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Forest fragmentation alters microhabitat availability for Neotropical terrestrial insectivorous birds

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ABSTRACT

Many insectivorous birds of the tropical rainforest understory, particularly terrestrial species, are prone to local extinctions in fragmented forests. We evaluated the hypothesis that vegetation structural changes in rainforest fragments reduce the availability of microhabitats used by terrestrial insectivores. Near Manaus, Brazil, we compared the vegetation in forest fragments to the vegetation in a continuous forest site where nine species of terrestrial insectivores were observed foraging. Our focal species included those that are extinction prone in fragments (*Myrmornis torquata* [Wing-banded Antbird], *Grallaria varia* [Variegated Antbird], *Hylopezus macularius* [Spotted Antpitta]), a fragmentation-tolerant species (*Myrmothera campanisona* [Thrush-like Antpitta]), and species that have an intermediate response (*Myrmeciza ferruginea* [Ferruginous-backed Antbird], *Formicarius colma* [Rufous-capped Antthrush], *Formicarius analis* [Black-faced Antthrush], *Conopophaga aurita* [Chestnut-belted Gnatcatcher], and *Corythopis torquata* [Ringed Antpipit]). To quantify vegetation, we measured sixteen habitat variables in 8-m radius plots where birds were observed foraging as well as random points in continuous forest and forest fragments of 1-, 10-, and 100-ha. Four principal components were produced from a principal component analysis and we selected a variable (leaf litter depth, plant cover 3–10 m, density of plants 1–2 m, and plant cover >20 m) from each principal component for our fragment vs continuous forest comparisons. Using Markov chain Monte Carlo (MCMC) simulation, we estimated the probabilities that the density of plants 1–2 m, proportion of plant cover 3–10 m, and leaf litter depth increased with decreasing fragment area and also exceeded the values associated with fragmentation-sensitive species. We also tested the prediction that plant cover >20 m decreased in forest fragments and that those sites became more open than typical sites used by our focal species. Our predictions were strongly supported: decreasing fragment size was correlated with increasing density of tall plants, increasing mid-story vegetation cover, decreased canopy cover, and increasing leaf litter depth. Even if our focal species are able to disperse to small forest fragments, our results suggest that they may not find enough appropriate habitat.

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1. Introduction

Many Neotropical insectivorous birds of the forest understory respond negatively to forest fragmentation, selective logging, and second growth (Barlow et al., 2006; Johns, 1991; Stouffer and Bierregaard, 1995). Of the understory insectivorous birds, those that forage on or near the ground are particularly sensitive (Powell et al., 2015; Stouffer and Bierregaard, 1995; Stratford and Stouffer, 1999). For example, most of the terrestrial insectivores that were in 1- and 10-ha forest plots before isolation were absent

after the plots became isolated (Stratford and Stouffer, 1999). However, a small number of understory insectivores persist and may even benefit from limited human disturbance (Boyle and Sigel, 2015; Canaday and Rivadeneira, 2001; Stouffer and Bierregaard, 1995; Thiollay, 1997).

Many hypotheses have been proposed to explain the variation in sensitivities among understory insectivores (Robinson and Sherry, 2012; Stratford and Robinson, 2005). A number of these hypotheses are related to the biotic and abiotic changes that occur in fragments, including variation among species in response to increased nest predation (Visco and Sherry, 2015), altered abiotic conditions (i.e., microclimate) (Pollock et al., 2015), and prey abundance (Şekerciöğlu et al., 2002). Abiotic conditions in fragments become altered as a result of edge effects – the changes that occur

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along the edges of forest fragments, such as increased temperature and insolation, lower humidity, and greater exposure to wind (Didham and Lawton, 1999; Kapos et al., 1997; Murcia, 1995). For example, increased light levels in forest fragments may inhibit their use by understory insectivores (Stratford and Robinson 2005; Pollock et al., 2015), which may avoid bright microhabitats (Patten and Smith-Patten, 2012; Walther, 2002).

Forest fragmentation affects a large number of biotic parameters that are associated with edge effects include increasing density of small trees, seedlings, and lianas (see reviews in Laurance et al. (2002) and Murcia (1995)). Edge effects on vegetation, such as increased tree mortality, may exceed 200 m and alter vegetation throughout smaller fragments (Laurance et al., 2002). These vegetation changes alter the structure of the vegetation where understory birds forage and may potentially alter their choice of foraging microhabitat (Collins et al., 1982; James, 1971; Mitchell et al., 2006). We use the term microhabitat to describe the relatively fine-scale vegetation structure where birds forage within a territory (James and Wamer, 1982; Stratford and Stouffer, 2013).

Neotropical terrestrial insectivores have narrow microhabitat preferences (Borges, 2013; Cintra and Naka, 2012; Marra and Remsen, 1997; Powell et al., 2013; Stratford and Stouffer, 2013). In a previous study (Stratford and Stouffer, 2013), we compared foraging microhabitats in continuous forest to microhabitats in second growth for nine species of terrestrial insectivores. We showed that species absent from second growth were associated with elements of primary forest vegetation that were not typical of second growth. For example, terrestrial insectivores were associated with shallower leaf litter and greater density of large trees than were found in second growth forest.

Here we extend our previous study (Stratford and Stouffer, 2013) by comparing microhabitats available in forest fragments with the microhabitats where terrestrial insectivores were observed foraging in continuous forest. We nine selected species with varying degrees of fragmentation sensitivity, ranging from *Myrmornis torquata* (Wing-banded Antbird), a species that was missing from all the forest fragments studied by Stratford and Stouffer (1999) and has never recolonized any fragment, to *Myrmothera campanisona* (Thrush-like Antpitta) a species that colonizes forest fragments. With the exception of *M. campanisona*, the study species that were absent from smaller fragments avoid shrubby areas and prefer areas with a relatively thin leaf litter and large trees (Stratford and Stouffer, 2013). *M. campanisona*, however, prefers areas with a higher density of vegetation and is typically found in large tree falls (Stouffer, 2007).

Based on described edge effects on vegetation and litter, observed patterns of fragment use by the study species, and microhabitat associations from continuous forest from the same bird observations (Stratford and Stouffer, 2013), we made the following predictions. First, we predicted that as fragment size decreases, available microhabitats will become increasingly dissimilar to the microhabitats used by fragmentation-sensitive terrestrial insectivores in continuous primary forest. In particular, the vegetation structure in small (1- and 10-ha) fragments will be most different from those sites where terrestrial insectivores use for foraging. Second, we predicted that microhabitats in small fragments will become more similar to the microhabitats associated with *M. campanisona*.

2. Methods

2.1. Study site

We investigated terrestrial insectivore microhabitat selection and vegetation structure of fragments and continuous forest from

July 1994 to January 1995 in *terra firme* forest at the Biological Dynamics of Forest Fragments Project (BDFFP), 60 km north of Manaus, Brazil (see <http://pdbff.inpa.gov.br/> and Bierregaard and Gascon (2001) for maps and a detailed description of the project). The continuous forest site is part of vast undisturbed forest to the north of the BDFFP. The forest fragments were created in collaboration with local ranchers by clearing forest around the fragments in the early 1980s. Fragments available for study included two 100-ha, four 10-ha, and five 1-ha fragments.

We chose our nine focal species (Table 1) because they have varying responses to forest fragmentation and are relatively easy to detect (Stratford, 1997). The ecology of these species has been the focus of several studies at the fragment and landscape scales (Powell et al., 2013; Stouffer, 1997, 2007; Stratford and Stouffer, 1999, 2013). The focal species are found throughout continuous forests in the Manaus area, but rarely use second growth (Borges and Stouffer, 1999). Some of their microhabitat preferences were evaluated in Stratford and Stouffer (2013), and larger scale habitat preferences have been quantified (Cintra and Naka, 2012; Johnson et al., 2011).

2.2. Vegetation sampling

Microhabitat samples were taken within 8 m radius circular plots of ~0.02 ha. The protocol, modified from James and Shugart (1970), is described in detail in Stratford and Stouffer (2013). Within each plot, all woody plants >2 m were counted and categorized as trees in five size classes based on their dbh: ≤7 cm, 7–15 cm, ≥15–23 cm, ≥23–30 cm, ≥30 cm. However, trees in the largest three size classes were sparse and were collapsed into a single size class, creating three size classes: small (≤7 cm), medium (7–15 cm) and large (≥15 cm). We counted all palms (>1 m in height) and vines (including lianas, dangling roots, and non-woody vines) in three size classes (≤0.5 cm, >0.5–2 cm, >2 cm) measured at 1.5 m. For vines on the ground, we measured the maximum thickness occurring in the plot.

The number of dead leaves pierced by a pin and leaf litter depth were measured at 10 random points along a transect from the plot center to the plot edge (Stratford and Stouffer, 2013). Another 10 random leaf litter samples were taken along a second transect oriented 90° from the random transect. At the same random points, we determined the presence or absence of vegetation in five height bands: ≤0.5 m, >0.5–3 m, >3–10 m, 10–20 m, >20 m. The presence of vegetation from 0 to ≤0.5 m was determined by placing a

Table 1
Study species, number of observations, and their fragmentation sensitivity based on Stratford and Stouffer (1999).

Species	N	Fragmentation-sensitivity
<i>Myrmornis torquata</i> (MYTO) Wing-banded Antbird	12	High
<i>Myrmeciza ferruginea</i> (MYFE) Ferruginous-backed Antbird	23	Moderate
<i>Formicarius analis</i> (FOAN) Black-faced Antthrush	12	Moderate
<i>Formicarius colma</i> (FOCO) Rufous-capped Antthrush	17	Moderate
<i>Hylopezus macularius</i> (HYMA) Spotted Antpitta	3	High
<i>Grallaria varia</i> (GRVA) Variegated Antpitta	4	High
<i>Myrmothera campanisona</i> (MYCA) Thrush-like Antpitta	8	Low
<i>Conopophaga aurita</i> (COAU) Chestnut-belted Gnateater	4	Moderate
<i>Corythopsis torquatus</i> (COTA) Ringed Antpipit	13	Moderate

1.27 cm diameter pole at the sample point and observing if vegetation touched the pole. Above 0.5 m, we determined the presence of vegetation directly above the sample point by looking through a tube held vertically. We also estimated canopy height at the each of the twenty points with a rangefinder. All plants <2 m were counted in a 15.75 m² strip on both sides of each of the transect and placed into small (≤ 1 m) or tall (>1 m) plant categories.

To quantify the microhabitats used by terrestrial insectivores, we took microhabitat samples where birds were observed foraging in a continuous forest area of about 500 ha from July 1994 to January 1995 (Stouffer, 2007; Stratford and Stouffer, 2013). Data from continuous forests sites were used in Stratford and Stouffer (2013) to compare sites used by birds in continuous forest to random sites second growth. Here we compare the same samples from the foraging sites to random sites in forest fragments. The location of the first observed foraging event became the center of each microhabitat plot. All observations within a species were at least 500 m apart to increase the probability that different individuals were being sampled. Although some of our focal species were found in fragments, most individuals there were detected with playback (Stratford and Stouffer, 1999) and could not be used for foraging observations.

To quantify vegetation in forest fragments, we randomly placed four, eight, and sixteen vegetation plots in 1, 10, and 100-ha forest fragments, respectively. In 1-ha fragments we randomly placed a microhabitat sample in each 0.25 ha section. We divided 10-ha and 100-ha fragments into eight and sixteen equal sized sections, respectively, and randomly placed a plot in each section. We replaced random points that fell <25 m from edges with new points. We sampled 44 random points in a 200 ha continuous forest plot within the bird sampling area (Stratford and Stouffer, 2013). Each point was placed within a unique 1 ha area determined by gridded trails.

2.3. Analysis

To identify suites of correlated vegetation variables, we used the principal function in the R (3.0.1) package psych (1.3.2) with

Table 2

Microhabitat variables and their loading on four components. Bold numbers indicate the variables that are considered to be associated with that component. Underlined variables were selected for the Bayesian analysis. We reported the posterior probabilities as very unlikely ($p < 0.05$), unlikely ($0.05 < p < 0.33$), likely ($0.66 < p < 0.95$), and very likely ($p > 0.95$). For $0.33 < p < 0.66$, we claim lack of evidence to support or reject our predictions and consider those groups to be similar. This semiquantitative approach was modeled from the Intergovernmental Panel on Climate Change and facilitates the interpretation of uncertainty (see http://www.ipcc.ch/publications_and_data/ar4/wg1/en/ch1s1-6.html).

Variable	PC1	PC2	PC3	PC4
Plants 1–2 m	<u>0.67</u>	0.08	–0.18	0
Trees < 7 cm dbh	0.62	0.47	0	0.31
Plants < 1 m	0.59	–0.1	0.18	–0.1
Vines < 2 cm	0.58	0.2	–0.04	0.45
Cover 0.5–3	0.58	–0.02	0.06	–0.22
Cover < 0.5 m	0.56	–0.29	–0.25	–0.09
Cover 3–10 m	0.11	<u>0.68</u>	0.04	0
Vines 2–4 cm	0.1	0.65	–0.21	0.11
Vines > 2 cm	–0.02	0.52	0.06	0.33
Trees 7 cm < dbh < 15 cm	–0.26	0.51	0.05	–0.05
Cover > 20 m	0.06	–0.35	0.73	0.01
Canopy height	0.03	–0.3	0.65	0.07
Trees > 15 cm dbh	–0.01	0.23	0.61	–0.26
Cover 10–20 m	–0.1	0.18	0.51	0.05
Leaf litter depth	–0.14	0.08	–0.12	0.78
Leaf litter number	–0.1	0.15	0.12	0.75
Palm density	–0.15	0.33	0.4	–0.47
Cumulative variance explained	0.14	0.27	0.38	0.5

varimax rotation. We used a scree analysis to determine the number of components (4) with all variables in the analysis (Hair et al., 2010). From each of the principal components, we selected the top loading variable for the comparisons among birds, fragments and control sites (Table 2). These variables included leaf litter depth, plants 1–2 m tall, plant cover 3–10 m, and plant cover >20 m. By selecting a single variable from each component for analysis, we can interpret differences between foraging points and random points despite the complex nature of the habitat we sampled (James and McCulloch, 1990; James and Shugart, 1970).

We estimated medians, 5%, 25%, 75% and 95% credible intervals for leaf litter depth, plants 1–2 m, plant cover 3–10 m, and plant cover >20 m using Bayesian analysis in JAGS(R Programming Language). For our prior distribution of medians for leaf litter depth, we used a log normal distribution, which constrains estimates to be >0. Leaf litter depth cannot be negative, but birds can be associated with areas with no litter; we assume a normal response to leaf litter depth. We used a Poisson distribution for the prior distribution of plants 1–2 m. Like the log normal distribution, the Poisson constrains counts to >0; we assumed plant density had Poisson response to count variables. For plant cover 3–10 m and >20 m, we assumed a binomial distribution.

We directly assessed the hypotheses that medians of vegetation variables differed among fragment points, continuous forest points, and foraging points by using the step function in JAGS. The step function counts the number of simulations where the estimate of one specified group (e.g., 1-ha fragment) median exceeds the median of another specified group (e.g., Wing-banded Antbird). Though we had small sample sizes for a few species, we use vague priors to make our assessments more conservative. Based on Malcolm (1994), we predicted the densities of plants 1–2 and plant cover 3–10 m would increase in forest fragments and exceed the densities associated with fragmentation-sensitive focal species. We also predicted fragments would have thicker leaf litter and less plant cover >20 m than sites associated with fragmentation-sensitive focal species based on Bierregaard et al. (1992) and Malcolm (1994), respectively.

3. Results

3.1. Effects of fragmentation on microhabitats

For plants 1–2 m, we found no strong evidence there was any consistent effect of fragmentation (Table 3, Fig. 1A). As we predicted, it was likely that plant cover 3–10 m increased in fragments, and increased with decreasing fragment size (Table 3, Fig. 1B). We predicted leaf litter would increase in fragments; our results were likely consistent with this prediction, with the exception of 100-ha fragments, which were similar to continuous forest (Table 3, Fig. 1C). We found no evidence that 100- and 10-ha forest fragments had less plant cover >20 m than continuous forest, but it was very likely that 1-ha had more open canopies (Table 3, Fig. 1D).

3.2. Bird preferences vs microhabitat availability in fragments

There were likely more plants 1–2 m in forest fragments than at foraging points for most of the focal species, although the results were not entirely consistent (Table 3, Fig. 1A). For example, *Formicarius analis*, *Grallaria varia*, and *C. torquatus* were associated with plant densities similar to that found in all fragment size classes. We also predicted *M. campanisona* would be associated with sites that have densities of plants 1–2 m that were similar to fragments (posterior probabilities of differences 0.33–0.66); however, this species was associated with sites that were very likely to have a higher density of plants than in forest fragments. The

Table 3
Posterior probabilities of our predictions. We first compare vegetation in forest fragments to continuous forest, then fragments of different sizes to each other, then fragments to each of the focal species. The likelihood of our predictions being correct are color coded as dark green for extremely likely, light green for likely, plain text for about as likely than not, pink for unlikely and red for extremely unlikely.

Hypotheses	Plants 1-2 m	Cover 3-10 m	Leaf litter Depth	Hypotheses	Cover >20 m
1ha > continuous	0.41	1.0	0.92	1ha < continuous	0.98
10ha > continuous	0.51	0.99	0.75	10ha < continuous	0.58
100ha > continuous	0.77	0.83	0.39	100ha < continuous	0.49
1 ha > 100 ha	0.20	0.91	0.93	1 ha < 100 ha	0.98
1 ha > 10 ha	0.41	0.91	0.77	1 ha < 10 ha	0.97
10 ha > 100ha	0.26	0.91	0.81	10 ha < 100ha	0.62
100 ha > MYFE	0.87	0.64	0.99	100 ha < MYFE	0.32
100 ha > MYTO	0.94	0.71	0.83	100 ha < MYTO	0.41
100 ha > COAU	0.91	0.21	0.66	100 ha < COAU	0.22
100 > COTA	0.78	0.72	0.72	100 < COTA	0.55
100 ha > FOAN	0.51	0.60	0.96	100 ha < FOAN	0.67
100 ha > FOCA	0.99	0.46	0.93	100 ha < FOCA	0.36
100 ha > GAVA	0.52	0.75	0.96	100 ha < GAVA	0.75
100 ha > HYMA	0.87	0.32	0.82	100 ha < HYMA	0.84
100 ha < MYCA	0.99	0.62	0.08	100 ha > MYCA	0.98
10 ha > MYFE	0.70	0.94	1.0	10 ha < MYFE	0.43
10 ha > MYTO	0.86	0.95	0.95	10 ha < MYTO	0.50
10 ha > COAU	0.85	0.54	0.80	10 ha < COAU	0.27
10 > COTA	0.62	0.95	0.89	10 ha < COTA	0.64
10 ha > FOAN	0.31	0.91	0.99	10 ha < FOAN	0.76
10 ha > FOCA	0.96	0.86	0.98	10 ha < FOCA	0.46
10 ha > GAVA	0.41	0.94	0.99	10 ha < GAVA	0.80
10 ha > HYMA	0.81	0.67	0.90	10 ha < HYMA	0.87
10 ha < MYCA	0.99	0.25	0.21	10 ha > MYCA	0.98
1 ha > MYFE	0.59	0.99	1.00	1 ha < MYFE	0.96
1 ha > MYTO	0.78	0.99	0.98	1 ha < MYTO	0.95
1 ha > COAU	0.81	0.85	0.88	1 ha < COAU	0.78
1 > COTA	0.53	0.99	0.96	1 ha < COTO	0.98
1 ha > FOAN	0.25	0.99	1.00	1 ha < FOAN	0.99
1 ha > FOCA	0.91	0.98	0.99	1 ha < FOCA	0.95
1 ha > GAVA	0.36	0.99	1.00	1 ha < GAVA	0.98
1 ha > HYMA	0.77	0.91	0.94	1 ha < HYMA	0.98
1 ha < MYCA	0.99	0.05	0.38	1 ha > MYCA	0.72

probabilities that plant cover 3–10 m associated with foraging points differed from the plant cover in fragments increased with decreasing fragment size (Table 3, Fig. 1B). It was likely that plant cover 3–10 m in 100-ha fragments exceeded plant cover for *M. torquata*, *Corythopsis torquata*, and *G. varia* but not of these probabilities exceeded 0.75. It was very likely that plant cover 3–10 m in 1- and 10-ha fragments for most species except *Conopophaga aurita* and *M. campanisona*. As predicted, *M. campanisona* was associated with plant cover that did not differ from the plant cover in forest fragments.

The probabilities that leaf litter depth in fragments exceeded leaf litter associated with foraging points increased with decreasing fragment size (Table 3, Fig. 1C). It was very likely that leaf litter depth in fragments of all size classes for *Myrmeciza ferruginea*, *F. analis*, and *G. varia*. It was at least likely that the leaf litter depth in 1- and 10-fragments exceeded the leaf litter depth associated with all species except *M. campanisona*. We found it unlikely that the leaf litter associated with *M. campanisona* was thicker than the leaf litter in 100- and 10-ha fragments. However, we found the leaf litter in 1-ha fragments was similar to *M. campanisona* foraging points.

Plant cover >20 m in 10- and 100-ha fragments was similar to foraging points for most of the focal species, except it was likely

that *F. analis*, *G. varia*, and *Hylopezus macularius* foraged where plant cover >20 m was more dense (Table 3, Fig. 1D). However, none of these probabilities exceeded 0.87. In 1-ha fragments, it was very likely that plant cover >20 m was less than at foraging locations for *M. ferruginea*, *M. torquata*, *C. torquata*, *F. analis*, *Formicarius colma*, *G. varia*, and *H. macularius*, and likely for *C. aurita*. *M. campanisona* foraging sites were associated with plant cover >20 m that was very likely less dense than plant cover in 10- and 100-ha forest fragments and was likely less dense than plant cover in 1-ha forest fragments.

4. Discussion

We found that forest fragmentation alters a suite of vegetation variables related to forest structure. With decreasing fragment area, we found the vegetation in fragments becomes increasingly dissimilar to vegetation in continuous forest. We found these effects despite our vegetation samples being in the fragment centers and not along edges where vegetation changes were likely to be more drastic (Laurance, 2000). Compared to continuous forest and 100-ha fragments, smaller (1- and 10-ha) fragments had

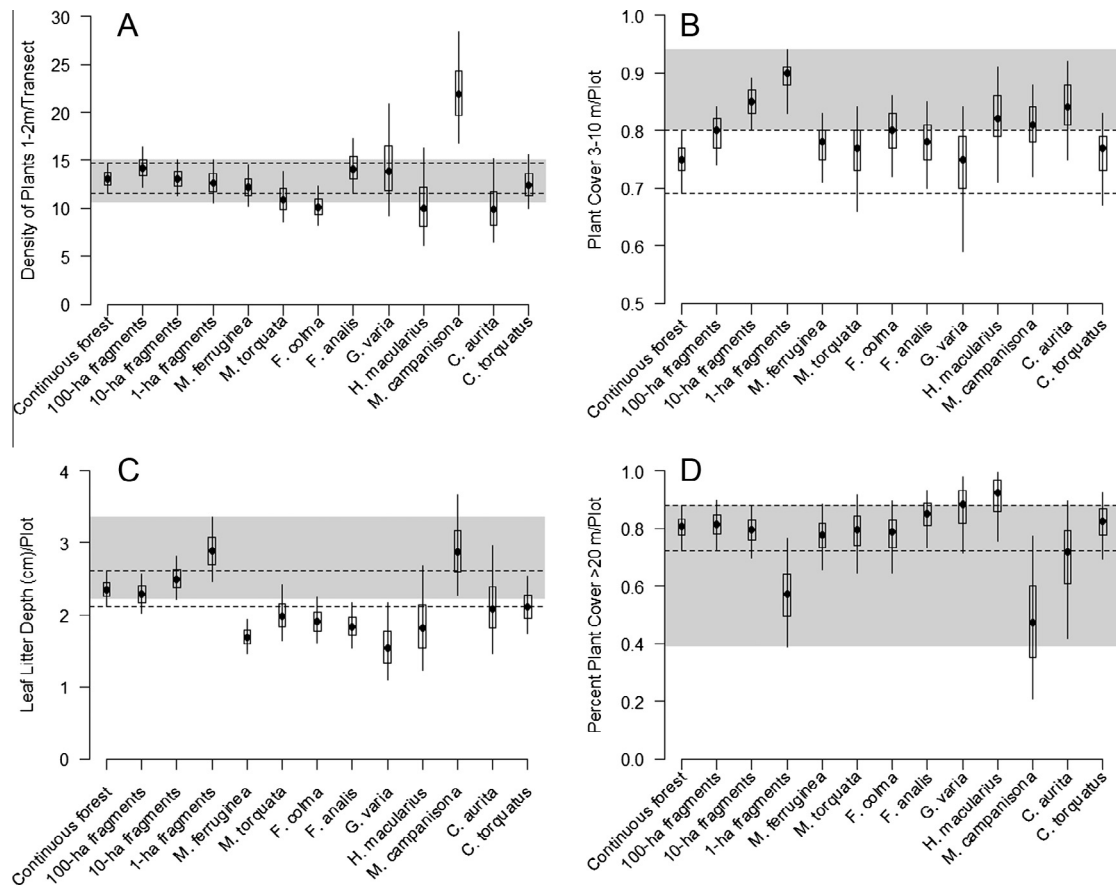


Fig. 1. Posterior estimates of medians (points), 50th percentile (box), and 90th percentile (whiskers) credible intervals for (A) plants 1–2 m, (B) proportion of plant cover 3–10 m, (C) leaf litter depth, and (D) proportion of plant cover >20 m. The dashed horizontal line represents the 90th percentile of the continuous forest sites and the shaded area represents the 90th percentiles of the small (1- and 10-ha) fragments.

increased plant cover in the mid-story but more open canopies. Additionally, leaf litter was thicker in smaller fragments than the large (100-ha) fragments. These results are consistent with other results from the same site (Laurance et al., 2011) and other tropical sites (Laurance, 2000; Laurance and Curran, 2008; Williams-Linera, 1990). Surprisingly, fragmentation did not seem to strongly affect the density of plants 1–2 m. Malcolm (1994) found that foliage density at this height did not increase past 25 m from the edge, so the interiors of small fragments may not experience higher densities of plants 1–2 m.

Do the microhabitat changes in fragments, particularly smaller fragments, make them unsuitable for fragmentation-sensitive terrestrial insectivores? Our results demonstrate the vegetation structure in fragments becomes increasingly dissimilar to those sites where fragmentation sensitive species forage. Changes in plant cover from 3 to 10 m, litter depth, and cover >20 m generally altered microhabitat availability in a direction dissimilar from sites chosen by foraging terrestrial insectivores in continuous forest. Most species used sites with average or lower plants 3–10 m, thinner litter depth, and average or higher plant cover >20 m (see also Stratford and Stouffer, 2013). Of all the microhabitat features we included, leaf litter depth is most likely to directly affect terrestrial insectivores, as they usually forage on this substrate. However, without experimentation, the importance of leaf litter remains unknown. Leaf litter is also thicker in *Cecropia*-dominated second growth, where these species are absent (Stratford and Stouffer, 2013) and fragmentation-sensitive species also avoided areas of thick leaf litter in continuous forest (Cintra and Naka, 2012). Although there was no difference in prey abundance between fragments and continuous forest in the BDFFP fragments (Mestre et al.,

2010) or elsewhere (Şekercioglu et al., 2002), the thicker leaf litter layer in fragments may be a physical impediment to ground foraging birds.

M. campanisona was an exception to the other terrestrial insectivores. This species, which uses large treefall gaps in continuous forest and colonizes or persists in fragments (Stratford and Stouffer 1999; Stouffer 2007), differed strongly from the other terrestrial insectivores in its preferences. *M. campanisona* uses microhabitats with over twice the density of plants 1–2 m than other terrestrial insectivores and was associated with open canopies. Although *Myrmothera* diverged strongly from the other terrestrial insectivores, only its litter depth preference corresponded strongly to changes associated with fragmentation. Its canopy association closely matched canopy in 1-ha fragments, where it was able to colonize at the time of our study (Stratford and Stouffer 1999).

Our experimental design did not test the mechanisms of local extinctions in forest fragments. Area requirements in continuous forest are >1 ha for all species, and >10 ha for *M. torquata*, *F. analis*, and *H. macularius*, providing a simple explanation for absence from small fragments (Ferraz et al., 2007; Johnson et al., 2013; Stouffer, 2007). Several species of terrestrial insectivore have been able to recolonize 10- and 100-ha fragments in the years since our field data were collected (Powell et al., 2013). We do not know how canopy cover or the density of understory plants has changed in fragments over those years. After fragmentation, forest fragments may develop dense vegetation along their edges, possibly buffering interiors from edge effects (Murcia, 1995; Williams-Linera, 1990) though this hypothesis remains untested for our focal species. Second growth that was almost universally unacceptable for terrestrial insectivores at the time of our study (Borges and Stouffer,

1999; Stratford and Stouffer, 2013) is now sometimes used by terrestrial insectivores (Campos e Silva et al., 2012), but our data demonstrated that these species prefer vegetation characteristics that are associated with undisturbed forest. If the vegetation in fragments remains disturbed or vegetation structure continues to be modified, then strategies promoting dispersal (e.g., forested corridors) may not be effective, since terrestrial insectivores may not find appropriate habitat in forest remnants.

Although our vegetation data is consistent with the pattern of bird distribution in a fragmented landscape, we cannot rule out the direct influence of microclimate effects on birds. Changes in vegetation structure in fragments alters microclimate (Didham and Lawton, 1999; Kapos, 1989; Murcia, 1995) and birds are potentially responding to these variables, such as increased insolation and temperatures (Stratford and Robinson, 2005). Pollock et al. (2015) found that understory insectivores were not selecting sites based on microclimate, but their study did not include edge areas, which have more extreme microclimates (Didham and Lawton, 1999). Indeed, Patten and Smith-Patten (2012), found that birds associated with darker areas were more sensitive to forest edges than birds willing to use brighter microhabitats. The links among microclimate (including light levels), microhabitat structure, and understory bird microhabitat use deserves much more attention (Robinson and Sherry, 2012; Stratford and Robinson, 2005). Fine-scale manipulations of canopy structure, understory plant density, and microclimate would be key in discriminating between competing explanations.

Our results for terrestrial insectivores in the BDFFP landscape conform to other work showing terrestrial insectivores to be particularly sensitive to microhabitat changes associated with disturbance to rainforest. Vegetation changes could be the primary reason tropical terrestrial insectivores are lost from selectively logged areas (Aleixo, 1999; Barlow et al., 2006; Bicknell and Peres, 2010; Canaday, 1997; Edwards et al., 2013). The microhabitat hypothesis has mixed support in temperate forests. Long-distance migrants and forest specialists appear to be more sensitive to vegetation structure than temperate residents or synanthropic species (Ambuel and Temple, 1983; Fernandez-Juricic, 2004; Miller et al., 2004). Thus, the link between fragmentation, altered vegetation, and loss of forest interior birds may be a geographically and taxonomically widespread phenomenon.

Fragmentation alters vegetation structure across forest types (Fischer and Lindenmayer, 2007) and understory birds are closely linked to vegetation structure across the tropics (Oosterhoorn and Kappelle, 2000; Sewell and Catterall, 1998; Uezu and Metzger, 2011). Thus, it is very plausible that local changes in vegetation structure within forest fragments, along with area effects and landscape-level factors, play a strong role in the loss of understory insectivore diversity from tropical sites (Bregman et al., 2014; Harris et al., 2011). Combined with our previous results (Stratford and Stouffer, 1999, 2013), we show that forest fragmentation and the surrounding matrix alters the landscape to be unsuitable for our focal species.

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