Habitat and Life History Determinants of Antbird Occurrence in Variable-Sized Amazonian Forest Fragments

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ABSTRACT

The highest avian species richness on Earth is found in the Neotropics, with the speciose antbird superfamily (Thamnophilidae, Formicariidae, Grallariidae and Conopophagidae) accounting for 15 percent of South American passerine diversity. Antbird species have divergent life histories and ecological requirements, resulting in considerable interspecific variation in responses to anthropogenic habitat modification. Here, we examine interspecific differences in antbird responses to both habitat fragmentation and perturbation in a region of the so-called ‘Arc of Deforestation’ of southern Brazilian Amazonia in northern Mato Grosso. We surveyed the antbird community of 31 variable-sized forest patches and found that antbird species richness was predominantly affected by patch size and isolation, although forest patch quality was also important. Life history predictors were less important overall in determining patch occupancy and minimum patch area requirements with body mass and geographic range size the most important predictors. Foraging niche was also important; mixed flock followers, bamboo specialists and army-ant followers were all more prone to local extinction in small fragments. Although most Amazonian antbird species are not currently threatened, rates of interfluvial endemism are high and future forest loss may imperil many species currently considered to be of low conservation concern. Lessons learnt in the identification of fragmentation-sensitive genera and guilds may be applicable to other antbird species outside Amazonia, such as those in the Brazilian Atlantic Forest. Ensuring future survival of antbirds across neotropical forest landscapes that retain only a small percentage of their original primary forest cover will rest on protecting remaining large forest patches and maintaining structural and functional connectivity between them.

Abstract in Portuguese is available at http://www.blackwell-synergy.com/loi/btp

Key words: antpitta; antthrush; edge-specialists; extinction; formicariids; forest disturbance; Myrmotherula; tropical forests.

Antbirds are ubiquitous, charismatic, if sometimes ethereal inhabitants of neotropical forests from northern Mexico to northern Argentina. Antbird diversity is highest in the Amazonian basin, where differences in ecological specialization and microhabitat preferences permit sympatry of over 50 species at a single site (e.g., Zimmer et al. 1997). The Brazilian Amazon (which contains ~41% of the world’s remaining tropical forest) is, however, subject to the world’s fastest absolute tropical deforestation rate: currently ca 2 Mha/yr (INPE 2008). The antbird moniker incorporates three families within the furnariid radiation of the New World suboscine clade: the typical antbirds (Thamnophilidae), the antthrushes (Formicariidae), the antpittas (Grallariidae) and the gnatcatchers (Conopophagidae) (Remsen et al. 2008). Most thamnophilid species are arboreal or undergrowth inhabitants, with only a few species being clearly terrestrial, whereas terrestriality seems to be the commonest lifestyle for most members in the other three families.

Antbirds exhibit highly divergent interspecific responses to forest fragmentation and perturbation, along a gradient from highly fragmentation/disturbance tolerant to highly fragmentation sensitive. Interspecific responses are known to be determined primarily by life history characteristics: understory insectivores, mixed-species flock followers and obligate army-ant followers are known to be most vulnerable to local extinction in small patches (Stouffer & Bierregaard 1995, Sekercioglu et al. 2002, Ferraz et al. 2007, Stouffer 2007, Lees & Peres 2008a). Globally, sedentary birds like antbirds are far more extinction-prone than migrants and nomadic species and there is a tight correlation between specialization and extinction risk (Sekercioglu 2007).

Although only one Amazonian antbird species is currently listed as threatened (Birdlife International 2008a), future forest loss and climate change (Sekercioglu et al. 2008, Vale et al. 2008) may see many more species in the basin qualifying for threatened status. Moreover, understanding the responses at the generic level facilitates comparison with other threatened species with similar life history traits from other fragmented forest regions (e.g., Brazilian Atlantic Forest; Mesoamerica) and may inform a priori conservation decisions. In this study, we examine antbird community responses to fragmentation around the town of Alta Floresta, State of Mato Grosso, Brazil, which has one of the most species-rich antbird communities in the lowland Amazon in part owing to a high degree of habitat heterogeneity (52 species: Zimmer et al. 1997; A. Lees, unpubl. data). We attempt to ascertain the effects of forest patch and forest landscape characteristics on within-patch species richness and examine which antbird life history traits predispose extinction proneness.

METHODS

Study landscape.—The countryside around the town of Alta Floresta (09° 53’ S, 56° 28’ W) lies along the center of the notorious Amazonian ‘Arc of Deforestation’, the most aggressive tropical deforestation frontier in the world (Soares-Filho et al. 2006). This vast mosaic landscape of variable-sized forest patches is set in a matrix of active cattle pasture (Fig. S1) and provides an ideal landscape in which to study the effects of primary forest fragmentation.
and perturbation on bird communities. For a more detailed description of the study area, see Lees and Peres (2006).

ANTBIRD SURVEYS.—From June to September 2004 and May to June 2006, antbird species were recorded on a presence/absence basis during 930 unlimited-radius point-counts at 31 forest sites, including 30 fragments and 1 continuous, undisturbed forest site. Two large forest fragments (> 10,000 ha) were treated as pseudo-controls. The size of the 31 forest sites surveyed ranged from 1.2 to >100,000 ha (largest true isolate = 14,476 ha; mean ± SE = 5647 ± 4672 ha). Thirty point-counts were completed within each site over three mornings at points along transects spaced 200 m apart wherever possible, but this distance was inevitably reduced to 50 m in the smallest fragments due to severe area constraints. An equal amount of sampling time (10 point-counts of 15 min/d; total of 30 point-counts) was allocated to fragments of all size classes and the continuous forest site, thus small patches were more exhaustively sampled than large ones and the results should be regarded as conservative with respect to area effects, as some species may have been missed in large patches. Surveys were conducted during the dry season, the annual peak in avian vocal activity and when many antbird nests have been discovered (A. Lees, unpubl. data). For a detailed description of the sampling techniques and limitations, see Lees and Peres (2006, 2008a).

FOREST PATCH METRICS.—Following an unsupervised classification of a 2004 Landsat image (ETM 227/067), we unambiguously resolved eight mutually exclusive land-cover classes (ranging from closed-canopy forest to bare ground). Although no formal accuracy assessment was performed, we were able to extensively ground-truth these classifications at all sites. The image was georeferenced based on a 1996 satellite image with a 5 m accuracy and a spatial resolution of 15 m. Patch size and landscape metrics were extracted from the image using Fragstats v. 3.3 (McGarigal et al. 2002) and ArcView 3.2. For incompletely isolated forest patches (three of 30 surveyed patches), we artificially eroded the narrowest connections—usually consisting of riparian corridors to other forest patches—to calculate the total patch area. Erosion of connections was carried out across the narrowest groups of pixels. Patch metrics data for our largest (effectively ∞-sized) site, located within vast tracts of continuous forest north of the Teles Pires river, were based on an arbitrary area equivalent to one order of magnitude larger than our largest fragment and linear regression models based on all other patches (Lees & Peres 2006). A forest habitat quality index (HQI) was then calculated using a weighted mean value for all pixels within the patch. For each pixel, closed-canopy primary forest and bare ground were assigned the highest and lowest scores, respectively, with scores of six intermediate classes for disturbed forest and pasture subtypes based on their spectral quality which was correlated with aboveground vegetation biomass (C. A. Peres, F. Michalski and I. R. Lake, unpubl. data). We also calculated the percentage of forest habitat within 1 km of the perimeter of each sampled forest patch as an indication of the degree of isolation of the forest patch. Structural forest habitat variables quantified at each point-count station included mean understory density and canopy gap fraction (Lees & Peres 2006; Table 1).

REGIONAL ANTbird COMMUNITY COMPOSITION AND IDENTIFICATION OF TERRA FIRME SPECIES.—Of the 52 antbird species known from the region, five species (Hypocnemis hypoxantha, Dicranoeca cinera, Pyrigena leucophanta, Chamaea nobilis, and Conopophaga aurita) are currently only known from the east bank of the Teles Pires river (Zimmer et al. 1997; A. Lees, unpubl. data). One of our control sites was located on this bank, so we excluded records of these species (recorded from our east bank control site) from our analysis, even though the Teles Pires represents only a minor fluvial barrier (Bates et al. 2004). Our analysis only concerns the terra firme forest antbird community, thus excluding species found in transitional forest habitats: Thamnophilus stictochilus and Formicivora grisea; riverine species: Sakesphorus luctuosus, Myrmotherula multistriata, Herpetocichla rufomarginata, Hypocnemoides maculicuda, Scatella naevia, Schistochila rufacies and Hylophylax punctulatus; and nonforest matrix species: Thamnophilus doliatus (Zimmer & Isler 2003). We address the riparian avifauna of the region in a different study (Lees & Peres 2008b) and all the above-named riverine antbird species occurred in connected riparian forest corridors, with some species occupying even degraded sites. We failed to sample only one terra firme forest antbird species of the Alta Floresta landscape (Myrmornis torquata), but only two territories are known from the entire region (A. Lees, unpubl. data). This species has been shown to be extremely prone to extinction in small fragments (Stratford & Stouffer 1999). Another rare species, Grrallaria varia, was excluded from the analysis because it was only detected once during this survey, from a control forest site on the east bank of the Teles Pires. We therefore retain a baseline assemblage of 36 species of terra firme forest antbirds, following the exclusion of the above-mentioned 16 species.

LIFE HISTORY CHARACTERISTICS.—We assessed species susceptibility to extinction using eight life history characteristics: (1) body mass (after Terborgh et al. 1990, Hilty 2002); (2) sensitivity to disturbance (Parker et al. 1996) classified as 1, 2, or 3, where 3 is the most sensitive; (3) geographic range size (km²) (Birdlife International 2009); (4) number of habitats used (Parker et al. 1996); (5) flocking propensity (of mixed-species flocking species classified as either nonflocking, facultative or obligate flock following; Hilty 2002, Zimmer & Isler 2003); (6) foraging strata (Zimmer & Isler 2003); (7) relative abundance; and (8) patchiness (both derived from Parker et al. 1996).

DATA ANALYSIS.—To reduce the number of variables in the regression analysis and collinearity between them, a Pearson’s correlation matrix was calculated using potential independent variables. A tolerance threshold of pairwise $R^2$ values of 0.56 was used to determine unacceptable collinearity between independent variables, and we then eliminated either the less general or less biologically meaningful variable (Freckelton 2002). We excluded foraging guild from these correlations. To assess the relationships between patch and landscape characteristics and number of antbird species, we performed linear regression modeling considering all 31 sites. We
TABLE 1. Correlation coefficients among patch, landscape and life history variables where: AREA, log10 patch area (ha); SHAPE, Fragstats\textsuperscript{\textregistered} shape metric; CANOP, forest canopy cover; UNDR, understory density; HQI, pixel-weighted habitat quality index; CCFOR, percentage of closed canopy forest; FOR1KM, percentage of closed canopy forest within a 1 km external buffer; ISOL, distance to nearest ‘source’ patch > 1000 ha; SNST, sensitivity to disturbance; STRA, typical foraging stratum; BM, mean body mass (g); ABUN, relative abundance; PATC, patchiness; FLOCK, flock following propensity; HABITAT, number of habitat utilized; RANGE, geographic range size (km\textsuperscript{2}). Significance levels: *P < 0.05, **P < 0.01.

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log-transformed species body mass but used untransformed values for all other species traits. Categorical variables (flock and primary forest dependence) were converted into dummy variables for inclusion in the analysis. We investigated the variation in antbird community structure among forest patches using nonmetric multidimensional scaling (NMDS) ordinations, with the Bray–Curtis dissimilarity measure (sqrt-transformed and unstandardized) using the PRIMER software (Carr 1996). Species assemblage nestedness is a common response to faunal relaxation, so we used the nestedness calculator (Atmar & Patterson 1993) to determine whether patterns of antbird within forest fragments created nested species distributions. This approach calculates a matrix-wide value of heat disorder—the ‘nestedness temperature,’ which may vary between 0° for a perfectly nested system and 100° for a perfectly random system. This method is not without shortcomings (Fischer & Lindenmayer 2002) and although some absences within the matrix may be an undersampling artifact (Cam et al. 2000) this was only likely to be the case in the largest forest patches surveyed.

We employed model selection methods based on the Akaike’s information criterion (AIC; Burnham & Anderson 2002). To identify which (1) patch and landscape variables and (2) life history variables were the best predictors of patch occupancy, we used an all-subsets approach with general linear models assuming a Poisson distribution. Multimodel inference (MMI) approaches using model-averaged parameter estimates do not suffer from problems associated with stepwise model selection techniques, e.g., bias in parameter estimation, inconsistencies among model selection algorithms and an inappropriate focus or reliance on a single best model (Whittingham et al. 2006). Instead, competing models are compared by evaluating the relative support in the observed data for each model and models can be ranked and weighted, thereby providing a quantitative measure of relative support for each competing hypothesis. Furthermore, an averaged model is more appropriate than a single model when multiple models have similar levels of support from the data, in which case model averaging can be used to make robust parameter estimates and predictions (Johnson & Omland 2004, Whittingham et al. 2006). Models were first ranked by second-order AIC (AIC\textsubscript{c}—corrected for small sample size) differences (\(\Delta_i\); Burnham & Anderson 2002); the lower the AIC\textsubscript{c} value the more likely the model approximates the data. Models were ranked by rescaling the AIC\textsubscript{c} values such that the model with the minimum AIC\textsubscript{c} has a value of 0. Relative likelihood of each model in a candidate set was then estimated with Akaike weights (\(\omega_i\); Burnham & Anderson 2002). The \(\omega_i\) values for all models in a candidate set sum to one. Akaike weights were used to generate model-averaged parameter estimates. Model averaging is based on \(\omega_i\) values for each model, therefore including model selection uncertainty in the estimate of each parameter and its associated variance. We calculated the relative importance of any given variable (\(\Sigma \omega_i\)) by summing the Akaike weights for all models.
containing that variable (Burnham & Anderson 2002). Data analyses were undertaken with the STATA 8 statistical package (STATA Corp., College Station, Texas).

RESULTS

PATCH AND LANDSCAPE CHARACTERISTICS.—The size of the 31 forest sites inventoried (Fig. S1) ranged from 1.2 to > 100,000 ha. Forest patch quality was also highly variable with the pixel-scale percentage of closed-canopy forest within a patch ranging from 17.4 to 72.7 percent (mean = 49.5 ± 15.9% SD). Likewise, the landscape context in which these patches were embedded was highly variable; for instance, the proportion of closed-canopy primary forest within a 1 km buffer varied between 4.8 and 81.2 percent (24.4 ± 27.2%), and the distance to the nearest source patch > 1000 ha ranged from 0 to 10,301 m (3066 ± 2184 m). Collinearity was high among patch and landscape variables (Table 1); we were therefore forced to exclude metrics describing patch shape and core forest area (> 200 m from forest edges) in addition to the percentage of forest cover within a 1 km external buffer.

ANTBIRD RESPONSES TO FRAGMENTATION.—Antbird species richness ranged between 0 and 36 species per patch (mean = 13.4 ± 10.8 SD; N = 31), and increased over the entire size spectrum of forest fragments in the Alta Floresta region, generating a robust species–area relationship (R² = 0.824, P < 0.001, N = 31; Fig. 1A). Antbird species richness per patch also increased with increasing forest habitat quality (R² = 0.368, P < 0.001) and the within-patch proportion of closed-canopy primary forest (R² = 0.434, P < 0.001; Fig. 1B). Antbird species that were least sensitive to area effects (i.e., those that occupied the smallest patch size class) also occupied the greatest number of patches (Table S1). NMDS scores indicate that small patches were more dissimilar from one another in overall antbird assemblage composition. Antbird assemblages converged in similarity with increasing forest patch size, albeit with some exceptions provided by idiosyncratic small patches with high species richness (Fig. S2). The antbird patch occupancy data for all 31 sites filled 38.5 percent of the 1116 cells in the overall species-by-site matrix. The nestedness analysis calculated a temperature of 10.6°C for the observed matrix, whereas we obtained a mean temperature of 68.3°C (SD = 3.3°C) on the basis of 500 randomly drawn matrices. This suggests that local antbird extinction events, from the most species-rich to the most species-poor site, are relatively predictable across antbird species. The most idiosyncratic site was the control forest site on the east bank of the Teles Pires, which naturally lacks several edge species; the most idiosyncratic species was *Myrmeciza atrothorax*, a disturbance tolerant species that was absent from control forest sites lacking edge habitats.

The Akaike weights provide an overall measure of the importance of patch and landscape variables in explaining overall species richness.
LIFE HISTORIES.—As a nuclear species (sensu Moynihan 1962), Thamnomanes caesius and Thamnomanes saturninus play an important role in consolidating mixed-species flocks (Powell 1985). These relatively conspicuous flock leaders were missing from patches smaller than 16 ha (T. caesius) or 24 ha (T. saturninus). The minimum spatial requirements and patch occupancy of the two obligate flock following Myrmotherula antwrens are therefore inextricably tied to the flock’s home range and the presence of Thamnomanes, rather than the availability of food resources (Powell 1989). This dependence on Thamnomanes explains why facultative flock following Myrmotherula antwrens (e.g., Myrmotherula hauwelli) are able to occupy patches smaller than 10 ha. In fact, ‘flock dropout’ antbirds, such as M. hauwelli and Thamnophilus schistaceus, are among the most fragmentation insensitive of forest birds, and are thereby able to make much greater use of the fragmented landscape (Stouffer & Bierregaard 1995, Antongiovanni & Metzger 2005). Within the Alta Floresta landscape considered here, there are 999 completely isolated forest patches larger than 5 ha; 178 larger than 50 ha; and 35 larger than 500 ha. This fractal landscape, however, is still extensively forested at its periphery, such that an antbird that can occupy a 5 ha remnant is only able to occupy 13 percent more of the entire landscape (243,553 ha) than one restricted to patches larger than 500 ha. As the landscape becomes progressively more fragmented and large patches become rarer and more isolated, problems of metapopulation dynamics failure, demographic stochastic effects and genetic isolation will, however, become more exigent for area-sensitive antbird species (Diamond et al. 1987, Bates 2002). These will be most marked in the rarer species which show greater demographic fluctuations even within large tracts of primary forest (Stouffer 2007).

Eight antbird species were encountered in nonforest matrix habitats (principally scrubby second growth) during a separate study around Alta Floresta: Cymbilaimus lineatus, Taraba major, T. schistaceus, Thamnophilus aethiops, Cercomacra cinerascens, Myrmoborus leucophrys, M. astrothorax and Hyllopezus berlepschi (Mahood 2006). All of these species also occurred within small forest fragments, providing further evidence that matrix tolerance is an important factor enabling species persistence in small forest patches (cf., Lees & Peres 2009). None of these species are obligate flock followers or army-ant followers, and although some species have an affinity for bamboo patches (e.g., M. leucophrys and H. berlepschi), they are not tied to them (Zimmer & Isler 2003). Instead, they are probably dependent on habitats with a similarly dense vegetation structure, requirements that can apparently be met by degraded second growth habitats. The Alta Floresta region—a relatively recent deforestation frontier—is typically comprised of a binary landscape (i.e., primary forest or nonforest), without secondary forest patch buffers around the remaining primary forest remnants. Elsewhere in Amazonia, the presence of a more hospitable matrix may act as a buffer against local extinction of many forest-dependent bird species (Stouffer et al. 2006).

Hyllopezus berlepschi is unique among ground antbirds in its tolerance for degraded habitats. This species is relatively uncommon in edge and bamboo habitats within the matrix of undisturbed terra firme forest east of the Rio Teles Pires (Fig. S1; Zimmer et al. 1997), yet appears to proliferate in degraded linear forest remnants (Lees & Peres 2008b) and in small forest patches that provide this preferred vegetation structure. The data from our forest fragments do not reflect the species’ minimum patch requirements, as
we avoided preselecting patches that were highly degraded. The remaining terrestrial antthrushes and antpittas—all medium- to large-bodied species—were very sensitive to patch size effects; our results are consistent with those from the Projeto Dinâmica Biológica de Fragmentos Florestais (PDBFF) north of Manaus, Brazil, where local extinctions of terrestrial insectivores occurred in 68 percent of the 10 ha fragments and 31 percent of the 100 ha fragments (Stratford & Stouffer 1999). In comparing findings from these two Amazonian landscapes, however, it should be borne in mind that the PDBFF forest patches were only isolated from adjacent areas of primary forest by a relatively narrow strip of relatively benign second growth matrix, whereas our Alta Floresta forest patches were often isolated by more than 10 km of cattle pastures from large (> 1000 ha) forest patches. Stratford (1997) demonstrated that several species of terrestrial insectivores used microhabitats that are more prevalent in continuous forest areas than in small fragments. Decreased leaf litter desiccation rates, resulting in a deeper litter-layer, may occur both in small forest fragments (Didham 1998) and naturally in transitional forest regions, such as those found immediately south of Alta Floresta (Lees et al. 2008), thereby potentially limiting populations of terrestrial insectivores by making foraging difficult.

Restricted-range species.—We found that antbird species with small geographic ranges tend to be more fragmentation sensitive and hence more vulnerable to extinction (cf., Pimm et al. 1988, Gaston 1994, Purvis et al. 2000). For most birds, especially tropical species, global range sizes have major errors and are likely to be overestimates, with range-restricted, specialized and more threatened species’ ranges being most overestimated (Jetz et al. 2008, Schipper et al. 2008). True range size is likely to be even more important a predictor of local extinction. The antbird of greatest conservation concern in the region is the endemic Rhegmatorhina gymnops. In common with numerous other studies concerning obligate ant followers (e.g., Stouffer & Bierregaard 1995), this species only occurred in the largest patches (minimum patch size = 1907 ha). Rhegmatorhina gymnops formerly occurred within a 230 ha suburban forest patch on the outskirts of Alta Floresta (A. Whittaker, pers. commun.), but became extinct there in 1997, approximately 17 yr after the isolation of this patch and following the local extinction of host army-ant (Ection burchelli) swarms. Its range currently occupies an area of 157,738 km², although this is predicted to contract by 38 percent to 98,598 km² by 2020 due to deforestation (Vale et al. 2008). The other ‘fully obligate’ army-ant follower in the region (Phelegopsis nigromaculata) was encountered in forest fragments as small as 84 ha, and this species continues to persist in the same 230 ha patch where the local extinction of R. gymnops has already been documented. In the absence of Ection swarms, P. nigromaculata presumably parasites (sensu Wrege et al. 2005) swarms of the smaller-bodied ant (Labidus sp.). Phelegopsis nigromaculata was also more frequently encountered in riparian forest corridors than R. gymnops (Lees & Peres 2008b), although both species were observed crossing non-forest gaps equally frequently (Lees & Peres 2009). Rhegmatorhina gymnops is thought to have larger territory requirements than P. nigromaculata (Zimmer & Isler 2003) and this might contribute to its higher fragmentation sensitivity.

Cerocyma manu is a bamboo (Guadua sp.) specialist restricted to extensive, mature bamboo thickets (Fitzpatrick & Willard 1990) and in Alta Floresta it was never encountered in patches < 915 ha. This species has been forecast to lose 20 percent of its habitat by 2020 (Vale et al. 2008), leaving it occupying a range of 240,399 km². Bamboo specialists such as Epinecrophylla ornatei, C. manu and Drynophila devillesi, which search for insects in live bamboo stands, rely heavily on the spatiotemporal distribution of scattered bamboo patches within the terra firme forest matrix (Janzen 1976). Bamboo specialists may also be particularly sensitive to forest fragmentation; local die-offs of bamboo may occur on scales of thousands of square kilometers (Nelson & Bianchini 2005), thus encompassing whole forest patches. Given the general reticence of antbirds to cross the hostile nonforest matrix, such species will be unable to track the spatiotemporal distribution of bamboo stands and may face local extinction if they are unable to exploit resources other than bamboo (Ribon et al. 2003). Both species of Epinecrophylla antwren occurring in the region—E. ornatei and Epinecrophylla leucophthalma—appear to be highly fragmentation sensitive. Epinecrophylla ornatei is a bamboo specialist, but both species are also arboreal dead-leaf searchers (Remsen & Parker 1984), a trait that may also render them extinction-prone. The rarity of E. leucophthalma, however, even within large forest patches away from the Teles Pires river may be governed by as yet unclear landscape scale factors; a pattern reflected locally in a handful of other bird species such as Pionites leucogaster and Platyrinchus platyrhynchos (A. Lees, pers. obs.).

Antbirds are an excellent indicator group to illustrate the effects of tropical forest fragmentation and perturbation because (1) their relatively frequent bouts of singing makes them easily detectable to trained observers (Stotz et al. 1996) and (2) they encompass a wide range of foraging strategies and habitat preferences that predisposes them to be affected asymmetrically by these anthropogenic processes. We have already highlighted the fact that many species are of immediate conservation concern in the highly fragmented Atlantic Forest. Further lessons learnt from Amazonia may serve to highlight which species may be under immediate threat of extinction at different spatial scales. We have identified obligate flock following members of the genus Myrmotherula as being particularly fragmentation sensitive; there are five threatened species of Myrmotherula spp. in the Atlantic Forest, including the critically endangered Myrmotherula snowi, which clings to survival in a handful of small remnant fragments of northeastern Brazil (Mazar Barnett et al. 2005). Bamboo specialists such as the vulnerable Biaea nigrispectus and ant followers such as the critically endangered Pyrgilena atra are equally vulnerable owing to their life histories. Without conservation attention we would expect the extinction of these restricted-range specialists to be much more likely than for more disturbance tolerant (but still restricted-range) genera such as Myrmeciza. For instance, the endangered Myrmeciza ruficauda has been recorded in degraded second growth (Birdlife International 2008b), which buffer many primary forest isolates. Guarding against the global extinction of endemic antbirds in the
Atlantic Forest (Ribon et al. 2003, Uezu et al. 2005), and local extinctions of Amazonian antbird populations (which may represent evolutionary significant units) within variegated and fragmented landscapes (Lees & Peres 2006, 2008b), will depend on maintaining structural and functional connectivity between sufficiently large forest remnants.

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**SUPPORTING INFORMATION**

Additional Supporting Information may be found in the online version of this article:

**TABLE S1.** Minimum patch area requirements and patch occupancy for 36 species of terra firme forest antbirds across 31 forest patches surveyed.

**TABLE S2.** Model weights from information-theoretic analysis of patch and landscape predictors of antbird species richness in variable-sized forest patches, and life history predictors of minimum patch size occupied.

**FIGURE S1.** Location of the study region around Alta Floresta, northern State of Mato Grosso, Brazil, showing the 31 forest sites surveyed, Alta Floresta, surrounding forest areas and the non-forest matrix dominated by cattle pastures.

**FIGURE S2.** Antbird assemblage composition as a function of forest patch size for all species occurring within the 31 forest patches sampled.

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