounded by *Vismia* spp. and *Cecropia* spp. (Forest Fragments Project region, north Manaus)

Species	Frag. *Vismia* spp. ($N = 18$) vs. Frag. *Cecropia* spp. ($N = 17$) (df = 1) – including 100-ha fragments	Frag. *Vismia* spp. ($N = 9$) vs. Frag. *Cecropia* spp. ($N = 8$) (df = 1) – excluding 100-ha fragments
P. rufifrons	NS	NS
H. cantator	NS	NS
T. caesius	NS	$G = 7.7$; $P = 0.005$
F. colma	NS	NS
H. ochraceiceps	$G = 7.4$; $P = 0.006$	NS
T. ardesiacus	NS	NS
C. arada	$G = 4.2$; $P = 0.039$	NS

NS: Not significant, Frag. *Vismia* spp.: Fragments surrounded by *Vismia* spp.; Frag. *Cecropia* spp.: fragments surrounded by *Cecropia* spp.

However, this pattern changed when these comparisons were carried out excluding the two 100-ha fragments (Table 5). In this case, *T. caesius* was significantly more frequent in the fragments surrounded by *Cecropia* spp. than in those surrounded by *Vismia* spp. (Table 5). No significant differences in occurrence were observed for the other species (Table 5).

3.4. Effect of distance

Distance from continuous primary forest did not affect any species' occurrence in either *Vismia* spp. regrowth, *Cecropia* spp. regrowth, or both regrowth types considered together. *P. rufifrons*, *H. cantator*, *T. caesius* and *F. colma* were detected throughout the secondary forest study area. *H. ochraceiceps* and *T. ardesiacus* were only reported within the first 50 m of continuous forest and *C. arada* was never reported in areas of secondary forest.

4. Discussion

In our analyses three groups of species can be distinguished. The first consists of species that occurred more frequently in secondary growth areas and in fragments than in continuous primary forest. *H. cantator* and *P. rufifrons* fall into this group and we will refer to them as the "positively affected species" (Tables 3 and 4). These species are known to be especially abundant in clearings, such as tree fall gaps, inside primary forest (Stouffer and Bierregaard, 1995). The second group consists of species that are negatively and moderately affected by fragmentation (moderately sensitive species). This group is composed of *T. caesius* and *F. colma*, which were detected in all landscape elements, but had the lowest frequency in 1 and 10 ha fragments and secondary growth areas. Both positively affected and the moderately sensitive species use the whole extent of the matrix. The third group is composed of *C. arada*, *H. ochraceiceps*, and *T. ardesiacus*, which occurred almost exclusively in areas of primary forest larger than 10 ha. These species just use matrix areas near to the primary forest and apparently avoid second growth forests. We found these species to be very sensitive to the negative effects of fragmentation and we refer to species in this group as highly sensitive species.

4.1. Synergistic effects of matrix and fragment size

Species identified as either positively affected or moderately sensitive, *H. cantator*, *P. rufifrons*, *F. colma*, and *T. caesius*, were found to occur throughout the entire extent of the inter-habitat matrix. Conversely, those identified as highly sensitive, *C. arada*, *H. ochraceiceps* and *T. ardesiacus*, were largely absent from the inter-habitat

matrix, and their occurrence was mainly restricted to continuous forest and fragments of 100 ha. This suggests that a species occurrence in small fragments is directly related to the effects of the matrix.

This synergetic effect appears when we compare highly and moderately sensitive species. Highly sensitive species, *C. arada, H. ochraceiceps*, and *T. ardesiacus*, that were reported in most of the fragments immediately after isolation, soon disappeared in small fragments, remaining absent in many fragments even after the surrounding forests had regenerated (Stouffer and Bierregaard, 1995). These species appear to be unable to recolonize the fragments because they do not use the matrix at all (*C. arada*) or they only use regions of the second growth forest immediately adjacent to the continuous primary forest. *H. ochraceiceps* and *T. ardesiacus* were observed accompanying mixed flocks only at the edge between the continuous forest and the second growth forest, using matrix areas only as an extension of their foraging area. They appear to be unable to establish territories in distant portions of the matrix. In our samples, there were no reports of any of these species in the 1 ha fragments. *H. ochraceiceps* did not occur at all in fragments of 10 ha, and *T. ardesiacus* was reported only once, in the least-isolated 10 ha fragment (60 m from continuous forest).

On the other hand, the moderately sensitive species, *F. colma* and *T. caesius*, in spite of having suffered a decline with the isolation of the fragments (Stouffer and Bierregaard, 1995), and even temporarily disappeared in some (Forest Fragments Project unpublished data, but for *F. colma* see Stratford and Stouffer, 1999), seem to have been able to (re)occupy the fragments of all sizes. Both species were reported in fragments as small as 1 ha. It appears that the factor determining their occurrence in small fragments is not related to the size of the patches, since 1 and 10-ha fragments are smaller than the minimum territory size of those species (Stouffer and Bierregaard, 1995; Stratford and Stouffer, 1999). Their capacity to use the inter-habitat matrix appears to be fundamental in their re-colonization of small fragments. Probably, both species remained or re-colonized the smaller fragments only because they recognized the matrix as habitat, although, perhaps of inferior quality.

It appears that the highly sensitive species remain locally extinct in the large majority of 1 and 10 ha fragments. This is likely due to these fragments not meeting the minimum area requirements for territory establishment. Moreover, these species are not able to disperse among smaller portions of the inter-habitat matrix effectively. The moderately sensitive species, on the other hand, despite having territory sizes larger than the size of the smaller fragments, very probably re-colonized these fragments because they can utilize the matrix as additional habitat. Finally, the positively affected species, *P. rufifrons* and *H. cantator*, use the matrix extensively and were not found to be locally extinct in any of the fragments. On the contrary, they were positively affected by the fragmented landscapes, occurring more frequently in the fragments than in the continuous forest.

These results confirm that the high vulnerability of some understory insectivorous birds to fragmentation is closely related to the low capacity of those species to exploit matrix habitats (Stouffer and Bierregaard, 1995).

4.2. Influence of matrix type

The positively affected species, *P. rufifrons* and *H. cantator*, were able to utilize the entire extent of the secondary growth areas very efficiently, regardless of the type of dominant tree species.

However, for moderately and highly sensitive species the occupation or re-colonization of some forest fragments by some species can be strongly influenced by the type of matrix. When the 100 ha fragments are considered, the frequency of occurrence of *C. arada* and *H. ochraceiceps* appear significantly greater in fragments surrounded by *Vismia* spp., than those surrounded by *Cecropia* spp. This result could be related to the fact that individuals of these two species persist in the 100 ha fragment surrounded by *Vismia* spp. that was isolated in 1990 (Forest Fragments Project unpublished data). When only the smaller fragments are considered, where certain species have gone locally extinct, more species recolonize fragments surrounded by *Cecropia* spp. than fragments surrounded by *Vismia* spp. *T. caesius* occurred more frequently and was more abundant in small fragments (1 and 10-ha fragments) surrounded by *Cecropia* spp. than in fragments surrounded by *Vismia* spp. The only two occurrences of *T. caesius* in 1 ha fragments were in fragments 3114 and 1112, which are surrounded by *Cecropia* spp. There is evidence that *T. caesius* became locally extinct in these two fragments at some point in time following isolation, indicating that this species may recognize *Cecropia* spp. regrowth as a usable habitat type (Stratford and Stouffer, 1999).

F. colma and *T. ardesiacus* also appear to be able to use *Cecropia* spp.-dominated matrix. The only 1 ha fragment where *F. colma* was detected (fragment 1112) is located within a secondary growth dominated by mature *Cecropia* spp. *F. colma* occurred in this fragment prior to its isolation in 1983. In the first months following its isolation, however, the species disappeared, remaining locally extinct until 1992 (Stratford and Stouffer, 1999). The area surrounding this fragment was not disturbed following the initial isolation event and a secondary-growth forest dominated by mature *Cecropia* spp. trees developed. By 1992, the *Cecropia* spp.-dominated secondary growth was apparently sufficient for *F. colma* to pass through the habitat and re-colonized fragment 1112 (Stratford and Stouffer, 1999).

The same occurred with *T. ardesiacus* in fragment 1207 (10 ha), which is also completely surrounded by *Cecropia* spp. regrowth. This fragment is approximately 60 m from the nearest continuous forest. Shortly following isolation, the species disappeared from the fragment. The low degree of isolation of this fragment was apparently not sufficient in itself to allow re-colonization by *T. ardesiacus*. This is not surprising, as a dirt road of approximately 20 m has been shown to be sufficient to inhibit the movement of this species between two areas of primary forest (Develey and Stouffer, 2001; Laurance et al., 2004). It was only when the *Cecropia* spp.-dominated regrowth matured that *T. ardesiacus* re-colonized fragment 1207.

In our study, moderately sensitive and some highly sensitive species, *F. colma*, *T. ardesiacus* and *T. caesius*, were able to successfully re-colonize fragments of 1 and 10 ha that were surrounded by secondary growth dominated by *Cecropia* spp. This suggests these species are better able to utilize *Cecropia* spp. secondary growth areas as dispersal routes than those dominated by *Vismia* spp. Previous studies have found that re-establishment of the understory insectivorous bird community occurs more rapidly in fragments surrounded by *Cecropia* spp.-dominated secondary vegetation than in those surrounded by *Vismia* spp.-dominated vegetation (Stouffer and Bierregaard, 1995; Stouffer and Borges, 2001). Abundance of these species is also higher in second growth areas dominated by *Cecropia* spp., than in second growth areas dominated by *Vismia* spp. (Stouffer and Borges, 2001).

The type of secondary growth that develops in an area depends on the deforestation method used and the different growth strategies of the main pioneer species in this region, *Cecropia* spp. and *Vismia* spp. The practice of cutting and burning forest, frequently used when creating cattle ranches, favors the establishment of *Vismia* spp. and makes re-growth by other species more difficult by reducing the size of the local seed bank (Uhl et al., 1981; Buschbacher, 1986). Similar to bushes, *Vismia* spp. individuals branch extensively during the first years after germination, which helps them dominate the area by inhibiting the sprouting of other species (Uhl and Jordan, 1984; Maury-Lechon, 1991). They are also well adapted to drier places. *Cecropia* spp. individuals have a very different development strategy. They display faster vertical growth, develop fewer lateral ramifications, and invest little in mechanical structures. As a consequence, second growth areas dominated by this pioneer grow taller and develop a more closed canopy in a shorter amount of time than *Vismia* spp.-dominated regrowth. *Cecropia* spp.-dominated regrowth also tends to be more species-diverse than areas dominated by *Vismia* spp. (Williamson et al., 1998). These differences in growth habits help explain why moderately to highly sensitive understory bird species tend to recolonize areas dominated by *Cecropia* spp. regrowth more frequently than *Vismia* spp.-dominated regrowth.

5. Conclusions and implications for conservation

With the tendency of growing occupation and expansion of agricultural frontiers, the landscapes in the Amazon Basin will become increasingly fragmented, where forests will be progressively substituted by agriculture and livestock (Fearnside, 2001). In this context, it is very important to pay particular attention to the type of inter-habitat matrix, mainly in areas where the forest remnants are of reduced size.

Our results support the idea that the matrix type is very important to determine the occurrence of species in small fragments ($\leqslant$10 ha), in particular for the moderately sensitive species. Three hypotheses can be considered to explain this pattern. First, mature matrices can offer a barrier to edge effect, increasing the effective interior area of fragments. Although we do not have data to sustain this idea, it is already known that, depending on its quality, the matrix may function as a buffer zone to the edge effect in the fragments (Didham and Lawton, 1999; Mesquita et al., 1999). Second, more developed matrices may facilitate the flows of individuals in the landscape (Aberg et al., 1995), increasing its permeability and thus the movement between continuous forest and fragments. Third, matrices dominated by *Cecropia* spp. may be used as additional habitat by forest species in small fragments. In particular for the moderately sensitive species, their success in re-colonizing the 1-ha fragments depended not only on their ability to move through but also in their capacity to use the *Cecropia* spp. areas as a complement of their territory. Otherwise, matrices originated without the use of fire, like those dominated by *Cecropia* spp., display a faster regeneration time of the vegetation, increasing the landscape permeability and the possibility of such matrices to act as a complementary habitat. In this way, the regeneration process of altered areas can strongly influence the maintenance of species in fragmented landscapes. Our results suggest that the maintenance of a permeable and high quality matrix can help to mitigate some of the adverse effects of habitat fragmentation.

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