BIODIVERSITY RESEARCH

Twenty years of understorey bird extinctions from Amazonian rain forest fragments: consistent trends and landscape-mediated dynamics

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ABSTRACT

Aim We analysed presence/absence data for understorey bird species in rain forest fragments sampled from 1979 through 2001. Here we consider extinctions between 1992, when most fragments had been isolated for at least 8 years, and 2001. Our objectives were to determine whether high extinction rates documented soon after isolation continued through up to 20 years after isolation, and to examine fragment size and landscape effects on extinction.

Location Biological Dynamics of Forest Fragments Project, near Manaus, Brazil.

Methods Through 1992, birds were surveyed with standardized mist net sampling in ten 1- to 100-ha fragments. We repeated the mist net protocol in 2000–01. We also added remote taping of the dawn chorus and tape playback surveys for species captured in 1991–92 but not in 2000–01.

Results Between 1992 and 2001, 37 species went extinct in at least one fragment. As expected, extinction rate decreased with increasing fragment size. Over 30% of species went extinct in 1-ha fragments, compared to about 5% in 100-ha fragments. Extinction followed a predictable pattern: most species lost from 100-ha fragments between 1992 and 2001 had already gone extinct in smaller fragments before 1992. Despite extinctions, fragments gained species between 1992 and 2001, apparently due to species moving through the developing second growth matrix. Fragments surrounded by old second growth had lower extinction rates than predicted based on fragment size alone.

Main conclusions Sequential extinctions occurred for at least 20 years. Some additional species previously lost from smaller fragments may continue to go extinct in 100-ha fragments. At the same time, species assemblages in 1- and 10-ha fragments mostly reflect second-growth dynamics by 20 years after isolation. High species loss predicted from the first few years after isolation has not occurred, almost certainly because of recolonization.

Keywords
Amazonia, bird communities, extinction, forest fragmentation, landscape dynamics, rain forest, rescue effect.

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INTRODUCTION

From of the earliest studies of bird communities in forest fragments, an area effect on species richness has been documented (e.g. Galli et al., 1976; reviewed in Ewers & Didham, 2006). This relationship can be viewed as a manifestation of the same processes that lead to the familiar species–area relationship on islands (MacArthur & Wilson, 1967), but with the complicating effects of surrounding landscape composition and dynamics (Ewers & Didham, 2006; Kupfer et al., 2006). Obviously, understanding how many species, and which species, can be supported in a fragment of a given size has fundamental importance for conservation planning.

Following isolation, classical island biogeography predicts that the number of species in a fragment should relax to a new equilibrium determined by the fragment's area and degree of

isolation (MacArthur & Wilson, 1967). This perspective assumes that fragments behave like actual islands. For fragments, matrix dynamics also play a pivotal role in determining community structure (Ewers & Didham, 2006). A completely deforested matrix may function much like a water barrier, seriously impeding immigration of birds into fragments, and reducing the probability of immigrants rescuing small populations (*sensu* Brown & Kodric-Brown, 1977). On the other hand, developed second growth allows species to recolonize small fragments, and to have territories that include fragments and second growth (e.g. Stouffer *et al.*, 2006; Sekercioglu *et al.*, 2007). Development of second growth is generally associated with increasing species richness in fragments (e.g. Stouffer & Bierregaard, 1995a; Renjifo, 2001). Colonization of fragments by forest specialist species appears to be facilitated as second growth develops, although not all species respond equally (Renjifo, 2001; Castellon & Sieving, 2006; Stouffer *et al.*, 2006).

In most studies, actual loss of species from fragments cannot be determined directly because fragments were not surveyed repeatedly. Instead, species present in larger fragments but absent in smaller fragments are assumed to have been lost from the smaller fragments. A weakness of this approach is that it can confuse extinct species with species that were not in the fragment at the time of isolation. Both area effects and isolation effects influence the number of species present (e.g. Stratford & Stouffer, 1999; Ferraz *et al.*, 2007).

Extinctions have been documented directly at several Neotropical sites. An exceptionally long record of species loss comes from Barro Colorado Island, Panama (BCI), a hilltop that has been surveyed repeatedly since it became an island after construction of the Panama Canal between 1911 and 1914. At BCI, forest interior species continue to be lost, including those that apparently persisted through the 1960s (Robinson, 1999). Over 40 years, La Selva, Costa Rica, has also seen the disappearance or drastic population reduction of some forest bird species, even though the lowland peninsula of rain forest remains connected to a large middle-elevation reserve (Sigel *et al.*, 2006; Sigel, 2007; chapter 3).

The Biological Dynamics of Forest Fragments Project

The Biological Dynamics of Forest Fragments Project (BDFFP), a *terra firme* forest site near Manaus, Brazil (2°30′ S, 60° W), also provides long-term history of species present in forest fragments. Eleven continuous forest plots were sampled and then isolated as 1- ($n = 5$), 10- ($n = 4$) and 100-ha ($n = 2$) fragments beginning in 1980 (Gascon & Bierregaard, 2001 provide details of the site selection and isolation processes).

The most consistently collected data on birds at the BDFFP come from a standardized mist netting program that began in 1979. Capture data suggest an area-dependent loss of species from these fragments through about the first 12 years after isolation (Ferraz *et al.*, 2003). Unfortunately, these capture data can only be used directly for species that are reliably captured if they are present. For most species, detection probability needs to be explicitly considered to allow interpretation of the netting results (Ferraz *et al.*, 2003).

Ferraz *et al.* (2003) modelled species loss from the fragments from isolation through 1992 under four scenarios for patterns of population decay and potential for recolonization. From these scenarios, they calculated t_{50}, the time to lose half the species originally present. Their first method, the minimum, assumed that 'species are immediately extinct following their last capture and never return.' Their second method, the Bayesian decay, considered population decay to extinction species-by-species. Their third method, the runs test, used the capture sequence for each species within each fragment to calculate the probability that the species was actually absent when it was not detected. These three methods all modelled species going extinct only once; that is, recolonization was not included. False absences following the last capture were permitted for the Bayesian and runs-test methods. The three methods produced similar results, with rapid loss of species and a continued decline through 1992. The Bayesian method was also used to predict extinctions beyond the 1992 sampling, and showed a continuing trajectory of extinction for every fragment. A fourth method, the jackknife, used annual estimates of species richness based only on species captured during the various sampling days within that year. Thus, the estimated number of species in a year was independent of the calculations from the preceding year, and could potentially increase due to recolonization. Like the other methods, for every fragment the jackknife estimate showed species loss following isolation. Unlike the other methods, it showed stable or even increasing species richness by 1992.

Here we consider local extinctions in the BDFFP fragments by comparing species captured during extensive netting in 1991–92, at the conclusion of the sample included in Ferraz *et al.* (2003), with species present in 2000–01. The later sample includes mist-net results as well as analysis of remote audio recordings and field surveys including tape playback for species that were not netted. Because of this comprehensive sampling effort, we are confident that the species we determined to be absent in 2000–01 were not simply overlooked.

Objectives

Our objectives were to document local extinctions that occurred at the BDFFP fragments between the 1991–92 and 2000–01 samples, and to examine how patterns of species loss varied among fragments. We also wanted to compare our empirical results with the patterns predicted by Ferraz *et al.* (2003). More specifically, we asked the following questions grouped into three general categories. First, how many species from 1992 were still present in 2000–01? Which species detected in 1991–92 were not detected in 2000–01? Did the 2000–01 communities show a pattern of ongoing decay, as predicted from the first three models of Ferraz *et al.* (2003), or did species richness equilibrate due to reduced extinction rate or recolonization, following the jackknife estimates of Ferraz *et al.* (2003)? Second, how did extinction differ among fragments? Did the absolute number or proportion of species that went extinct differ among fragment size classes? Were species lost from smaller fragments also lost from larger fragments? Had the species lost from larger fragments between

1992 and 2001 already gone extinct in smaller fragments before 1992? Third, in addition to effects of fragment size, can variation in extinctions among fragments be explained by variation in matrix structure or other landscape effects?

METHODS

Mist net samples come from lines of eight or 16 nets (NEBBA type ATX, 36-mm mesh, 12 × 2 m) set up along established trails through the interior of fragments, as well as from lines of four nets along four sides of each fragment. Each line was netted for 1 day at a time from 0600 to 1400 h. In the 1991–92 sample (hereafter '1992'), each fragment was sampled eight times, usually with a 1- to 2-month interval between samples. In 2000–01 (hereafter '2001'), each fragment was sampled six times, also at about a 1- to 2-month interval between samples. No mist net sampling was done from 1993 through 1999. To look for extinctions before the 1992 sample, we use capture data collected with the same protocol between 1979 and 1990, usually including regular sampling for about a year before and after isolation. Before 1991, these samples did not include nets on fragment borders. We include data from 10 of the 11 BDFFP fragments; one of the 1-ha fragments (2107) had incomplete sampling in 1992.

The major weakness of mist net sampling for determining presence of bird species is that birds are not detected until they are captured, but capture probability differs among species (e.g. Blake & Loiselle, 2001). Thus, we cannot reliably say whether differences among samples result from local extinctions or colonizations, or simply from failure to capture species. We compensated for this problem in the 2001 data by using two other methods to detect species that were not captured during the mist net sampling. First, we made a 1-h passive tape recording of the dawn chorus for most days of netting ($n = 70$ days), from which we made a list of species heard. Species identification on recordings was facilitated by comparison with Naka et al. (2008). We recorded with a Sony TCM-5000 tape recorder (Sony Corporation of America, New York, NY, USA) and a Sennheiser ME62 omnidirectional microphone (Sennheiser GmbH & Co. KG, Wedemark, Germany). We mounted the microphone about 1 m off the ground, directed upwards. In 10- and 100-ha fragments we changed the location of the recording on each day of netting, with the apparatus always 30–500 m from an edge. In 1-ha fragments the recordings were made from the central part of the fragment. Especially in 1-ha fragments, the recordings probably included birds outside the fragment, but for our analysis of forest birds we assume that any birds potentially tape recorded from nearby second growth were also using the fragment.

Second, we defined the potentially overlooked species in each fragment as those that were netted in 1992 but not in 2001. After we completed the mist-net sampling in 2001, we used tape playback surveys to search each fragment for missing species (e.g. Stratford & Stouffer, 1999). We searched for missing species over multiple visits for about a week in each fragment. LNN and PCS conducted these searches between July 2001 and January 2002. We did not consider a bird to be absent until we had searched for it with playback. Thus we did as much as we could to insure that

the species we did not detect were actually absent in 2001. Our approach represents an attempt to increase sampling effort targeted at specific species rather than trying to estimate probability of occurrence with analytical tools (e.g. MacKenzie et al., 2005). Obviously, we cannot say that presence in both 1992 and 2001 means continuous occupation during the entire period.

We used an information-theoretic approach to examine the effects of landscape variation among fragments on extinctions between 1992 and 2001. Based on a previous analysis of bird communities in the fragments (Stouffer et al., 2006), we considered the following variables for each fragment: distance from the forest to continuous forest (distance to forest); age of second growth bordering the fragment to a distance of at least 50 m in 2000 (border age) and age of second growth in a broader area of matrix 50–1000 m beyond the fragment (matrix age). We considered four models to explain the proportion of species that went extinct between 1992 and 2001. One model used fragment size as a categorical predictor. Three models used distance to forest, border age and matrix age each as linear predictors. For each model, we calculated the maximum-likelihood sum of squares and the Akaike Information Criterion for small samples (AICc). We ordered the AICc values to calculate the differences between the best model and each of the others (ΔAICc) and calculate Akaike weights (ω) and evidence ratios for each model (see Anderson & Burnham, 2002; Burnham & Anderson, 2002). We only examined the 1- and 10-ha fragments because so few species went extinct in the two 100-ha fragments (see Results).

We report results only for forest species (as defined in Cohn-Haft et al., 1997). We also exclude raptors, kingfishers, migrants and large ground foragers. These species formed a minimal proportion of the net captures, and would have been difficult to survey by other techniques. We regularly captured hummingbirds, but we were reluctant to assume that our surveys were adequate to demonstrate their absence, so we include hummingbirds only when we list the species known to persist in fragments.

RESULTS

Our netting samples for analysis included 90 forest species in 1992 and 93 species in 2001. Despite two fewer samples/fragment in 2001, a pairwise test revealed more species/fragment in 2001 (Fig. 1; Wilcoxon signed-rank test, $n = 10$ fragments, $S = 20.5$, $P = 0.037$). Even with stable or increasing species richness in the net samples between 1992 and 2001, all fragments lost some species between the two samples. Of the forest birds we considered, 37 species were not detected in 2001 in at least one fragment where they had occurred in 1992 (Table 1). Five species went extinct in two fragments, but only *Cyanocompsa cyanoides* was lost from three fragments. Our surveys following the netting were essential for sampling species absent from the net sample. From the surveys and passive tape recordings, we found species in all but one fragment that were absent from the 2001 net sample but had been present in 1992. On average, of the species netted in 1992 but not in 2001, we added back 3.7 additional species/fragment with our playback and remote taping surveys. Without augmenting the net sampling, these species would have
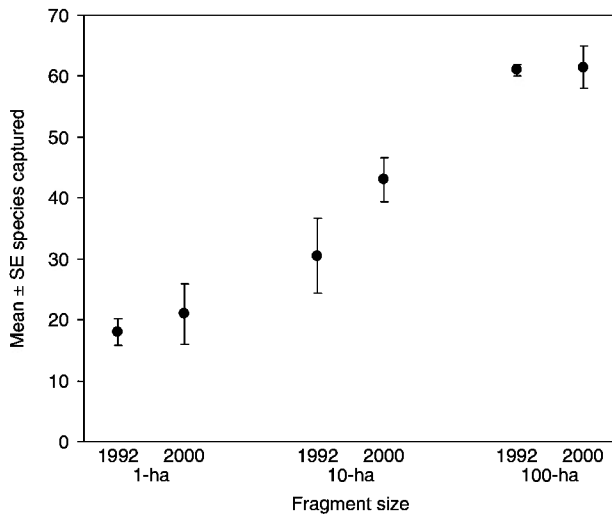
Figure 1 Mean ± standard error (SE) number of species captured in 1992 and 2001 ($n = 4$ 1-ha fragments, $n = 4$ 10-ha fragments, $n = 2$ 100-ha fragments).
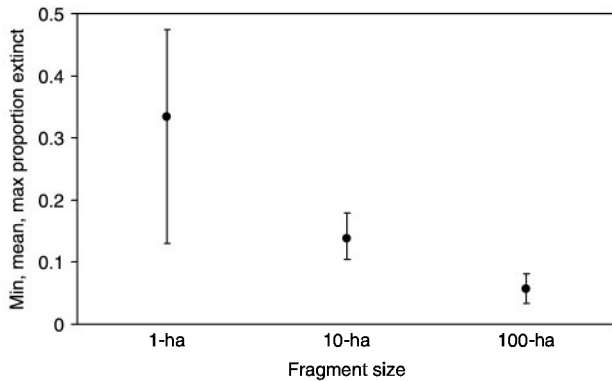

Figure 2 Mean, minimum and maximum proportion of species captured in 1992 that were not detected in 2001 ($n = 4$ 1-ha fragments, $n = 4$ 10-ha fragments, $n = 2$ 100-ha fragments).

mistakenly been considered to have gone extinct between 1992 and 2001.

As expected, smaller fragments lost more species than larger fragments (Table 1). Two to three times as many species went extinct in 1- and 10-ha fragments as in 100-ha fragments. Because the number of species detected in 1992 increased with fragment size, the proportion of species that disappeared differed even more dramatically among size classes, varying from 3 to 8% in the two 100-ha fragments to nearly 50% in one of the 1-ha fragments (Fig. 2). We found significant heterogeneity in the proportion of species that went extinct for all pairwise comparisons of fragment size classes (all $G > 3.9$, d.f. = 1, $P < 0.046$).

We considered whether the species that disappeared from at least one fragment were also lost from other fragments. In this analysis, we only used species that were present in 1992 and disappeared from at least one fragment by 2001. We then considered these species in 2001 across all fragments where they were

present in 1992 (Table 2). Many of the species lost from 1-ha fragments between 1992 and 2001 were present in 10- and 100-ha fragments in 2001, so they could be considered in this analysis. For these species, local extinction occurred 81% of the time in 1-ha fragments, but only 13% of the time in 10-ha fragments, and never in 100-ha fragments. For species that went extinct in 10-ha fragments, extinction rate dropped from 56% in 10-ha fragments to 5% in 100-ha fragments. Species that went extinct in 10-ha fragments between 1992 and 2001 were only present six times in 1-ha fragments in 1992, but they went extinct in 50% of these occasions by 2001.

The six species lost from 100-ha fragments between 1992 and 2001 were mostly absent from smaller fragments in 1992 (Table 1). From netting data collected before 1992, we asked if these species had ever been recorded in the smaller fragments, and had gone extinct before 1992. These species had been collectively recorded 11 times in 10-ha fragments and 14 times in 1-ha fragments before the 1992 sample. Only one occurrence of these species was recorded in 1- and 10-ha fragments in 1992. Thus of 25 possible extinctions, 24 (96%) had already occurred before the 1992 sample. The species lost from 10-ha fragments between 1992 and 2001 fared slightly better than the species lost from 100-ha fragments. These 15 species had been recorded 35 times in 1-ha fragments before 1992, but only six times in the 1992 sample, for an extinction rate of 83%. Some of these species could have been present but eluded capture in 1992, so these estimates are probably slightly inflated. Despite variation in sampling intensity, the long-term data show a sequential pattern of extinction for many species, with local extinction proceeding from smallest to largest fragments.

Only a small suite of species consistently persisted in fragments of all sizes, based on the net sample from 1992 and the net sample plus surveys in 2001 (Table 3). Five species occurred in all fragments in both samples. Another six species were absent from only one or two fragments in each sampling period. None of the species in Table 3 were absent from a 100-ha fragment in either period. Even among these ubiquitous species, two extinctions were recorded between 1992 and 2001 in 1-ha fragments (*Myrmotherula axillaris* and *Tachyphonus surinamus*). This list also includes hummingbirds, which were excluded from previous analyses.

This analysis does not represent a complete list of species persisting, as it does not include species that were not netted in 1992. For example, the canopy vireonid *Cyclarhis gujanensis* was detected by voice in all fragments in 2001, but was only captured in four fragments in 1992. At the same time, the list in Table 3 accurately represents the few species that regularly occur in the understorey.

The best model explaining proportion of species extinct was fragment size alone ($\omega = 0.640$), but border age also had some support (ΔAICc = 1.5, $\omega = 0.30$, evidence = 2.1). These results can be interpreted as indicating that fragment size was 2.1 times more likely to be the best model (of those tested) than was border age. The other two models had less support (ΔAICc > 5.8, $\omega < 0.04$, evidence > 18). *A posteriori* we also considered a model with both fragment size and border age, but this model had less support than either of the univariate models (ΔAIC = 3.1).

Table 1 Species captured in 1992 that were lost from at least one fragment in 2001. For each fragment size, the 1992 column shows the number of fragments where the species was captured in 1992, and the 2001 column shows how many of the fragments where the species was captured in 1992 still contained the species in 2001. Empty cells indicate that the species was not captured in that size fragment in 1992, and therefore was not considered in 2001. Taxonomy follows Remsen *et al.* (2008).

Species	1-ha fragments		10-ha fragments		100-ha fragments		Total extinctions
	1992	2001	1992	2001	1992	2001	
Piaya melanogaster			1	0			1
Notharclus tectus			1	0			1
Malacoptila fucsa			2	1	2	2	1
Galbula albirostris	1	1	2	1	2	2	1
Dendrocincla fuliginosa	2	1	4	4	2	2	1
Deconychura longicauda	1	0	1	1	2	2	1
Sittasomus griseicapillus	1	0	1	1	1	1	1
Dendrocolaptes picumnus	1	0					1
Lepidocolaptes albolineatus			1	0			1
Synallaxis rutilans			1	0	2	1	2
Xenops minutus	1	0			2	2	1
Sclerurus rufigularis			2	1	2	2	1
Frederickena viridis			2	1	2	2	1
Myrmotherula guttata					2	1	1
Myrmotherula axillaris	3	2	3	3	2	2	1
Myrmotherula menetriesii	1	0			2	2	1
Schistocichla leucostigma	1	0	1	1	2	2	1
Pithys albifrons	2	1	1	1	2	2	1
Hylophylax naevius	1	0					1
Dichropogon poecilinotus	1	1	4	3	2	2	1
Formicarius analis					2	0	2
Hylopezus macularius					2	1	1
Rhynchocyclus olivaceus			2	1	2	2	1
Platyrinchus saturatus	1	0	2	1	2	2	2
Terenotriccus erythrurus	1	0	3	2	1	1	2
Laniocera hypopyrra	1	0	1	0			2
Pachyramphus marginatus	1	0					1
Tyraneutes virescens	1	0					1
Microcerculus bambla	1	1	2	1	2	2	1
Vireo olivaceus	1	0					1
Arremon taciturnus	1	0					1
Saltator grossus	1	0					1
Cyanocompsa cyanoides	3	0	3	3	2	2	3
Tachyphonus cristatus					2	1	1
Tachyphonus surinamus	2	1	4	4	2	2	1
Cyanerpes caeruleus			1	0			1
Phaeothlypis rivularis					2	1	1
Total species lost		20		15		6	37

Despite the equivocal results of the analysis, for both 1- and 10-ha fragments, the fragment surrounded by the oldest border had the lowest extinction rate (Fig. 3). For the 1-ha fragment surrounded by 17-year-old second growth, the proportion of species that went extinct was comparable to the 10-ha fragments, and about one-third of what we found in the 1-ha fragments were surrounded by 0- to 6-year-old second growth. The two fragments surrounded by 17-year-old second growth also had the highest number of species netted within their size class.

DISCUSSION

The bird species present in the BDFFP fragments remained in flux through 20 years after isolation. Species went extinct in every fragment between 1992 and 2001. During the same period, all fragments also gained species, and the total number of species in most fragments increased or remained constant (Fig. 1). Unfortunately, our sampling cannot directly show whether the putative colonizations were species present but undetected in

Table 2 Proportion of potential extinctions that actually occurred. Extinctions are analysed by fragment size based on the data in Table 1: the first line considers only the species that went extinct in 1-ha fragments; the second line considers only the species that went extinct in 10-ha fragments and the third line considers only species that went extinct in 100-ha fragments (although some species may be considered multiple times if they went extinct in multiple size classes). The cells indicate the proportion and possible number of extinctions for that group of species. For example, the species that went extinct in 1-ha fragments had 27 potential extinctions in 1-ha fragments, and went extinct 81% of the time. Those same species had 24 potential extinctions in 10-ha fragments, but went extinct only three times (13%). These species had 22 possible extinctions in 100-ha fragments, but never went extinct.

	Proportion (possible) extinctions		
Species that went extinct in:	1 ha	10 ha	100 ha
1 ha	0.81 (27)	0.13 (24)	0.00 (22)
10 ha	0.50 (6)	0.56 (27)	0.05 (19)
100 ha	– (0)	1.0 (1)	0.67 (12)

Table 3 Species that occurred in at least eight of 10 fragments in both 1992 and 2001.

	Fragments detected	
Species	1992	2000
Glyphorynchus spirurus	10	10
Thamnophilus murinus	10	10
Mionectes macconnelli	10	10
Pipra pipra	10	10
Phaethornis superciliosus	10	10
Phaethornis bourcieri	10	9
Thalurania furcata	9	8
Hypocnemis cantator	8	10
Percnostola rufifrons	8	10
Myrmotherula axillaris	8	9
Tachyphonus surinamus	8	9

1992, so we emphasize the extinctions. Because of our extensive surveys with multiple techniques, we are confident that the species we report to be absent were indeed absent, rather than simply undetected (possible exceptions include *Piaya melanogaster* and *Platyrinchus saturatus*, two inconspicuous species that seldom vocalize).

Comparison with predictions

How do these empirical results compare with the estimates and predictions of Ferraz *et al.* (2003) for the same fragments? Clearly, the three models that included no recolonization did not match the data; extinctions appeared to be generally balanced by
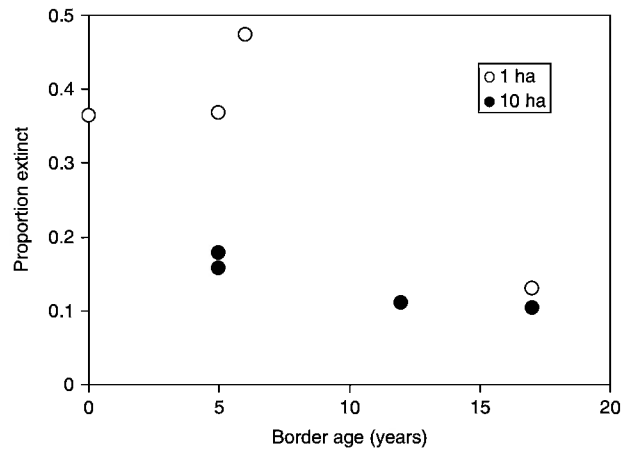

Figure 3 Border age in 2000 and proportion of species that went extinct between 1992 and 2001.

recolonization between 1992 and 2001 (Fig. 1). The minimum model showed the lowest number of species in 1992. It also showed an ongoing downward trend that was particularly pronounced in one of the 100-ha fragments, which was estimated to have < 30 species by 1992. As suggested by Ferraz *et al.* (2003), this model represents an extreme case as a lower bound on extinctions. Its failure implicates recolonization as an important driver of species richness in fragments. The Bayesian decay and runs test models gave very similar results through 1992, generally showing a parallel trend to the minimum model, but with more species at any given time. Only the Bayesian decay model was used to predict species richness beyond 1992. Bayesian decay seemed to match our results best for 1-ha fragments, showing most species to already be lost by 1992, but with a relatively flat trajectory at that point and beyond. For 10-ha and especially 100-ha fragments, this method predicted a continued strong decline in species that did not match our empirical data. For example, the 10-ha fragments were all expected to have 20–35 species by 1996, but we netted an average of over 40 species per fragment in 2001. These models represent an improvement over the minimum model, as they accounted for imperfect detection. Even so, recolonization apparently reversed the trend these models implied.

The jackknife estimates, which did not assume a decay in the number of species from year to year, and therefore permit recolonization, best match the pattern we observed. These estimates were generally stable or increasing (but with large confidence intervals) by 1992. Our data also suggest that the number of species in the fragments had stopped declining by 1992. The loss in species immediately after isolation generally matches the t_{50} predictions from the jackknife and other models for 1- and 10-ha fragments, but even the jackknife t_{50} overestimated the rate of extinction in 100-ha fragments. We suspect that this is because the landscape became increasingly favourable for recolonization over time as second growth developed in the matrix surrounding the fragments (see Landscape effects).

Fragment size effects

Extinctions in the fragments followed a predictable pattern based on fragment size. The rate of extinction, as proportion of species lost, varied inversely with fragment size, from about 6% in the two 100-ha fragments to 47% in one of the 1-ha fragments (Fig. 2). The sequence of species lost also followed a pattern. The species that disappeared from 100-ha fragments between 1992 and 2001 had mostly already been lost from smaller fragments before 1992. For example, about 95% of the species that disappeared from 100-ha fragments between 1992 and 2001 were already absent from 1-ha fragments by 1992. These species had been detected in the 1-ha fragments after isolation, but were quickly lost. Of the species present in both larger and smaller fragments in 1992, species that disappeared from larger fragments also tended to disappear from smaller fragments (Table 2).

Species lost from all fragment size classes reflect the species available to be lost based on the 1992 surveys. In 1-ha fragments, these include a collection of forest specialists that would be unlikely to persist in small fragments, such as the large woodcreeper *Dendrocolaptes picumnus,* the mixed-species flock species *Deconychura longicauda, Xenops minutus* and *Myrmotherula menetriesii*, and the streamside specialist *Schistocichla leucostigma* (ecological classifications from Cohn-Haft *et al.*, 1997). Species that went extinct in 1-ha fragments also include more generalist species found in second growth and along edges, and thus expected to occur in small fragments, such as *Dendrocincla fuliginosa, Vireo olivaceus* and *Saltator grossus.* In contrast, 10-ha fragments contained more forest specialist species in 1992, and most of the species lost were forest interior insectivores, such as *Malacoptila fusca, Sclerurus rufigularis* and *Dichropogon poecilinotus.* In 100-ha fragments, species lost were nearly all terrestrial insectivores (see also Comparison with other Neotropical sites).

Netting data and our surveys revealed a consistent core group of 11 forest species present in nearly all fragments (Table 3). These species made up about 50% of the understorey species detected in the most species-poor 1-ha fragments, where fewer than 20 species were netted (Fig. 1). Three of these species, *Thamnophilus murinus, Hypocnemis cantator* and *Percnostola rufifrons*, prefer edges and gaps and are among the most commonly netted species in second growth (Borges & Stouffer, 1999). Altered physical structure of fragments, with increased tree mortality and increased abundance of lianas (e.g. Laurance *et al.*, 2001), probably provides suitable habitat for them, and may also increase the abundance of understorey fruits consumed by the omnivores *Pipra pipra* and *Mionectes macconnelli*, also among the most commonly netted species in second growth (e.g. Levey, 1988). The three hummingbirds had been shown to be generally unaffected by fragmentation at the PDBFF through 1993 (Stouffer & Bierregaard, 1995b). *Glyphorhynchus spirurus* may be the most common species in undisturbed forest at our sites, with territories as small as 4–5 ha (Philip C. Stouffer, unpublished data). These modest space requirements, perhaps coupled with the lack of competition, apparently allow it to persist in even isolated 1-ha fragments. Low sensitivity to area was also identified by Ferraz *et al.* (2007) for some of the persistent

species, although at least one species, *Tachyphonus surinamus*, showed high sensitivity to area in that analysis and probably persisted due to its low vulnerability to isolation. These persistent species all use relatively young second growth, so movements of birds through matrix probably rescues the small populations in the fragments (Borges, 1995; Borges & Stouffer, 1999).

Landscape effects

In addition to the strong effect of fragment size, variation in landscape context among fragments appeared to have some influence on the rate of extinction, with fragments bordered by older second growth losing fewer species (Fig. 3). Higher extinction rates were recorded in the fragments where the borders were cleared between our samples (borders < 7 years old in Fig. 2) than in the fragments where the borders grew without additional disturbance (borders > 7 years old). The weak effect of border cutting is somewhat surprising, given the strong influence of local landscape effects on overall bird abundance and species composition in the fragments (Stouffer & Bierregaard, 1995a; Stouffer *et al.*, 2006). We suspect that part of the difference may also be due to logistical constraints in our 2001 sampling. The borders around four fragments were cut between when the net sampling began and when we surveyed for species absent from the net sample. We used the border age at the time sampling began, but recognize that the landscape was manipulated within our sample. At the same time, the lack of strong landscape effects on extinction, despite strong effects on abundance (Stouffer *et al.*, 2006), may reveal that the number of species can be decoupled from overall abundance. Abundance may depend on birds moving in and out of the fragment through second growth, while the number of species detected at least once may depend on persistence or recolonization, including rare events. For example, we know that the common army ant follower *Pithys albifrons* disappears from fragments isolated by open pasture or young second growth (Stouffer & Bierregaard, 1995b). Despite this pronounced and consistent pattern, however, *Pithys albifrons* did occur in one well-isolated 1-ha fragment in our sample, based on a single, surprising, capture.

Data from the two fragments with the most favourable conditions for recolonization suggest landscape context affects extinctions. The second growth surrounding fragments 1112 (1 ha) and 1207 (10 ha) has not been cut since the fragments were isolated in 1983. The proportion of species that went extinct in 1112, 13%, was less than half that of any other 1-ha fragment, and was lower than the mean proportion in 10-ha fragments (Fig. 2). Moreover, this fragment had the highest number of species netted in a 1-ha fragment in 1992 and in 2001. The proportion of species that went extinct in 1207 was comparable to the mean for other 10-ha fragments, but it also had the most species netted in both 1992 and 2001.

Ferraz *et al.* (2007) attempted to disentangle the effects of area and isolation for the birds of the BDFFP. Of the 12 species that went extinct in our sample that were also included in their species-by-species analysis (their fig. 4), nearly all were identified as being highly sensitive to area. On the other hand, fewer than

half of the species that went extinct in our sample were identified as being highly vulnerable to isolation. The species that were most vulnerable to isolation, according to Ferraz *et al.* (2007), had generally already gone extinct by 1992, at least in 1- and 10-ha fragments. We suggest that this pattern further implicates extinction/recolonization dynamics rather than just vulnerability to isolation as driving species richness 20 years after isolation.

Comparison with other Neotropical sites

Species loss from the BDFFP fragments shares some patterns with other Neotropical sites for which comparable data are available. As at BCI, we observed the rate of species loss to decline over time (Robinson, 1999). Similarly, as predicted by classical island biogeography, extinctions at the BDFFP and BCI were balanced somewhat by colonizations (or recolonizations). The inverse relationship we observed between extinction rate and fragment size demonstrates greater turnover in smaller fragments, a result also shown from repeated sampling in Costa Rican fragments (Borgella & Gavin, 2005). Another consistent trend among sites with repeated surveys is the loss or decline of terrestrial insectivorous species in particular and forest insectivores in general (Willis, 1974; Sieving, 1992; Kattan *et al.*, 1994; Robinson, 1999; Sigel *et al.*, 2006). For example, of the six species lost from 100-ha fragments (Table 1), all but *Tachyphonus cristatus* are insectivores that forage either on the ground or on the lowest vegetation stratum. These species had already been lost from smaller fragments, and other members of this guild had already been lost from 100-ha fragments by 1995 (Stratford & Stouffer, 1999). We should point out, however, that our sampling does not include the entire community, so we do not mean to imply that other guilds suggested to be vulnerable in other studies (e.g. large frugivores) would not also be vulnerable at the BDFFP.

The presence of a distinct set of extinction-resistant species at the BDFFP differed from results on islands created by construction of Lago Guri, Venezuela (Terborgh *et al.*, 1997; Feeley, 2003). Those islands showed that no species shared among all islands, either among 12 islands surveyed 7 years after isolation (Terborgh *et al.*, 1997) or among 26 islands surveyed about 14 years after isolation (Feeley, 2003). In the later sample, only three species occurred on even half the islands. We agree with Feeley (2003) that the communities on the Guri islands appear to be largely structured by extinction processes. We suggest that the difference between those true islands and the BDFFP fragments reflects the presence of a second growth matrix that permits recolonization more readily than the water barriers surrounding the Guri islands. Feeley (2003) found little evidence for interspecific competition structuring the Guri communities; it remains to be seen if competition acts more strongly in our system, where recolonization permits more interactions.

CONCLUSIONS

Overall, the results from the BDFFP fragments over 20 years empirically demonstrate some important patterns of bird species loss in rain forest fragments that have generally been inferred without the benefit of repeated sampling. First, a time lag in extinctions means that species continue to be lost long after the original isolation event, even in relatively small fragments, and even after the number of species has stabilized (e.g. Sodhi *et al.*, 2004). Second, these extinctions are predictable, and follow a sequence from smaller to larger fragments, thus confirming the mechanism thought to lead to nested subsets of communities (Wright *et al.*, 1998). Third, stabilization of species richness in these fragments occurs only because of recolonization, accounting for the difference between our results and predictions in Ferraz *et al.* (2003) from models that assumed only decay. In the absence of recolonization, it appears that species richness would continue to decline (see also Ferraz *et al.*, 2007). The BDFFP fragments have an unusual landscape setting; they are surrounded by dynamic second growth imbedded in vast areas of continuous forest. Other 1- to 100-ha fragments isolated by greater distance or more hostile matrix would likely become extremely depauperate, rapidly in 1- to 10-ha fragments, and more gradually in 100-ha fragments.

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