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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

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