Long-Term Landscape Change and Bird Abundance in Amazonian Rainforest Fragments

PHILIP C. STOUFFER, *† RICHARD O. BIERREGAARD JR., *‡ CHERYL STRONG, *§ AND THOMAS E. LOVEJOY*††

*Biological Dynamics of Forest Fragments Project, Instituto Nacional de Pesquisas da Amazônia, CP 478, Manaus, AM 69011–0970, Brazil
†School of Renewable Natural Resources, RNR 227, Louisiana State University, and Louisiana State University Agriculture Center, Baton Rouge, LA 70803–6202, U.S.A., email pstouffer@lsu.edu
‡Biology Department, University of North Carolina, Charlotte, NC 28223, U.S.A.
§San Francisco Bay Bird Observatory, PO Box 247, Alviso, CA 95002, U.S.A.

Abstract: The rainforests of the Amazon basin are being cut by humans at a rate >20,000 km²/year, leading to smaller and more isolated patches of forest, with remaining fragments often in the range of 1–100 ha. We analyzed samples of understory birds collected over 20 years from a standardized mist-netting program in 1- to 100-ha rainforest fragments in a dynamic Amazonian landscape near Manaus, Brazil. Across bird guilds, the condition of second growth immediately surrounding fragments was often as important as fragment size or local forest cover in explaining variation in abundance. Some fragments surrounded by 100 m of open pasture showed reductions in insectivorous bird abundance of over 95%, even in landscapes dominated by continuous forest and old second growth. These extreme reductions may be typical throughout Amazonia in small (<10 ha), isolated fragments of rainforest. Abundance for some guilds returned to pre-isolation levels in 10- and 100-ha fragments connected to continuous forest by 20-year-old second growth. Our results show that the consequences of Amazonian forest loss cannot be accurately described without explicit consideration of vegetation dynamics in matrix habitat. Any dichotomous classification of the landscape into “forest” and “nonforest” misses essential information about the matrix.

Keywords: fragmentation, matrix effects, patch size effects, landscape effects, Neotropical birds, bird communities, secondary forest

Conservación a Largo Plazo en el Paisaje y la Abundancia de Aves en Fragmentos de Bosque Lluvioso en la Amazonía

Resumen: Los bosques lluviosos en la cuenca del Amazonas están siendo talados por humanos a una tasa de >20,000 km²/año, provocando que los parches sean más pequeños y aislados, con fragmentos remanentes en el rango de 1-100ha. Analizamos muestras de aves de sotobosque recolectadas durante más de 20 años en un programa estandarizado de colocación de redes de niebla en fragmentos de bosque lluvioso de 1- a 100ha en un paisaje Amazónico dinámico cerca de Manaus, Brasil. En los gremios de aves, la condición de vegetación secundaria que rodea a los fragmentos a menudo fue tan importante como el tamaño del fragmento o la cobertura forestal local para explicar la variación en abundancia. Algunos fragmentos rodeados por 100 m de pastizal abierto mostraron reducciones de más de 95% en la abundancia de aves insectívoras, aun en paisajes dominados por bosque continuo y vegetación secundaria madura. Estas reducciones extremas pueden ser típicas en la Amazonia en fragmentos de bosque lluvioso pequeños (<10 ha) y aislados. La abundancia de algunos gremios retornó a niveles pre-aislamiento en fragmentos de 10- y 100- ha conectados a bosque continuo por vegetación secundaria de 20 años. Nuestros resultados muestran que las consecuencias de la pérdida de bosques en la Amazonía no pueden ser descritas con precisión sin considerar explícitamente a la

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The future of Amazonian biodiversity depends on the amount of forest remaining and on how rainforest organisms respond to degradation, particularly loss of primary rainforest. Analysis of remote sensing data shows that the present rate of Amazon deforestation is >20,000 km²/year (Fearnside 2005). The pace of Amazon degradation has fluctuated somewhat, and will respond to development programs of the Brazilian government (Laurance et al. 2004; Fearnside 2005; Young 2005). Under some scenarios, disturbance could reach two-thirds of the Brazilian Amazon within the next 15 years. Reduction in forest cover inevitably leads to smaller and more isolated patches of forest (Fahrig 2003). In Amazonia, the process of anthropogenic disturbance typically leads to patches in the 1–100-ha range (Gascon et al. 2000; Peres 2000).

Conceptual advances have modified our view of how habitat loss affects species in the habitat fragments that remain. Early research, extended from studies of actual islands, emphasized area effects (Galli et al. 1976; Willis 1979). Although many studies continue to be published based only on analysis of fragment area, other factors have been shown to be important for explaining population or community patterns in fragments. Consideration of time since isolation illustrates that biotic responses do not occur instantaneously when fragments are isolated (Brooks et al. 1999; Ferraz et al. 2003). Landscape-level analyses have led to the suggestion that fragment size by itself may have little to do with the species present in the fragments; rather, patterns at the patch scale may be driven by the amount of habitat lost at the landscape scale (Fahrig 2003). Despite these advances in the temporal and spatial context in which fragments are viewed, many researchers continue to limit their studies because they consider the matrix surrounding fragments as a homogeneous and static component of the landscape (Lindenmayer et al. 2003).

When matrix habitat has been included in analyses of fragments, it has often helped to explain results from fragments. Matrix habitat may facilitate movement among patches by acting as a corridor of habitat that is at least suitable for travel (Rosenberg et al. 1997). Although corridors remain difficult to define, most researchers examine remnants that make direct connections between patches.
clustered in groups of two or three that had comparable landscape histories. Minimal disturbance occurred around four fragments, where trees were cut but the resulting debris was abandoned, a result most comparable to logging. Regeneration occurred rapidly, leading to an overstory of Cecropia sciadophylla Mart. within a few years. At seven other fragments, the areas around the fragments were burned and used as cattle pastures, although one fragment was partially surrounded by abandoned, unburned matrix. Depending on the intensity of grazing, the matrix gradually regenerated into patchy scrub dominated by Vismia spp. In later years, the fragments were reisolated by burning or cutting, either by farmers reestablishing pasture or by the BDFFP. The BDFFP cleared the matrix explicitly to maintain the isolation of the fragments, generally by cutting a band of 50–100 m (see Gascon and Bierregaard [2001] for more information on the history of the fragments).

We present results of long-term bird sampling in this dynamic Amazonian landscape. The landscape setting of our fragments allowed us to distinguish among the effects of fragment size, time since isolation, forest configuration in the local landscape, and second-growth (matrix) dynamics in determining bird abundance over a 20-year period.

Methods

Sampling

Sampling began in fragments before the fragments were isolated. In all cases, mist nets (NEBBA type ATX, 36-mm mesh, 12 x 2 m) were set up in lines along established trails, with the bottom of the net at ground level. The number of nets differed among fragments. In 1-ha fragments, only eight nets could be accommodated in a single line. In 10-ha fragments, we used 16 nets in a single line. In 100-ha fragments, we used three lines of 16 nets each. We netted each line for 1 day at a time, always beginning at 0600 and continuing until 1400 hours, unless heavy rains forced us to close the nets. Intervals between samples varied over the years. From 1979 through 1992, sites were generally sampled at intervals of at least 6 weeks, although fragments were often sampled more often for about 1 year before and after isolation. No sampling was done between 1993 and July 2000. In July 2000, the original protocol was resumed until May 2001.

Our site exhibited the tropical pattern of high species richness and low abundance of individual species. As a result, individual species could have been undetected in mist net samples, with detection probability varying among species (Ferraz et al. 2003). Rather than attempting to analyze individual species, we analyzed social or foraging guilds following guild assignments used in previous publications from the BDFFP (e.g., Stouffer & Bierregaard 1995a; Stouffer & Borges 2001; see Supplementary Material, below). We discarded raptors, kingfishers, and large ground omnivores, such as tinamous and cracids. These species are either rare or cannot be reliably sampled with mist nets. We also excluded Geotrygon montana, the only common migratory species in the understory (Stouffer & Bierregaard 1995). We divided the remaining birds into four broad guilds: nonforest species, strict insectivores, frugivores/omnivores, and hummingbirds. Nonforest species included any understory species absent inside but present outside unbroken forest, regardless of foraging guild (Cohn-Haft et al. 1997).

We subdivided insectivores into seven guilds. The 35 most common species in the presiation sample were divided among six guilds: obligate army-ant followers; obligate mixed-species flock participants; flock dropouts (species that could be found in most flocks but also occurred outside of flocks, especially in fragments); gap specialists; terrestrial species (species that forage while walking); and arboreal species (a loose collection of species that forage off the ground). The seventh insectivore guild, “other insectivores,” were forest insectivores not among the 35 most common species in the presiation sample. This guild includes both rare understory species, such as Phaeothlypis rivularis, and common midstory species that seldom descend to net level, such as Tolmomyias assimilis. We included these rarely netted species to allow us to examine whether the loss of commonly captured understory species was accompanied by an increase in capture rate by less-common species, either through behavioral shifts to use the understory or through numerical increase.

We subdivided frugivores/omnivores into nine species that regularly occur in the understory (core frugivores) and other frugivores. Other frugivores were generally midstory and canopy species that seldom descend to net level.

Our measure of bird abundance was capture rate/1000 mist-net hours in each fragment, excluding same-day recaptures. Capture rate normalizes unequal sampling effort among fragments. Capture rate should be considered a measure of bird activity in the lower understory and compared within guilds across time and fragments, rather than interpreted as a measure of absolute abundance.

Statistical Analyses

in each fragment. Because some fragments had been sampled for years before isolation, we truncated their preisolation samples to approximately 1 year. The only exception was one fragment that was only sampled three times before isolation. Time series analyses for each guild followed methods from our analyses of the data through 1992 (Stouffer & Bierregaard 1995a, 1995b; Stouffer & Borges 2001). We used repeated-measures analysis of variance (ANOVA), with fragment size as a categorical main effect. Time (preisolation, 1991–1992 [hereafter 1992], or 2000–2001 [hereafter 2001]) and its interaction with fragment size were analyzed as within-fragment effects, with \( p \) values adjusted according to the value of the Huynh–Feldt epsilon (Stevens 1990). In these analyses we log-transformed capture rate to reduce the correlation between variance and mean within samples.

Second, we used 44 bird-netting samples from the 11 fragments in an information-theoretic analysis to evaluate variables leading to variation among samples after isolation (Burnham & Anderson 2002). The information-theoretic approach allows independent evaluation of alternative models and inferences from multiple candidate models (Anderson et al. 2000; Burnham & Anderson 2002). We delimited the samples for the information-theoretic analysis by at least 5 days of netting in a 1-year interval, except for six samples with 1–3 days of netting. We also limited the samples to periods for which unambiguous landscape data were available (see below). The time period included in the samples began 1 year after isolation and continued through 2001. We did not include the first year after isolation, because of the brief spike in bird captures immediately after isolation (Bierregaard & Lovejoy 1989). The borders of some fragments were cleared one or more times out to a distance of 50–100 m. We defined samples so that border clearing always occurred between sample periods, not within them. These border-clearing events led to the six samples with \(<4\) days of netting.

We calculated values for seven fragment or landscape variables for each sample. We included three variables intrinsic to the fragment (fragment size, fragment age, and tree mortality rate), two variables related to the second-growth surrounding the fragment (age of the second growth along the fragment’s border and maximum age of any path to continuous forest), and two variables from the neighboring continuous forest (amount of continuous forest within 800 m of the fragment, and minimum distance of continuous forest to the fragment). We chose 800 m because this distance maximized the variance among fragments. Furthermore, forest cover within this distance is important for birds in fragments (Graham & Blake 2001; Bender et al. 2003).

We calculated values of the variables for second growth and continuous forest from satellite images provided by the BDFFP (available at the BDFFP Web site: www.pdbff.inpa.gov.br) and by M. Antongiovanni da Fonseca and E. Martins Vinticinque (both formerly at the BDFFP GIS lab). We also used fragment histories (from the BDFFP Web site) and personal observations to determine the history of the landscape around each fragment. The satellite images clearly distinguished fragments and continuous forest from second growth. The images also unambiguously showed areas that had been cut within about 1 year. The timing of these clearing events could also be corroborated with records at the BDFFP. After determining when cutting occurred, we could then track the area’s age through subsequent satellite images until it was cleared again. We used ArcView 3.3 with the Image Analysis (ESRI, Redlands, California; www.esri.com) and X-tools extensions (Oregon Department of Forestry, Salem, Oregon; www.odf.state.or.us) to calculate continuous forest area within 800 m and nearest distance to continuous forest. The information-theoretic analyses required the same data set for each model, so we chose samples to avoid missing data. The exception was tree mortality (data for permanent plots provided by W. Lauerance), which was never measured in fragments 1112 or 1207. For samples from these fragments, we substituted mean mortality for fragments of the same size and age.

In the information-theoretic analysis, we treated each sample independently, using all possible maximum-likelihood least-squares models with the seven independent variables as continuous predictors of capture rate (127 total models). We evaluated models based on their information content, as measured by Akaike’s information criterion for small samples (AIC\(_c\)), which balances the fit of a maximum-likelihood least-squares model [\(\log(L)\)] against the number of estimable parameters in the model (K). Multimodel inference (Burnham & Anderson 2002) from these information-theoretic analyses revealed how fragment size, time, and landscape changes interact to affect fragment biota over a 20-year period. Multimodel inference requires data from all possible candidate models, meaning we had to include models that seemed unlikely (Burnham & Anderson 2002). This process is not multivariate fishing; by using all possible models, we put all variables on equal footing to calculate relative variable weights (Burnham & Anderson 2002). We log-transformed fragment size but used untransformed linear values for all other variables. We used untransformed predictors and capture rates because we wanted linear parameter estimates for the predictor variables. We were not interested in parameter estimates for fragment size, because this was the only variable that remained static for each fragment over the course of the study. We used reduced sets of models to calculate slopes and unbiased standard errors (Burnham & Anderson 2002). We chose the confidence set of models with the cutoff of \(\Delta\text{AIC}_c<6\) because the best model is approximately 20 times as likely as a model with \(\Delta\text{AIC}_c = 6\).
Figure 1. Capture rates of understory birds in Amazonian forest fragments (hexagons, 100 ha; squares, 10 ha; triangles, 1 ha) in three time periods grouped by social or foraging guilds (a–l). Significant fragment size (S), year (Y), and interactive (S × Y) effects are from repeated-measures analysis of variance (*p < 0.05; **p < 0.01; ***p < 0.001). The x-axis is the same for all guilds (see j–l).

Results

Time Series Analysis

Capture rates of birds varied dramatically among fragments over time (Fig. 1). Among 12 guilds, 8 showed significant fragment-size effects, year effects, or interactions (Table 1). For example, in 1992, mean capture rates of all insectivores were only 16% of the mean preisolation rate in 1-ha fragments, 26% in 10-ha fragments, and 62% in 100-ha fragments. By 2001, however, capture rates increased for most guilds. The recovery was not equal across guilds or across fragments, even among fragments of the same size. For example, ant followers, flocking insectivores, and terrestrial insectivores were completely absent from at least one fragment in 2000, despite their mean increase across fragments between 1992 and 2000.

Table 1. Repeated-measures analysis of variance results (F and adjusted p values) for all bird guilds examined in rainforest fragments.

<table>
<thead>
<tr>
<th>Guild</th>
<th>Size F2,8</th>
<th>p</th>
<th>Time F2,16</th>
<th>p</th>
<th>Size × time F4,16</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>All insectivores</td>
<td>3.95</td>
<td>0.0642</td>
<td>24.16</td>
<td>0.0001</td>
<td>3.20</td>
<td>0.0465</td>
</tr>
<tr>
<td>ant followers</td>
<td>3.33</td>
<td>0.0889</td>
<td>14.98</td>
<td>0.0002</td>
<td>4.01</td>
<td>0.0194</td>
</tr>
<tr>
<td>arboreal insectivores</td>
<td>4.12</td>
<td>0.0589</td>
<td>11.86</td>
<td>0.007</td>
<td>2.20</td>
<td>0.0115</td>
</tr>
<tr>
<td>flock obligates</td>
<td>5.70</td>
<td>0.0289</td>
<td>15.62</td>
<td>0.0002</td>
<td>6.47</td>
<td>0.0027</td>
</tr>
<tr>
<td>flock dropouts</td>
<td>1.24</td>
<td>0.34</td>
<td>5.65</td>
<td>0.0139</td>
<td>1.50</td>
<td>0.25</td>
</tr>
<tr>
<td>gap specialists</td>
<td>0.95</td>
<td>0.425</td>
<td>2.26</td>
<td>0.140</td>
<td>1.51</td>
<td>0.25</td>
</tr>
<tr>
<td>terrestrial</td>
<td>4.55</td>
<td>0.0479</td>
<td>74.97</td>
<td>0.0001</td>
<td>11.09</td>
<td>0.0002</td>
</tr>
<tr>
<td>other insectivores</td>
<td>2.24</td>
<td>0.169</td>
<td>3.04</td>
<td>0.0759</td>
<td>1.56</td>
<td>0.233</td>
</tr>
<tr>
<td>All frugivores</td>
<td>3.04</td>
<td>0.104</td>
<td>6.16</td>
<td>0.0111</td>
<td>3.44</td>
<td>0.0545</td>
</tr>
<tr>
<td>core frugivores</td>
<td>4.81</td>
<td>0.0426</td>
<td>4.89</td>
<td>0.022</td>
<td>2.61</td>
<td>0.0745</td>
</tr>
<tr>
<td>other frugivores</td>
<td>1.65</td>
<td>0.251</td>
<td>0.47</td>
<td>0.634</td>
<td>0.65</td>
<td>0.633</td>
</tr>
<tr>
<td>Hummingbirds</td>
<td>1.86</td>
<td>0.2167</td>
<td>3.54</td>
<td>0.0534</td>
<td>0.75</td>
<td>0.5712</td>
</tr>
</tbody>
</table>
Nonforest species did not invade the fragments. Because these species were absent from most samples, the guild had too many zero values for parametric analysis. These species reached maximum capture rates of 11.4 in 1992 and 9.0 in 2001. These maxima were both in 1-ha fragments, where net lines began within 10 m of the border. These species were seldom netted inside larger fragments, where net lines began farther from the edge. Among forest species, we have no evidence for a general increase in use of the lower understory in fragments by birds that generally occur at higher strata or are otherwise uncommon in continuous forest (other insectivores and other frugivores in Fig. 1). These results demonstrate that the overall changes in understory bird abundance were driven by forest understory insectivores and, to a lesser extent, forest understory frugivores (Fig. 1).

Information-Theoretic Analysis

Capture rates among the 44 postisolation samples varied by over an order of magnitude for some guilds, even among fragments of the same size (Fig. 2). From these samples, guilds with significant long-term variation in the time series analysis (Fig. 1, Table 1) were included in the information-theoretic analysis.

For each guild, the confidence set of models with $\Delta$AIC$_{c}$ < 6 included at least 17 models, with all possible variables always included in the candidate models (Tables 2 and 3). This suggests that bird abundance over the 20 years of sampling responded to the interactions of the fragment and the temporal dynamics of the surrounding landscape. Considering the most informative models for each guild, size alone (the model capture rate $= \text{fragment size}$) was generally uninformative. This simple model was well supported ($\Delta$AIC$_{c}$ < 4) for only one guild, terrestrial insectivores.

Because we used all possible candidate models, we were able to calculate unbiased Akaike weights ($w_i$) for each variable based on the sum of the weights of all models in which the variable appeared, regardless of the other variables included in each of those models. This process begins by ranking the models by their information content, in this case AIC$_{c}$ scores (Table 3). From this, the $w_i$ for each model is calculated. $\sum w_i = 1.0$ across all 127 models, but will accumulate rapidly among the most informative models. In the example of flock insectivores (Table 3), the 24 models in the confidence set reached $\sum w_i = 0.89$, with $\sum w_i > 0.5$ for the six best models. The $w_i$ for any given model may be summed for all variables included in the model. In the example, size was included in all of the models shown, so $\sum w_i$ for size was equal to $\sum w_i$ for all models. Border age was included in all but four of the models shown, so its $\sum w_i$ was slightly less than $\sum w_i$ for all models. Because each variable was included in an equal number of models, variables with high $\sum w_i$ were included in better models than were variables with low $\sum w_i$. Had a simple model (such as capture rate = fragment size) been far more informative than alternatives, multimodel inference would not be needed to interpret the pattern (Burnham & Anderson 2002), but only multimodel inference can describe the pattern in our data.

Following our initial information-theoretic analysis, we tried to reduce the number of models in the analysis (Anderson & Burnham 2002) by including only the variables that were more informative than fragment size, either alone or in combination with fragment size. This approach allowed us to eliminate one to three variables for each guild, reducing the number of models to 15–63, but did not strongly alter the variable weights. We included the full set of models for each guild so we could present the analysis and the results more directly.

Among the eight guilds, fragment size and age of the second growth on the border of the fragment were consistently the most important variables (Table 2). Fragment size was weighted >0.95 for five guilds, and border age was weighted >0.95 for two guilds and >0.8 for an additional three guilds. No other variable was weighted >0.85 for any guild. Distance to continuous forest was marginally the most highly weighted variable for core frugivores (0.85 vs. 0.84 for border age), the only guild for which a variable other than fragment size or border age was most highly weighted. Despite the overwhelming importance of fragment size and border age, every other variable had an intermediate weight (0.4–0.8) for at least one guild.

Slope estimates from the information-theoretic analyses provide measures of the effects of landscape variables, which can be used to describe how landscape dynamics influence birds (Table 2). Each year of growth of the
Table 2. Model weights and parameter (slope) estimates from information-theoretic analysis of bird guilds with significant long-term responses to time since isolation of fragment size × time since isolation in Table 1.

<table>
<thead>
<tr>
<th>Guild</th>
<th>Number of models</th>
<th>Fragment size [\Sigma w_i]^a</th>
<th>Fragment age [\Sigma w_i]</th>
<th>Tree mortality [\Sigma w_i]</th>
<th>Border age [\Sigma w_i]</th>
<th>Second-growth age [\Sigma w_i]</th>
<th>Distance to forest [\Sigma w_i]</th>
<th>Amount of forest [\Sigma w_i]</th>
</tr>
</thead>
<tbody>
<tr>
<td>Insectivores</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>all</td>
<td>25</td>
<td>0.98</td>
<td>0.36</td>
<td>0.21</td>
<td>0.96</td>
<td>3.66 ± 1.18</td>
<td>0.39</td>
<td>0.24</td>
</tr>
<tr>
<td>ant followers</td>
<td>31</td>
<td>0.85</td>
<td>0.64</td>
<td>0.47 ± 0.25</td>
<td>0.22</td>
<td>0.99</td>
<td>1.17 ± 0.77</td>
<td>0.39</td>
</tr>
<tr>
<td>arboreal</td>
<td>41</td>
<td>0.79</td>
<td>0.27</td>
<td>0.35</td>
<td>0.81</td>
<td>0.89 ± 0.40</td>
<td>0.29</td>
<td>0.54</td>
</tr>
<tr>
<td>flock obligations</td>
<td>24</td>
<td>1.00</td>
<td>0.25</td>
<td>0.23</td>
<td>0.89</td>
<td>1.15 ± 0.43</td>
<td>0.42</td>
<td>0.22</td>
</tr>
<tr>
<td>flock dropouts</td>
<td>67</td>
<td>0.24</td>
<td>0.24</td>
<td>0.46</td>
<td>0.65</td>
<td>0.65 ± 0.34</td>
<td>0.38</td>
<td>0.64</td>
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<tr>
<td>flock terrestrial</td>
<td>41</td>
<td>1.00</td>
<td>0.29</td>
<td>0.25</td>
<td>0.41</td>
<td>0.29</td>
<td>0.64</td>
<td>0.26</td>
</tr>
<tr>
<td>Frugivores</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>all</td>
<td>23</td>
<td>0.98</td>
<td>0.64</td>
<td>0.70 ± 0.34</td>
<td>0.20</td>
<td>0.78</td>
<td>0.98 ± 0.44</td>
<td>0.51</td>
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<tr>
<td>core</td>
<td>17</td>
<td>0.99</td>
<td>0.42</td>
<td>0.20</td>
<td>0.84</td>
<td>1.00 ± 0.42</td>
<td>0.76</td>
<td>0.99 ± 0.42</td>
</tr>
</tbody>
</table>

^a Key to column heads: fragments size, log of fragment size (ha); fragment age, time since isolation (years); tree mortality, mean annual mortality rate for all permanent plots within the fragment; border age, age of second growth immediately (50–100 m) surrounding the fragment (years); second-growth age, maximum age of any direct path to continuous forest (years); distance to forest, minimum distance from any point in the fragment to continuous forest (100 m); amount of forest, total amount of continuous forest within 800 m of the fragment (1000 m²).

^b Confidence set of models with ΔAICc < 6.

^c The \[\Sigma w_i\] (Akaike weights) for all models with a given variable.

^d Slope ± SE for variables with \[\Sigma w_i\] > 0.5. Response is captures/1000 mist-net hours.
Table 3. Example (for mixed-species of flock insectivores) of a confidence set of models for capture rate, ranked by increasing $\Delta AIC_c$.

<table>
<thead>
<tr>
<th>Model</th>
<th>log($L$)</th>
<th>$K$</th>
<th>$AIC_c$</th>
<th>$\Delta AIC_c$</th>
<th>$w_i$</th>
<th>$\sum w_i$</th>
<th>fragment size (fs)</th>
<th>border age (ba)</th>
<th>second-growth age (sg)</th>
<th>amount of forest (af)</th>
<th>fragment age (fa)</th>
<th>tree mortality (tm)</th>
<th>distance to forest (df)</th>
</tr>
</thead>
<tbody>
<tr>
<td>fs ba</td>
<td>333.3</td>
<td>4</td>
<td>342.4</td>
<td>0.0</td>
<td>0.197</td>
<td>0.197</td>
<td>0.197</td>
<td>0.197</td>
<td>0.000</td>
<td>0.000</td>
<td>0.000</td>
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second-growth surrounding the fragment increased the capture rate of insectivores by 3.66 ± 1.18, or about 2% of the preisolation rate. Ant followers increased by about 3% of their preisolation rate, and core frugivores by 4% of their preisolation rate, with each year of growth around the fragment. Conversely, increasing the distance to continuous forest by just 100 m reduced capture rate by 6.47 ± 3.38 for arboreal insectivores and by 2.44 ± 1.3 for terrestrial insectivores. For both of these guilds, this reduction was >13% of the preisolation rate for every 100 m added between fragment and forest.

Discussion

Our results demonstrate that bird capture rates in these fragments are not due simply to fragment size or dynamics within the fragments, even in combination with forest cover in the landscape. Distance to continuous forest or amount of continuous forest influenced capture rates in fragments, but second-growth variables, particularly border age, were generally more informative (Table 2). Bird abundance in the fragments was neither a simple nor a threshold function of the overall amount of forest in the local landscape (Fahrig 2002, 2005), because capture rates varied enormously despite little influence of the continuous forest variables in this heavily forested area. Certainly we expect that reduction in forest cover throughout the landscape of the fragments would eventually lead to permanent extinction in the fragments, but we also know that fragments can be devoid of birds without extreme forest loss in the landscape (e.g., Fig. 2). For some guilds, the larger landscape was rendered inconsequential by the isolation imposed by several hundred meters of open pasture.

Slope estimates for landscape variables (Table 2) cannot be extended linearly in space and time beyond this study, but they suggest that fragments isolated from continuous forest by even a few kilometers of open space without regenerating second growth would have greatly reduced bird abundance for the major guilds of understory birds. We hypothesize that these conditions would lead to capture rates of forest birds even below the minimum we found in our landscape, which were already as low as 5% of mean preisolation capture rates for insectivores and frugivores (Fig. 2). On the other hand, fragments surrounded by developing second growth and within 1 km of continuous forest would be expected to follow a trajectory of increasing abundance for most guilds, as we saw between 1992 and 2001 (Fig. 1).

The increases in abundance we observed between 1992 and 2001 occurred despite continued structural deterioration of the fragments (Laurence et al. 1997, 2002). Tree mortality was never a highly weighted variable in our analysis, suggesting that birds respond more strongly to area, matrix, and landscape effects. Graham and Blake (2001) reached a similar conclusion after analyzing bird abundance and vegetation structure in a Mexican rainforest.

Previously, we pointed out a strong effect of matrix structure on recolonization by birds (Stouffer & Bierregaard 1995a). Second growth dominated by *C. sciadophylla*, which occurs when cut areas are not burned, was traversed sooner than second growth dominated by *Vismia* spp., which typically follows burning and pasture abandonment (Mesquita et al. 2001). We did not include this variable in the present analysis, because the design became unwieldy owing to multiple disturbances in the matrix at most fragments. Furthermore, our observations suggest that the difference between the two types of second growth, at least for bird movements, becomes less pronounced after about 10 years of growth (Borges & Stouffer 1999). Several fragments with high bird abundance in 2001 were connected to continuous forest by 10- to 20-year-old *Vismia*. This result leads to the encouraging prediction that even abandoned cattle pastures can sometimes develop second growth suitable for bird movements. In general, birds appear to increase their use of any second growth as it ages, probably allowing them to move among forest patches and incorporate matrix into territories centered in fragments. The strong border effects reinforce the observation that even a narrow deforested strip can impede movements, effectively isolating a fragment for many species (Develey & Stouffer 2001; Launce et al. 2004; Launce & Gomez 2005).

Important differences among guilds illustrate variation in response to landscape change (Fig. 1, Table 2). Flock dropout insectivores, gap specialists, and hummingbirds are relatively unaffected by fragmentation (see also Stouffer & Bierregaard 1995a, 1995b; Antongiovanni & Metzger 2005). These species appear to use second growth, allowing them both to recolonize fragments and to expand activity beyond fragments into second growth, thus reducing fragment size effects (e.g., Tubelis et al. 2004). Ant followers require large areas (Willson 2004) but move readily through second growth to reach small fragments, as do army ants (Stouffer & Bierregaard 1995a; Blake & Loiselle 2001). Frugivores show strong fragment size effects but also appear to increase in abundance as the second-growth ages and increase in fragments in response to the amount of forest in the local landscape. Frugivore guilds may include species that readily use second growth, which allows them to move through the entire landscape (e.g., *Mionectes macconnelli*), and species that are relatively restricted to mature forest (e.g., *Turdus albicollis*; Bierregaard & Stouffer 1997). At the other extreme, terrestrial insectivores are sensitive to area effects and have the slowest recovery as border ages. Some of these species may be persisting in fragments, rather than recolonizing, accounting for the strong area effect (Stratford & Stouffer 1999; see also Robinson 1999; Blake &
Loiselle 2001). This guild has been repeatedly shown to be extremely sensitive to fragmentation (e.g., Stouffer & Bierregaard 1995a; Renjifo 2001). Similarly, the strong area effects on flocking insectivores probably relates to their requirement of ∼10 ha of mature forest for flock territories (Develey & Stouffer 2001), although they occur at relatively high densities in 100-ha fragments

Understanding the effects of landscape change on forest biota has been hampered by landscape variation among fragments that can be difficult for researchers to control. For example, small fragments typically occur in less-forested landscapes than larger fragments, confounding fragment size effects with effects of forest loss in the landscape (Fahrig 2003). In fact, studies accounting for both effects suggest that landscape effects contribute more to fragment biota than do fragment size effects (Fahrig 2003). Our results show strong effects of fragmentation per se because fragment size consistently provided the most heavily weighted variable for explaining bird capture rates, even for fragments adjacent to each other (Table 2). We believe this pattern in fragmented landscapes may be typical of birds in Amazonia, where most birds are nonmigratory, have large area requirements, and have strict habitat requirements (Terborgh et al. 1990; P.C.S., unpublished data).

Regardless of the role of fragment size or forest cover, our observation that the temporal variation in bird capture rates within and among fragments was driven by changes in the matrix suggests that fragmentation analyses based on landscapes divided into only forest and non-forest may be missing important information, especially in systems with dynamic second growth (Stouffer & Bierregaard 1995a; Blake & Loiselle 2001; Ricketts 2001). Although some studies at relatively small spatial scales have considered matrix effects explicitly (e.g., Sisk et al. 1997; Ricketts 2001; Tubelis et al. 2004), even the most sophisticated spatial analyses of bird abundance at large scales generally categorize habitat as only forest or nonforest (e.g., Donovan & Flather 2002). We suggest that research at the landscape level should explicitly include matrix structure and dynamics whenever possible (Lindenmayer & Franklin 2002).

Our guild-based analyses leave many open questions about the vulnerability of individual species and about the ramifications of variation in bird abundance to community function. An analysis of individual species through 1992 showed that species richness had declined across fragments through about the first 10 years after isolation (Ferraz et al. 2003). We now know that overall bird abundance increased in many fragments between 10 and 20 years after isolation (Fig. 1). Even so, some species went extinct in that interval (P.C.S., C.S., and L.N. Naka, unpublished data), and the overall pattern of species richness has not been examined. We have no quantitative data on the effects of fragmentation on canopy species, except that these species do not drop into the understory in fragments. Our observations suggest that vagile canopy species such as parrots move readily across the BDFFP landscape, whereas other species, especially small insectivores and omnivores, do not. Differences among species in area and habitat requirements, vagility, and metapopulation structure certainly influence persistence and re-colonization (Sisk et al. 1997; Renjifo 2001; Vandermeer & Carvajal 2001). More detailed demographic and dispersion data for individual species (Terborgh et al. 1990; Robinson et al. 2000) would allow better modeling of landscape effects on selected species (e.g., Donovan & Flather 2002). Similarly, more information on interactions between birds and their food, including fruits and arthropods (Şekercioğlu et al. 2002), would likely demonstrate ecological consequences of reduced abundance of understory birds in isolated fragments (e.g., Silva & Tabarelli 2000; Cordeiro & Howe 2003; Şekercioğlu et al. 2004).

The BDFFP fragments represent an unusual situation in the Amazon-protected fragments near continuous forest in a largely regenerating second-growth landscape. More typically, fragments become increasingly isolated (Skole & Tucker 1993; Imbernon & Branthomme 2001), and second growth returns only after agricultural activities are abandoned (Moran et al. 1994). Matrix habitat generally includes roads, homesteads, pastures, and other land uses that would be less conducive to movements of forest birds than the abandoned pastures or logged forests we studied. Accessible forest, such as most typical fragments, also often suffers effects of logging, fire, and hunting (Nepstad et al. 1999; Laurance & Cochrane 2001; Sodhi et al. 2004). These differences between our study sites and typical anthropogenic fragments lead us to the unfortunate conclusion that the conditions favoring high bird abundance rarely will be met in fragments in degraded areas of the Amazon (Laurance et al. 2001). Understory bird abundance in isolated fragments should show a downward trajectory, regardless of the proximity of continuous forest. One simple conservation implication emerges from our results: permitting second growth to reconnect fragments back to continuous forest may be the only way for understory birds to persist in small fragments in Amazonia. Management directed at matrix reforestation should produce positive results for birds in fragments if an uninterrupted path connects small fragments to larger forest patches.

Acknowledgments

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Supplementary Material

The following supplementary material is available as part of the online article from http://www.blackwell-synergy.com: Table S1. Guild assignments of species included in

Literature Cited


