Avian life-history determinants of local extinction risk in a hyper-fragmented neotropical forest landscape

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Abstract

The fact that species vary in their vulnerability to extinction is well documented, but the reasons for these differences remain poorly understood. Why should some species/families/guilds decline rapidly with increasing anthropogenic disturbance, while others either tolerate or proliferate in disturbed habitats? We investigated the bird species composition in 31 primary forest patches of varying size in a region of the Amazonian 'Arc of Deforestation' and assessed which species life-history traits predisposed individual species to extinction. Medium-sized non-flocking canopy frugivores/omnivores of low primary forest dependence were least likely to go extinct in small patches, while small-bodied flock-following primary-forest-dependent terrestrial insectivores were most fragmentation sensitive. We found highly idiosyncratic relationships between the minimum size of forest patches occupied by different species and their territory size requirements estimated based on other Amazonian studies. This suggests that avian assemblages in forest fragments primarily comprise species that either have good dispersal abilities or are highly tolerant to the non-forest matrix, rather than those whose minimum spatial requirements can be met by the size of available forest fragments.

Introduction

Conservation biologists have invested considerable effort identifying the life-history traits that render certain species, guilds, families or communities vulnerable to extinction (see reviews in McKinney, 1997; Purvis et al., 2000; Henle et al., 2004). Identifying traits associated with increased extinction risk may facilitate the protection of species sensitive to disturbance (Lindenmayer et al., 2002; Martin & Possingham, 2005). Birds are often used as a model taxonomic group as they (1) form a diverse assemblage for which key life-history attributes are better known than for any other group; (2) are relatively easy to survey; (3) occupy spatial scales amenable to human perceptions. Despite recent macroecological progress in our understanding of the relationship between sensitivity to anthropogenic disturbance and life-history traits on a global or continental scale (e.g. Purvis et al., 2000; Fagan et al., 2001; O'Grady et al., 2004), few studies have investigated these relationships at the level of local assemblages within a given landscape. Traits commonly linked to local extinction proneness include geographic range size, population size and variability, body mass and life-history specialization. According to the classification scheme of Vos et al. (2001), species least vulnerable to fragmentation should be generalist species with high densities, small spatial requirements, high mobility and short generation times.

Although a considerable body of work on traits related to extinction risk focuses on population persistence following habitat fragmentation (e.g. Blake, 1991; Laurance, 1991; Terborgh et al., 1997; Davies, Gascon & Margules, 2001), the entire southern Amazonian region has received little attention. Gage et al. (2004) used a comparative macroecological modelling approach to investigate the threat of extinction to Neotropical birds, and for the southern Amazonian region concluded that the only weak predictors of threat were body size (larger species being more threatened) and number of habitats (species occupying more habitats being less threatened).

The Brazilian Amazon contains about 40% of the world’s remaining tropical rainforest and is subject to the world’s highest absolute tropical deforestation rate, currently averaging nearly 2 million hectares per year (INPE, 2007). Despite this, lowland Amazonia is not widely recognized as an area of current avian conservation priority (Fjeldså & Rahbek, 1998), on account of its low levels of endemicity – containing only five endemic bird areas (EBAs), of which two are on the western fringe close to the Andes (Stattersfield et al., 1998). Moreover, with habitat loss and fragmentation accelerating right across the continent, species threatened in the near future will also include many that are not currently considered to be range restricted. The Amazon is however an excellent model region in which to study the relationship between sensitivity to disturbance and life-history traits because of (1) its recent history of anthropogenic habitat fragmentation and degradation and (2) it is a vast, relatively uniform region with few endemics (thereby avoiding the confounding problems associated with
natural habitat heterogeneity), so that the effects of fragmentation and species life history can be teased apart.

This paper is the first avian study in a ‘real world’ Amazonian hyper-fragmented landscape – where the relative contribution of patch and landscape characteristics in structuring species assemblages is largely understood (Lees & Peres, 2006) – examining which behavioural and life-history traits determine species persistence in variably sized forest patches. We attempt to identify which species and guilds are most susceptible to the forest fragmentation process, and therefore dominate future conservation concerns.

**Methods**

**Study area**

Extensive road-paving and several large agricultural resettlement programmes during the 1970s catalysed massive forest clearance in southern Amazonia. The countryside around the town of Alta Floresta, State of Mato Grosso, Brazil (09°53'S; 56°28'W; Fig. 1), lies in the southern Amazonian ‘Arc of Deforestation’ and is an ideal model landscape in which to study the effects of habitat fragmentation and perturbation (Michalski & Peres, 2005). Before 1976, the region was entirely covered by undisturbed Amazonian terra firme forest of similar physiognomy (Soares-Filho, 1998). Subsequently the region has experienced extremely high deforestation rates, and by 2003 only 37% of the pre-frontier forest cover remained in the Alta Floresta region south of the Rio Teles Pires (Michalski & Peres, 2005). The remaining forest remnants vary extensively in size, shape and degree of connectivity, but are invariably surrounded by a matrix of managed cattle pasture. A more detailed description of the study landscape is presented elsewhere (Michalski & Peres, 2005; Lees & Peres, 2006).

The Alta Floresta region, which has been thoroughly surveyed ornithologically since 1989 (Zimmer et al., 1997), hosts one of the most species-rich avifaunas in South America with nearly 600 species recorded within 65 km of the town. The region supports many regional endemics and hitherto little-known taxa, but only a single species is considered to be threatened (Anodorhynchus hyacinthinus) and a further seven species considered near-threatened. This pattern is reflected across a great swathe of forest south of the Amazon and east of the Rio Madeira, which encompasses only four secondary EBAs, each protecting just one restricted range species (Stattersfield et al., 1998). However, this currently favourable status may be radically altered in the future by the processes of habitat loss and fragmentation, by a greater understanding of the region’s cryptic ornithodiversity and by the recognition of many restricted range subspecies as true phylogenetic species (e.g. Zimmer, 2002) or the discovery of new species (e.g. Whittaker, 2002).

**Sampling methods**

Between June 2004 and June 2006, one experienced observer (A. L.) completed 930 unlimited radius point counts (PCs) (Blondel, Ferry & Frochot, 1970) at 31 forest sites, including 30 fragments and one continuous, undisturbed control site (Fig. 1). Sampled fragments ranged in size from 1 to 14 476 ha. Two large forest fragments were larger than 10 000 ha and may be treated as continuous forest pseudo-controls. Most of the fragments included in the study were isolated from the wider skeletal forest matrix surrounding Alta Floresta with the exception of some of the larger
correlated range size, dispersal distance and body size) are known to be granivores. Many of these life-history attributes (e.g. home strata; (10) relative abundance (all derived from Stotz personal experience); (8) foraging guild; (9) preferred forai-
sity (of mixed-species flocking species) (after Hilty, 2002 and
species to warrant treating them separately.
We used model selection methods based on Akaike’s information criterion (AIC: Akaike, 1973; Burnham &
Anderson, 2002). To identify which life-history variables were the best predictors of gap-crossing ability, we used an all-subsets approach with general linear models assuming a Poisson’s distribution. Models were first ranked by second-
order AIC (AICc – corrected for small sample size) differ-
ences (Δr; Burnham & Anderson, 2002); the lower the AICc value, the more likely the model approximates the data. Models were ranked by rescaling the AICc values such that the model with the minimum AICc has a value of 0. Relative likelihood of each model in a candidate set was then estimated with Akaike weights (wi; Burnham & Anderson, 2002). The wi values for all models in a candidate set sum to one. Akaike weights were used to generate model-averaged parameter estimates and confidence sets. Model averaging is based on wi values for each model; therefore including model selection uncertainty in the estimate of each param-
eter and its associated variance. We calculated the relative variable importance (Σwi) by summing the Akaike weights for all models containing the variable (Burnham & Anderson, 2002). Data analyses were undertaken with the STATA 8-2 statistical package (STATA Corp., College Station, TX, USA).

We generated species-area relationships (logS vs. logA and S vs. logA) for each functional group in order to assess differences in response to fragmentation. We estimated the potential sensitivity to fragmentation for species with known territory size estimates (hereafter, TSest) by comparing these estimates with the observed minimum forest patch size (FPSmin) in which a given species was encountered. We thereby define the ratio TSest/FPSmin as the patch-size sensitivity of a given species. We used non-metric multi-
dimensional scaling ordinations (NMDS; Clarke & Green, 1988) to investigate variation in species composition among sites, using the Bray–Curtis dissimilarity measure based on the presence/absence matrix.

Results

Community analysis

We recorded a total of 338 bird species (excluding nocturnal species, aerial insectivores and waterbirds) and species occupancy per forest patch varied between 31 and 224 species (mean ± sd = 100.5 ± 54.3; Table 1). Most of the species recorded were year-round residents with only four austral migrants and 13 partial austral migrants recorded (after Stotz et al., 1996). We recorded all five Brazilian endemics present in the region: Mierastor minutus, Psophia viridis, Automolus paraensis, Sakesphorus luctuosus and Rhegmatornitha gymnops, although S. luctuosus was under-
sampled as it is predominantly a fringe riparian forest species. Species richness per fragment increased over the entire range of observed fragment sizes in the Alta Floresta region, generating a highly robust overall species–area relationship (r² = 0.926, P < 0.001, n = 31; Fig. 2). Small forest patches retained far fewer species than large patches, and NMDS scores indicate that they were also more dissim-
lar from one another in overall assemblage composition. In
other words, avian assemblages converged in similarity with increasing forest patch size (Fig. 3).

**Life-history characteristics and guild responses**

Correlations between the number of occupied fragments and geographic range size, number of zoogeographic regions occupied, relative abundance, degree of primary forest dependence, number of habitats used and preferred vertical stratum were mostly significant, but never exceeded 0.63 (Table 2). The most important predictor variables retained in the best models (Table 3) were foraging stratum, body mass, relative population abundance, foraging guild, primary forest dependence and whether or not a species was an obligate mixed-species flock attendant.

Species–area curves differed when bird species were split into six different feeding guilds (see Table 1 and Fig. 4). Placed in decreasing order of sensitivity to forest fragmentation, the species guilds were as follows: small insectivores, frugivores, nectarivores, large insectivores, omnivores and granivores.

**Forest patch size and territory size**

Twenty of the 65 species (17 non-passerines and 48 passerines) for which we compiled territory size estimates occurred in fragments equal to or smaller than their average territory sizes (Fig. 5). Of these species, 12 were non-passerines (60%) and eight were passerines (40%). Terborgh et al. (1990) classified five of these as edge species (Monasa nigrifrons, Electron platyrhynchum, Momotus momota, Melanerpes cruentatus and Campylorhynchus turdinus) and a further three (Thamnophilus schistaceus, Thamnophilus aethiops and Myrmeciza hemimelaena) were classified as gap specialists (Wunderle, Willig & Henriques, 2005). The remainder of this subset of 20 species included a forest raptor Micrastur ruficollis, a nunbird Monasa morphea, four frugivores/omnivores Trogon viridis, Pteroglossus beaumariasi, Ramphastos tucanus and Ramphastos vitellinus, two large woodpeckers Celeus elegans and Camppephilus rubricollis, one woodcreeper Xiphorynchus elegans, one antbird Cercomacra cinerascens, one flycatcher Myiornis ecaudatus and one oriole Icterus cyaneus.

Comparisons of the degree of fragmentation sensitivity for those species with known territory size estimates reveal the idiosyncratic species for which there was a large discrepancy between the TS<sub>est</sub> and FPS<sub>min</sub> values (Fig. 5). Most species exhibiting a very low patch-size sensitivity were small

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**Table 1** Species richness and linear species–area relationships for six functional groups of bird species with varying dietary requirements occurring at the 31 forest sites surveyed (P<0.001 for all groups)

<table>
<thead>
<tr>
<th>Feeding guild</th>
<th>Total number of species</th>
<th>Range per patch</th>
<th>Mean (± se) per patch</th>
<th>R&lt;sup&gt;2&lt;/sup&gt;-value (semi-log linear regression)</th>
<th>Z-value (semi-log)</th>
<th>R&lt;sup&gt;2&lt;/sup&gt;-value (double-log linear regression)</th>
<th>Z-value (double-log)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Frugivore</td>
<td>30</td>
<td>1–23</td>
<td>12.95 (5.49)</td>
<td>0.752</td>
<td>4.239</td>
<td>0.592</td>
<td>0.229</td>
</tr>
<tr>
<td>Granivore</td>
<td>36</td>
<td>7–26</td>
<td>9.10 (5.78)</td>
<td>0.617</td>
<td>3.677</td>
<td>0.538</td>
<td>0.117</td>
</tr>
<tr>
<td>Nectarivore</td>
<td>16</td>
<td>1–12</td>
<td>5.25 (2.66)</td>
<td>0.814</td>
<td>2.134</td>
<td>0.702</td>
<td>0.182</td>
</tr>
<tr>
<td>Omnivore</td>
<td>45</td>
<td>3–29</td>
<td>14.34 (7.16)</td>
<td>0.682</td>
<td>5.228</td>
<td>0.628</td>
<td>0.162</td>
</tr>
<tr>
<td>Large insectivore</td>
<td>37</td>
<td>2–20</td>
<td>10.32 (4.48)</td>
<td>0.780</td>
<td>3.588</td>
<td>0.616</td>
<td>0.173</td>
</tr>
<tr>
<td>Small insectivore</td>
<td>153</td>
<td>2–96</td>
<td>39.43 (27.59)</td>
<td>0.822</td>
<td>22.126</td>
<td>0.653</td>
<td>0.315</td>
</tr>
<tr>
<td>All species</td>
<td>337</td>
<td>31–224</td>
<td>99.06 (54.78)</td>
<td>0.924</td>
<td>44.801</td>
<td>0.842</td>
<td>0.191</td>
</tr>
</tbody>
</table>
Table 2 Correlation coefficients* among ecological, behavioural and life-history traits for all species (n=338)

<table>
<thead>
<tr>
<th></th>
<th>ZOOR</th>
<th>MASS</th>
<th>ABUN</th>
<th>PRDE</th>
<th>NHAB</th>
<th>STRT</th>
<th>SENS</th>
</tr>
</thead>
<tbody>
<tr>
<td>NFRA</td>
<td>0.185</td>
<td>0.179</td>
<td>-0.408</td>
<td>0.193</td>
<td>0.229</td>
<td>0.120</td>
<td>-0.097</td>
</tr>
<tr>
<td>ZOOR</td>
<td>0.069</td>
<td>0.111</td>
<td>0.012</td>
<td>-0.301</td>
<td>-0.456</td>
<td>-0.191</td>
<td>0.423*</td>
</tr>
<tr>
<td>MASS</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>ABUN</td>
<td>-0.327</td>
<td>0.373</td>
<td>0.425</td>
<td>0.577**</td>
<td>0.577**</td>
<td>0.443**</td>
<td>0.423**</td>
</tr>
<tr>
<td>PRDE</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>NHAB</td>
<td>0.019</td>
<td>0.012</td>
<td>0.019</td>
<td>0.089</td>
<td>0.062</td>
<td></td>
<td></td>
</tr>
<tr>
<td>STRT</td>
<td>0.093</td>
<td>0.295</td>
<td>0.295</td>
<td>0.295</td>
<td>0.295</td>
<td>0.295</td>
<td>0.625**</td>
</tr>
</tbody>
</table>

*Significance levels.
**P<0.01.
log-transformed.
NSRA, number of patches in which a particular species was detected; MASS, log₁₀ mean mass of species [g]; ABUN, relative abundance of species; PRDE, degree of primary forest dependence; NHAB, number of habitats in which a species can persist; STRAT, preferred vertical foraging stratum; SENS, sensitivity to disturbance.

Table 3 Model weights from information-theoretic analysis of life-history characteristics* of birds in variably sized forest patches

<table>
<thead>
<tr>
<th>Variable</th>
<th>Σw₁</th>
<th>β</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sensitivity to disturbance</td>
<td>0.294</td>
<td>0.078</td>
</tr>
<tr>
<td>Foraging strata</td>
<td>0.997</td>
<td>0.729</td>
</tr>
<tr>
<td>Body mass</td>
<td>0.920</td>
<td>1.69</td>
</tr>
<tr>
<td>Relative abundance</td>
<td>1.00</td>
<td>-3.886</td>
</tr>
<tr>
<td>Obligate flock-followers</td>
<td>0.691</td>
<td>-1.541</td>
</tr>
<tr>
<td>Facultative flock-followers</td>
<td>0.050</td>
<td>0.204</td>
</tr>
<tr>
<td>Foraging guild</td>
<td>0.720</td>
<td>-0.170</td>
</tr>
<tr>
<td>Primary forest dependence</td>
<td>0.618</td>
<td>-0.579</td>
</tr>
<tr>
<td>Number of habitats</td>
<td>0.395</td>
<td>-0.154</td>
</tr>
<tr>
<td>Number of zoogeographic regions</td>
<td>0.343</td>
<td>-0.041</td>
</tr>
</tbody>
</table>

*Model weights from a total of 1023 possible models.
Σw₁ (Akaike weights) for all models with a given variable.

insectivores and many were foraging niche specialists such as mixed-species flock-followers. Conversely, species exhibiting a high patch-size sensitivity were typically large-bodied generalist and edge species. Although body mass was a significant predictor of TSEst (R² = 0.491, P<0.001, n = 64) it was not a significant predictor of FPSmin (R² = -0.013, P = 0.694, n = 64), and TSEst and FPSmin values were not correlated (r = -0.16, P = 0.898, n = 64).

Discussion

The ability to identify and classify those taxa at risk from the twin processes of habitat fragmentation and perturbation based on their ecological attributes is a powerful tool for conservation biologists because it enables a priori management decisions. This study clearly shows that individual species, guilds and families vary widely in their responses to habitat fragmentation. There is no evidence to suggest that differences in plant species and faunal composition between sites were due to pre-existing differences in floristic composition and soil types (see Michalski, Nishi & Peres, 2007). Virtually all differences in forest patch occupancy can therefore be attributed to a combination of differences in forest patch size and quality (Lees & Peres, 2006) and intrinsic life-history characteristics of bird species.

Species with low relative abundance and/or small geographical range have long been recognized as rare (Darwin, 1859; Preston, 1948), and therefore vulnerable to extinction (e.g. Purvis et al., 2000). Species that occur at naturally low abundances may be disadvantaged within a fragmented landscape because when isolated in fragments their populations are reduced in comparison to co-occurring species with higher abundance, rendering them more extinction-prone to environmental or demographic stochasticity (e.g. Diamond, Bishop & van Balen, 1987). A severe reduction in the species richness of terrestrial/understorey foragers, as observed in this study, is consistent with most tropical forest fragmentation studies (e.g. Newmark, 1991; Stratford & Stouffer, 1999). Understorey species are usually poorer dispersers and ground-nesting species are more vulnerable to elevated numbers of small predators in small fragments (mesopredator release) than canopy species. In the Alta Floresta landscape, the degree of primary forest dependence and the number of habitats used by different species are extremely important in structuring the avian communities in forest patches (Lees & Peres, 2006). For example, forest species that tolerated second-growth and scrub habitats (e.g. Piaya cayana) and open-country species that invaded forest edges (e.g. Crypturellus tataupa) occurred in a larger number of patches compared with either primary forest or open-habitat specialist species.

The fact that assemblages of large-bodied species in the smallest fragments sampled around Alta Floresta were more species-rich than those of small-bodied species may seem counter-intuitive at first, considering the plethora of studies suggesting that large-bodied taxa are more vulnerable to extinction (e.g. Gaston & Blackburn, 1995; Purvis et al., 2000). In contrast, Bennett & Owens (1997) found that large body size is associated with increased extinction risk in birds from human persecution and introduced predators but not from reduced niche availability. Small-bodied birds are more vulnerable to extinction from habitat loss (Owens & Bennett, 2000). Unlike many other parts of lowland

Amazonia, large-bodied gamebirds are not extensively hunted for food in the Alta Floresta region primarily because of the high availability of bovine meat. This leaves mid-sized frugivores such as *Columba* spp., *Pteroglossus* spp. and *Ramphastos* spp. and large seed predators (e.g. *Ara* spp. and *Amazona* spp.) largely unmolested while traplining forest patches and tracking fluctuating fruit and seed resources even in the smallest forest fragments. Similar resource-tracking behaviour has also been demonstrated by avian frugivores in natural fragments in Australia (Price, 2004). Larger birds were less reluctant to cross open-habitat gaps than smaller species (cf. Grubb & Doherty, 1999), perhaps principally because bird vulnerability to predation by raptors is size dependent (e.g. Götmark & Post, 1996). Large canopy frugivores are usually considered to be extinction-prone (e.g. Willis, 1979; Kattan, Alvarez-López & Giraldo, 1994) but within the Alta Floresta landscape most species in this guild were under negligible hunting pressure and have been able to persist in 72% of all forest patches even after three decades of relentless forest conversion and fragmentation.

The intolerance to habitat fragmentation of most small insectivores corroborates a wealth of previous research (e.g. Newmark, 1991; Stratford & Stouffer, 1999; Beier, Van Drielen & Kankam, 2002; Sekercioglu et al., 2002). These included obligate flock-following species (especially...
dead-leaf gleaning species), small terrestrial species and obligate followers of army ants (Eciton spp.). Larger insectivores were slightly less fragmentation sensitive, most likely because most species are better dispersers and solitary, and do not assiduously join mixed-species flocks, which can amplify the spatial requirements of some species (Powell, 1989). Granivores are often hyper-abundant in small fragments (e.g. Donoso, Grez & Simontelli, 2003) and many of the granivores recorded within small fragments around Alta Floresta were usually species associated with the open-habitat matrix (e.g. Volatinia jacarina). A total of 47% of the granivores in this study were psittacids, and although some species were restricted to extensive patches of forest (e.g. Pionites leucogaster), most species were highly vagile, matrix-tolerant and fragmentation insensitive. Omnivores were also over-represented in small fragments, a finding echoed by other studies (e.g. Bierregaard & Stouffer, 1997). In fact, dietary switching may allow them to persist in small patches even if they have low dispersal capabilities.

The relatively high persistence rate of many frugivores is likely related to their higher innate dispersal abilities, larger body size and canopy habits. However, although the overall density of frugivorous birds may not change markedly in fragments because of an apparent ‘density compensation’ effect from other species (MacArthur, Diamond & Kaur, 1972; Willis, 1979), the degree of fragmentation tolerance was far from uniform across all species. For instance, some frugivores examined in this study (e.g. Selenidera gouldii, Cotinga cayana, Pipra spp.) were highly sensitive to fragmentation. Understorey hummingbirds occurred in fragments of all size classes and the encounter rates of some species (e.g. Phaethornis ruber) were greater in small fragments than in the largest fragments and continuous forest sites, a pattern consistent with observations from the Biological Dynamics of Forest Fragmentation Project (BDFFP) north of Manaus, Brazil (Stouffer & Bierregaard, 1995). Likewise, we encountered many canopy hummingbirds in small fragments as these species were also able to exploit habitat edges (cf. Stouffer & Bierregaard, 1995) and frequently traversed the non-forest matrix (A. C. Lees, pers. obs.). However, despite the fragmentation-insensitive responses of some species, we still found a strong overall species-area relationship for hummingbirds (Fig. 4c), which is at odds with the BDFFP findings – likely because of the greater size range and much greater spatial isolation of our forest fragments in Alta Floresta from extensive tracts of undisturbed forest.

Species feeding on patchy and ephemeral resources would appear to be pre-adapted to fragmented landscapes as they undertake foraging movements on a regular basis within undisturbed forest (e.g. Fleming, Breitwich & Whitesides, 1987). It is therefore somewhat surprising to find some small insectivorous and facultatively solitary midstorey and understorey antbirds (e.g. T. aethiops) in fragments that are only 20% the size of their territories in a mature floodplain forest of western Amazonia (Terborgh et al., 1990). For example, a 2.1 ha forest patch had one pair each of T. aethiops, T. schistaceus, C. cinerascens and M. hemimelaena. Three possible hypotheses can be invoked to explain this observed high density: (1) such small populations are the ‘living dead’ relics of much larger populations and may be expected to become extinct in the near future (Tilman et al., 1994; Hanski & Ovaskainen, 2002); (2) such patches represent sink populations (sensu Pulliam, 1988) that regularly receive immigrants from nearby areas of continuous forest (the patch used in this example was only 440 m from nearby continuous forest); (3) such species are able to persist in small patches because of release from competition (Debinski & Holt, 2000) with other sympatric insectivores, particularly resulting from the local extinction of mixed-species understorey flock attendants. The fact that this particular fragment has been isolated for at least 8 years (with some

reduction in size) and that similar-sized patches that were
more isolated retained fewer small insectivores suggests that
isolation, and thus hypothesis (2), may be more important.
This reinforces previous studies suggesting that patterns of
patch occupancy are primarily limited by dispersal opportun-
ties rather than by changes in the invertebrate prey-base
caused by fragmentation and edge effects (Sekercioglu et al.,
2002).
In order to better understand the importance of isolation,
 Further territory mapping in forest fragments and control
sites is required. The observation that minimum area re-
quirements of forest bird species were not correlated with
their observed minimum patch-size thresholds suggests that
such communities primarily comprise species that can either
 use multiple patches and/or the non-forest matrix, rather
than species whose minimum area requirements can be met
by the size of the remaining forest patches. Different species
therefore perceive the landscape differently – as fragmented,
variegated or continuous – depending on their life-history
characteristics and this ultimately determines the patterns of
patch occupancy in this heterogeneous landscape. This
supports the ‘continuum model’ of habitat use (Linden-
mayer, McIntyre & Fischer, 2003; Fischer & Lindenmayer,
2006), which recognizes large discrepancies between differ-
ent species’ ecological requirements – and especially the
value of landscape heterogeneity for biodiversity conserva-
tion. A deeper understanding of the relationships between
species life-history traits and habitat loss and fragmentation
can assist in the selection of which taxa to monitor as an
indicator species, and inform conservation planning deci-
sions. In the expanding deforestation frontier of Amazonia,
trade-offs should be considered between acquiring large
forest reserves to consolidate large patches of contiguous
habitat and improving the hostile matrix to re-establish
functional and (preferably) structural connectivity.

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