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Recovery potential of understory bird communities in Amazonian rainforest fragments

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RESUMO. **Potencial de recuperação de comunidades de aves de sub-bosque em fragmentos florestais da Amazônia**. Comunidades de aves de sub-bosque foram estudadas numa série de fragmentos próximos a Manaus, AM, ao longo de um período de 20 anos. Análises anteriores de capturas padronizadas com redes de neblina revelaram amplo dinamismo ao longo do tempo em taxas de captura, com comunidades em fragmentos respondendo ao crescimento ou corte da matriz de vegetação secundária ao redor dos mesmos. Este padrão foi avaliado em relação aos efeitos esperados nas diferentes classes de tamanho de fragmentos estudados (1, 10 e 100 ha). Neste trabalho, estendemos nossa análise precedente dos efeitos da paisagem analisando separadamente fragmentos de 1 e 10 ha, com o objetivo de descrever a recuperação de comunidades de aves de pequenos fragmentos isolados por floresta secundária abandonada. Nos fragmentos de 10 ha, a maioria das guildas, com exceção dos insetívoros terrestres, apresentou um padrão de recuperação da abundância inicial (antes do isolamento) em aproximadamente 40 anos. Embora algumas guildas apresentaram resultados parecidos em fragmentos de 1 ha, a composição das mesmas incluiu várias espécies também comuns em floresta secundária. Os resultados sugerem que o crescimento da matriz de vegetação secundária permite que a estrutura da comunidade de aves se aproxime daquela existente antes do isolamento em fragmentos de no mínimo de 10 ha, mas enfatizamos que esta conclusão representa o melhor resultado possível, devido à proximidade de amplas áreas de floresta não perturbada na paisagem onde trabalhamos.

PALAVRAS-CHAVE: Fragmentação da floresta, comunidades de aves, floresta secundária, ecologia da paisagem, Amazônia.

ABSTRACT. Understory bird communities have been studied in a series of Amazonian rainforest fragments near Manaus, Brazil for about 20 years. Previous analysis of standardized mist-net samples revealed considerable temporal dynamism in capture rates, with communities in fragments responding to growth or cutting of the second growth matrix. This pattern was superimposed on expected fragment size effects among the 1-, 10-, and 100-ha fragments. Here we extend our earlier analysis of landscape effects by separately considering 1- and 10-ha fragments, with the goal of describing the recovery of bird communities in fragments surrounded by abandoned second growth. Most guilds, with the exception of terrestrial insectivores, appear to be on a trajectory to return to pre-isolation abundance in 10-ha fragments within about 40 years. Although some guilds showed similar recovery in 1-ha fragments, these were mostly species also common in second growth. Our results suggest that matrix development can allow bird communities to approach pre-isolation structure in fragments of at least 10 ha, but we emphasize that this conclusion represents a best-case scenario facilitated by the proximity to primary forest of the fragments we studied.

KEY-WORDS: Forest fragmentation, bird communities, secondary forest, landscape ecology, Amazonia.

As primary rainforest in Amazonia is altered or removed, forest fragments will become increasingly important for conservation of Amazonian biodiversity. The current rate of deforestation has been estimated at >20000 km^2/year (Fearnside 2005), which could lead to disturbance over as much as 2/3 of the Brazilian Amazon by about 2020 (Laurance *et al.* 2004b, Fearnside 2005). The pattern of human activity in Amazonia generally produces forest remnants of 1-100 ha (Gascon *et al.* 2000, Peres 2000), so fragments in this size range will become an increasingly significant portion of the landscape.

Communities in isolated habitat patches have long been interesting to ecologists (MacArthur and Wilson 1967), but in about the past 30 years these studies have largely shifted from curiosity about real islands to concern over the capacity of remnant patches to contain the biodiversity formerly present in large, relatively undisturbed patches of habitat (Debinski and Holt 2000). Following the paradigm of island biogeography, conservation biologists have begun considering landscape context, generally the total amount of the habitat of interest, as important determinants of the biota in a given fragment (Fahrig 2003). The influence of matrix habitat on processes in fragments has received less attention, perhaps because classical island biogeography, based on true islands, does not consider the area between fragments to be variable among landscapes or dynamic over time.

Some recent studies have demonstrated that population processes and community structure in fragments respond strongly to matrix habitat. For example, species present in fragments tend to be those that can also use matrix habitat (Gascon *et al.* 1999, Lindenmayer *et al.* 2001). For these species, matrix can allow movement among fragments, or allow individuals to include both fragment and matrix within a territory or home range (Kupfer *et al*. 2006). Given that edge effects have a pervasive influence on fragments (Murcia 1995, Debinski and Holt 2000), increasing structural similarity between edge and matrix should help improve these generally negative effects (Laurance *et al*. 2002).

Our work with understory bird communities in a series of 1-100 ha rainforest fragments at the Biological Dynamics of Forest Fragments Project (BDFFP) near Manaus, Brazil, has documented the fate of birds over about a 20 year period, beginning before the fragments were isolated from continuous forest (Bierregaard *et al.* 2001, Laurance *et al.* 2002). In general, fragment size strongly affected overall abundance of birds, community composition, and rate of species loss (Stouffer and Borges 2001, Ferraz *et al.* 2003, Stouffer *et al.* 2006). Some species were much more strongly affected than others. For example, hummingbirds and gap specialist insectivores showed little response to dramatic landscape change, while terrestrial insectivores and mixed-species flock insectivores responded more strongly (Stouffer and Bierregaard 1995a, Stouffer and Bierregaard 1995b, Stouffer and Bierregaard 1996, Stratford and Stouffer 1999).

The matrix has been a dynamic and important part of our study system since the beginning of the study. Around some fragments, the felled forest was burned to establish cattle pastures, which were generally abandoned. Around other fragments, the cut forest was never burned, and regenerated into second growth forest dominated by *Cecropia sciadophylla* (Gascon and Bierregaard 2001). In addition to this pattern, some of the fragments have been periodically reisolated, either through the activities of ranchers or through the BDFFP itself (Gascon and Bierregaard 2001, see also pdbff.inpa.gov.br). Our analysis of bird communities in the fragments has shown strong effects of matrix dynamics. In general, increasing age of the matrix also increases the abundance of understory birds in the fragments, and reduces the rate of extinction compared to true isolation (Stouffer and Bierregaard 1995b, Ferraz *et al.* 2003, Stouffer *et al.* 2006). Matrix effects vary among guilds, but in some cases can be as important as fragment size effects. Moreover, clearing a band of second growth from around the edge of fragments led to dramatic reduction in bird abundance in fragments, even for fragments <1 km from continuous forest (Stouffer *et al.* 2006).

An encouraging prediction from our results is that bird communities can recover in fragments as the matrix develops. Species recolonize fragments, and the appropriate surrounding matrix probably increases the effective size of the fragment, thus allowing the fragment to support more species and more individuals (Kupfer *et al.* 2006). As matrix ages, it approaches the structure and composition of old-growth forest, and should support increasing numbers of forest birds, as has been found in a Costa Rican rainforest landscape (Blake and Loiselle 2001). In the BDFFP landscape, recolonization is facilitated by the proximity and extent of undisturbed forest; we emphasize that our conclusions about matrix regeneration are not intended to apply to fragments isolated by greater distances.

In this paper we extend our earlier analysis of landscape effects on bird communities in the BDFFP fragments to consider the best-case scenario for recovery of these communities- abandonment of second growth. We hope that our results will illustrate both the value and the limitations of small remnant patches for conservation of Amazonian rainforest birds. In addition to the role of the matrix, we also examine how variation in landscape-level forest cover affects the recovery of communities in fragments. More specifically, we ask the following questions. How do matrix development and forest cover affect bird communities in fragments? How does this recovery differ among species or guilds? What bird communities can we expect in fragments 25-50 years following abandonment?

METHODS

Bird and landscape sampling. The Biological Dynamics of Forest Fragments study site includes 11 fragments isolated from *terra firme* rainforest north of Manaus, Amazonas, Brazil (2^o 30' S, 60^o W). Fragments were isolated beginning in 1979, leading to 5 1-ha fragments, 4 10-ha fragments, and 2 100-ha fragments (see Gascon and Bierregaard [2001] for more details on the sites, and Laurance *et al.* [2002] for a summary of important results). Understory birds were sampled beginning before the fragments were isolated, with sampling continuing periodically through 2001.

Bird sampling followed a mist-netting protocol established at the beginning of the project. Nets (NEBBA type ATX, 36 mm mesh, 12x2 m) were set up in continuous lines of 8 (1-ha fragments) or 16 (10- and 100-ha fragments), with the bottom of the net at ground level. Nets were opened for one day at a time at each site, from 0600-1400, unless heavy rains interrupted sampling. Intervals between samples at each site varied over the course of the project, but were generally at least a month. No sampling was done from 1993 through 1999, but the original protocol resumed in 2000 and 2001. Based on the timing of samples and their relation to changes in the landscape surrounding the fragments, we divided the post-isolation capture data into 44 discreet samples. Our analysis here is based on capture rate, excluding same-day recaptures, which we calculated for each sampling period. Capture rate should be interpreted as a measure of bird activity in the understory useful for comparisons over time or among fragments. Capture rate is not a measurement of absolute abundance, nor does it sample the entire community (Remsen and Good 1996).

As expected for an Amazonian forest, our site shows high species richness but low abundance of individual species, making it difficult to analyze long-term patterns on a species-by-species basis. Our approach has been to subdivide the community into social or foraging guilds, which we have followed since before isolation (Stouffer and Borges 2001, Stouffer *et al*. 2006). Our landscape analysis excluded 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 and Bierregaard 1993). We divided the remaining birds into four broad guilds: nonforest species, strict insectivores, frugivore/omnivores, and hummingbirds (Appendix). Nonforest species included any understory species absent inside but present outside unbroken forest, regardless of foraging guild (Cohn-Haft *et al.* 1997). Insectivores were subdivided into seven guilds, ranging from small, tightly defined groups (e.g. the two species of gap specialists) to large, heterogeneous collections of species (e.g. 10 species of arboreal insectivores). Frugivore/omnivores could also be conveniently subdivided into nine species of core frugivores common in the understory, and all others, which included mostly canopy species that were rarely captured (see Stouffer *et al.* 2006 for more details of guild classification).

Our study here extends our previous analysis of the long-term capture data in relation to landscape change (Stouffer *et al.* 2006). Because the datasets are the same, and the analytical methods are similar, we refer the reader to that paper for more details. For each bird sample, we calculated values for seven variables describing the fragment or its landscape setting. In general, these data came from LANDSAT satellite images or PDBFF records (most available at the PDBFF website, pdbff.inpa.gov.br). We included three variables related to the fragment itself (fragment size, fragment age, and tree mortality rate), two variables from the matrix (age of the second growth along the fragment's border [border age], and age of a path from the fragment back to continuous forest [second-growth age]), and two variables from the surrounding continuous forest (minimum distance to continuous forest [distance to forest], and amount of continuous forest within 800m of the fragment [amount of forest]).

Analytical methods. We use an information-theoretic approach to evaluate alternative models for capture rate of various guilds in the fragments (Anderson *et al.* 2000, Anderson and Burnham 2002, Burnham and Anderson 2002). This technique allows the independent evaluation of candidate models and calculation of the relative importance of each independent variable. Important for our estimate of recovery over time, it also allows estimation of the slope and intercept, plus their standard errors, for continuous dependent variables (Burnham and Anderson 2002).

In Stouffer *et al.* (2006), we first identified the bird guilds that showed a long-term response to fragment size, time since isolation, or the interaction of size and time. Several guilds (non-forest species, gap insectivores, other insectivores, other frugivores, and hummingbirds) showed no meaningful pattern, and we did no further analysis. We then used the information-theoretic analysis to select appropriate models and identify the landscape variables most important for explaining the variation in capture rate among sites. In general, this analysis identified the following: a pervasive fragment size effect; a strong effect of border age for most guilds; a weaker effect of fragment age and distance to forest for some insectivores; a weaker effect of amount of forest and second growth age for some frugivores, and no effect of tree mortality.

Fragment size affected both the magnitude of decline in capture rate after isolation and the speed of recovery as second growth aged. One ha fragments displayed a rapid decline in capture rates for most guilds, and the slowest recovery; the reverse was true for 100-ha fragments (Stouffer *et al.* 2006). Given the strong effect of fragment size, our approach here is to individually analyze the 1- and 10-ha fragments (n=20 samples from 1-ha fragments and 18 samples from 10-ha fragments), and to reduce the subset of landscape variables to those that were shown to be highly weighted in our earlier analysis. The sample size from 100-ha fragments is too small to analyze individually.

For insectivore guilds, we considered the following variables: fragment age, border age, and distance to forest. For frugivores, we also used three variables: border age, second growth age, and amount of forest. We considered all possible maximum-likelihood least-squares models with any combination of these three variables as linear predictors of capture rate. These three variables produce seven possible candidate models, each with a value for Akaike's Information Criterion for small sample sizes (AIC*c*). The AIC*c* value weighs the fit of the model against the number of parameters in the model, allowing comparison of models with differing numbers of parameters, with a lower AIC*c* value indicating more information (Burnham and Anderson 2002). We then ranked the models based on their ΔAIC*c* from the best model, allowing us to calculate the Akaike weights (w_i) for each model and to identify a confidence set of models with ΔAIC*c* < 4.0. Any models beyond this threshold would be at least seven times less likely than the best model (Burnham and Anderson 2002, chapter 2). We then used multimodel inference from the confidence set of models to calculate the slope and intercept, with unbiased standard errors, for each variable (Burnham and Anderson 2002, chapter 4). The result of this process is identification of variables affecting each guild, and a plot of the variable's estimated effect on capture rate.

RESULTS

Insectivores. For insectivores, we analyzed the following guilds: all insectivores combined, obligate army-ant followers, arboreal insectivores, flocking insectivores, flock dropouts, and terrestrial insectivores. We analyzed 1- and 10-ha fragments separately except for flock dropouts, which showed no fragment size effect (but did show a time effect) in our earlier analysis (Stouffer *et al*. 2006). The cumulative variable weights (w_i) demonstrate that the strongest effect on capture rates for most insectivores was border age, with much less ef-

Table 1. Summarized results from information-theoretic analysis of capture rates from postisolation samples, partitioned by guild and fragment size class. 'Confidence set' is the number of models with ΔAIC*c* < 4.0. Akaike weights are the combined weights from all models with the variable. Highly-weighted variables appear in bold.

			Akaike weights (w_i)				
Guild	Size class	Confidence set	Fragment age	Border age	Second growth age	Distance to forest	Amount of forest
Insectivores							
All	1 ha	3	0.18	**0.98**		0.17	
	10 ha	5	0.56	**0.85**		0.17	
Ant followers	1 ha	3	0.19	**1.00**		0.16	
	10 ha	6	0.66	0.56		0.69	
Arboreal	1 ha	6	0.44	0.44		0.46	
	10 ha	3	0.18	**0.99**		0.33	
Flock obligates	1 ha	5	0.34	0.70		0.22	
	10 ha	3	0.26	**0.92**		0.29	
Flock dropouts	1 and 10 ha	4	0.24	**0.85**		0.74	
Terrestrial	1 ha	6	0.49	0.36		0.36	
	10 ha	6	0.21	0.49		0.63	
Core frugivores	1 ha	3		**0.95**	0.21		0.19
	10 ha	2		0.20	**1.00**		**0.97**

fect of fragment age or distance to forest (Table 1). The weight of the various landscape variables differed among guilds, and for some guilds differed between 1- and 10-ha fragments.

No insectivore guild showed one variable as highly weighted for 1-ha fragments and another for 10-ha fragments, but several analyses revealed useful explanatory variables for just one size class (Table 1). For ant-followers, border age was very highly weighted for 1-ha fragments, but no variable emerged for 10-ha fragments, suggesting that none of the models we tried performed appreciably better than the others for the 10-ha samples. The large confidence set of models also suggests that no models performed well compared to others (Table 1). The reverse pattern occurred for arboreal insectivores. For flock obligates, border age was also much more highly weighted in 10-ha fragments. In 1-ha fragments, border age was still over twice as highly weighted as any other variable, but with a w_i of only 0.70. For terrestrial insectivores, no variables were strongly weighted for either size class.

Fragment age and distance to forest never emerged as particularly meaningful variables, with the possible exception of distance to forest for flock dropouts, although it was still less highly weighted than border age. For arboreal insectivores and flock obligates in 10-ha fragments, model fit was not improved by adding other variables to the simple effect of border age, meaning that the confidence set of models could be reduced to just the border age model (Burnham and Anderson 2002:131). The same was true for all insectivores in 1-ha fragments.

Frugivores. Relatively few frugivore/omnivore species were captured beyond the core species, so we restricted our analysis to core frugivores. This guild showed strong variable weights, but with different variables for 1- and 10-ha samples. In 1-ha samples, border age alone was highly weighted. This guild also showed no improvement in model fit by adding parameters to the simple effect of border age, functionally reducing the confidence set to a single model. For 10-ha fragments, however, both second growth age and amount of forest were highly weighted, but border age was not.

Recovery over time. For each guild and each size class, we identified a candidate set of models with ΔAIC*c* < 4 for parameter estimates from multimodel inference (MMI). MMI provides an estimate of the intercept. For fragment age or border age, the intercept can be interpreted as the time of isolation. Slope estimates reflect the increase in capture rate over time as borders or second growth get older. If the standard error of the estimate does not overlap zero, the relationship can be interpreted as illustrating a meaningful trend (Burn-

Table 2. Estimates of the time necessary for capture rates to return to preisolation abundance in fragments, based on slope and intercept estimates from multimodel inference. Guilds include only those with strong temporal effects identified in Table 1. For core frugivores in 10-ha fragments, the predictor variable is second growth age. For all others, recovery time is based on border age. Preisolation rates are the means ± se across fragments.

Guild	Fragment size	Preisolation rate ± se	Time to recovery (years) Low	Mean	High
Insectivores					
All	1 ha	216.7 ± 19.2	34	46	70
	10 ha	144.5 ± 12.3	19	34	87
Ant followers	1 ha	43.5 + 5.7	22	26	33
Arboreal	10 ha	30.7 + 2.7	20	28	40
Flock obligates	10 ha	28.7 + 5.3	9	16	30
Flock dropouts	1 and 10 ha	17.9 ± 2.6	11	21	47
Core frugivores	1 ha	32.1 + 2.4	12	18	36
	10 ha	26.8 + 6.4	11	15	19

ham and Anderson 2002, chapter 4). By comparing this trend with the preisolation capture rate, we can estimate the time needed for the capture rate to return to preisolation levels, assuming a linear increase (Figure 1, Table 2). Although these relationships are not tidy, they do provide a starting point for evaluating effects of matrix regrowth.

For insectivores combined, the mean slope and intercept values lead to recovery to preisolation levels in 46 years, or a minimum of 34 years with the high slope estimate (Figure 1a,b, Table 2). In 10-ha fragments, which had a lower mean preisolation capture rate and a higher slope for border age, time to recovery with mean slope and intercept values was just 34 years. Using the high estimates reduced this to just 19 years, although the low estimate led to recovery only after 87 years.

The recovery of insectivores collectively depends on the recovery of individual guilds. Our analysis here includes the guilds that showed temporal variation, so we probably gain a better perspective on recovery by considering guilds individually than from insectivores collectively. Among insectivore guilds, we found meaningful border age effects for ant followers in 1-ha fragments, arboreal insectivores in 10-ha fragments, flock obligates 10 ha fragments, and flock dropouts in 1- and 10-ha fragments combined. Recovery time estimates among these guilds differed considerably, with some also showing strong differences between 1- and 10-ha fragments (Table 2). Ant followers were estimated to recover in 1-ha fragments in 22-33 years, faster than most guilds returned to 10- ha fragments. Flock species recovered rapidly, returning to preisolation abundance in 10-ha fragments in 9-30 years. Flock dropouts recovered in 11 to 47 years. Despite being a heterogeneous groups of species, arboreal insectivores in 10-ha fragments showed one of the tightest patterns, with recovery in 20-40 years (Figure 1c).

For core frugivores, second growth age was strongly weighted for 10-ha fragments, and led to recovery of preisolation capture rates in 11-19 years for core frugivores (Figure 1d, Table 2). Border age was more highly weighted for 1-ha fragments, and its growth led to recovery to preisolation levels within 12-36 years for core frugivores.

DISCUSSION

Landscape effects on guilds. Our results largely confirm that matrix effects have an extremely important influence on bird communities in 1- and 10-ha fragments at the BDFFP sites (Stouffer and Bierregaard 1995b, Stouffer *et al.* 2000). For every guild we tested, either border age or second growth age was the most highly weighted variable for 1- or 10-ha fragments, or for both (Table 1). Six of the 13 guild by size combinations we tested had 2-3 model confidence sets and $w_i > 0.92$ for border age or second growth age, suggesting that these variables had overwhelming support compared to the other variables we considered. Given that we removed the strong effect of fragment size and reduced the number of landscape variables in this analysis to those that had at least some support from our earlier study, these results suggest that matrix effects determine much of the differences among samples within fragment size classes.

For the few guilds in which matrix effects were not pro-

Figure 1. Representative capture rate relationships from multimodel inference plotted with empirical capture data from postisolation samples. In each figure, the upper line represents the high estimates of intercept and slope, the middle line represents the mean estimates, and the lower line represents the minimum. For preisolation abundance, see Table 2.

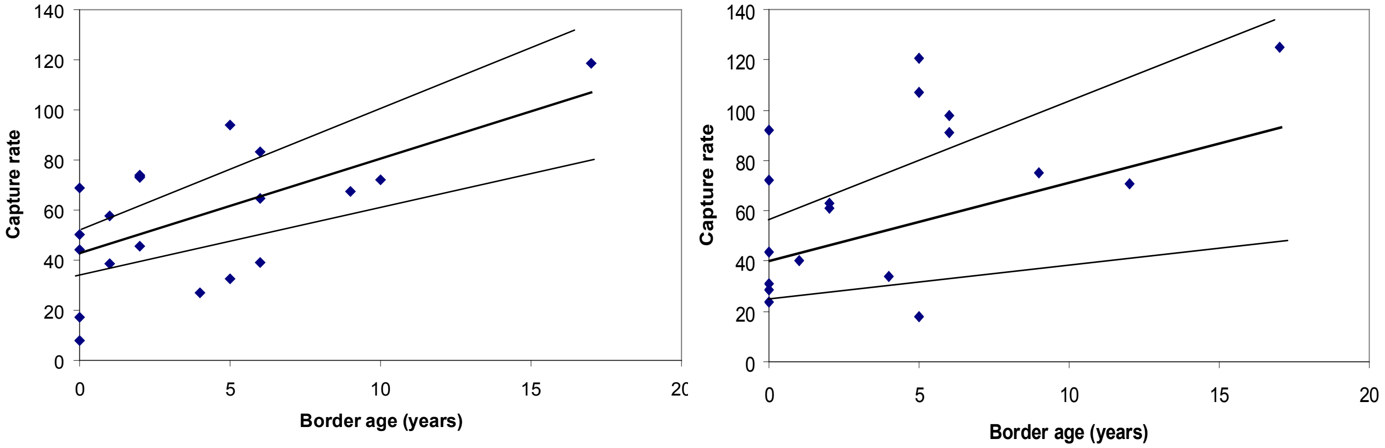
Figure 1a. All insectivores in 1-ha fagments

Figure 1b. All insectivores in 10-ha fragments

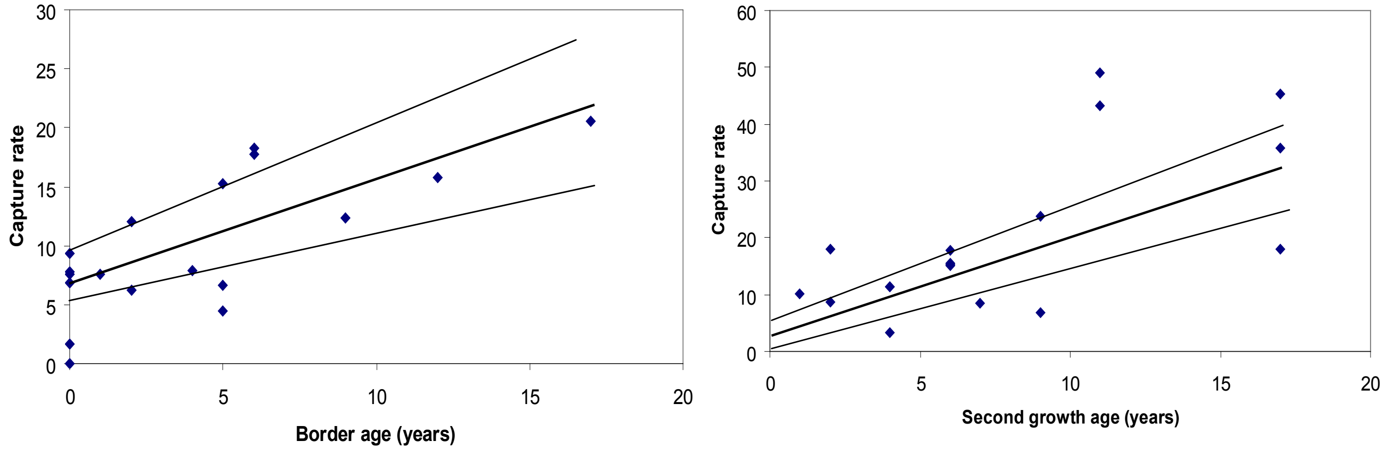
Figure 1c. Arboreal insectivores in 10-ha fragments

Figure 1d. Core frugivores in 10-ha fragments

nounced, no models or variables performed well. In some cases, these results revealed differences between 1- and 10-ha fragments that we would not have expected from our previous analyses. For ant followers, which showed rapid disappearance after isolation, followed by dramatic recovery in fragments surrounded by *Cecropia*- dominated second growth (Stouffer and Bierregaard 1995b), no model or variable emerged as useful for explaining the variation among 10-ha samples. No models were useful for flock obligates or arboreal insectivores in 1-ha fragments, probably because species from these guilds were seldom captured in 1-ha fragments under any conditions. Similarly, no models explained the variation in terrestrial insectivore captures. These species have shown almost no recovery in 1-ha fragments, and the slight recovery in some 10-ha fragments is apparently not well explained by the variables we considered.

An interesting pattern emerged in core frugivores, with border age apparently driving variation in 1-ha fragments, but with minimal effect of border age and a strong effect of second growth age in 10-ha fragments. This difference is difficult to interpret; perhaps these birds increase in abundance in second growth as it develops, but will move across younger borders to enter 10-ha fragments.

Recovery of understory communities in 1- and 10-ha fragments. Our analysis reveals how bird communities would be expected to recover in fragments at the PDBFF surrounded by abandoned matrix. Apparently, the variation in primary forest cover is generally not important in our system, where all fragments are within 800m of a vast area of continuous forest. Core frugivores in 10-ha fragments provide an exception to this generalization. Amount of forest within 800m was highly weighted for this guild, suggesting that the combination of close primary forest and old second growth facilitates diffusion back into fragments

Although the results from all insectivores combined suggest that preisolation capture rate can be attained even in 1-ha fragments, the responses of individual guilds give a better picture of the communities to be expected as matrix ages around the fragments (Table 2). As we've already seen from our empirical data, flock dropouts return to preisolation abundance quickly. Indeed, one of these species, *Glyphorynchus spirurus*, occurs in nearly every sample, and appears to persist even in 1-ha fragments isolated by active cattle pasture. We've documented the recovery of core frugivores over our sampling interval, as also predicted from multimodel inference. Arboreal insectivores and obligate flock insectivores show a different pattern. These guilds could be modeled only in 10-ha fragments, where they are predicted to recovered within 40 years, possibly quite less. In 1-ha fragments, however, these species have shown so little recovery so far that their eventual recovery cannot be estimated.

Collectively, our data suggest that within 25-50 years 10-ha fragments probably have bird communities comparable to preisolation for ant followers, arboreal insectivores, flock obligates, flock dropouts, and core frugivores (Table 2). Our earlier results showed rapid recovery, or even increased abundance, of gap specialists and hummingbirds following isolation (Stouffer and Bierregaard 1995a,b). If anything, we would expect abundance of these species to decline if gap formation stabilizes over time in fragments. Based on the data so far, terrestrial insectivores may be least likely to return to fragments. The response of terrestrial insectivores also illustrates an important limitation to our guild-based analysis: all species within a guild cannot be expected to respond similarly. *Formicarius colma* has persisted in several 10-ha fragments through 2001, and sometimes occurs in second growth, but *Sclerurus caudacutus* was quickly lost from fragments and has not returned (Borges 1995, Stratford and Stouffer 1999, unpublished data). Similar variation can be identified among species within the larger guilds, particularly arboreal insectivores.

The potential for return of typical forest species to 10-ha fragments makes sense based on what we know about area requirements of these species. Many, perhaps most, understory species require about 5-15 ha, so a 10-ha fragment can support about one pair (Terborgh *et al.* 1990, Develey and Stouffer 2001, Stouffer 2007). Certainly a local population of a single pair suffers demographic instability, so the developing matrix probably provides both a means for recolonization and an opportunity for forest species to extend territories beyond the border of the fragment (Kupfer *et al.* 2006). We know that both occur. For example, we documented a new mixed-species flock territory that included both undisturbed forest and second growth along a 25 year old roadside (Develey and Stouffer 2001). We've also seen the return of species that had previously been locally extinct (e.g. Stouffer and Bierregaard 1995a).

In 1-ha fragments, the community 25-50 years following matrix abandonment would include ant-followers, flock dropouts, core frugivores, gap specialists, and hummingbirds. These fragments would likely be missing many of the diverse suite of arboreal insectivores and terrestrial insectivores. Given that 10 year old second growth dominated by *Cecropia* yields comparable species richness and capture rates of these same species (Borges 1995, Stouffer and Borges 2001), we suspect that bird communities in 1-ha fragments will probably converge on the communities in the second growth. In other words, the forest bird community will return to these tiny fragments only when it returns to the matrix.

For any of these future scenarios, we should emphasize that the linear models we used cannot be expected to give useful predictions long into the future. Several studies from Central America suggest that second growth may recover forest species more rapidly than we found (Petit *et al.* 1999, Blake and Loiselle 2001), but bird densities are higher and second growth would be expected to recover more rapidly on these richer, more recent soils (Robinson *et al*. 2000, Williamson *et al.* 2005). We expect that some species that are increasing in our samples probably reach an asymptote at about their preisolation capture rates. Other species, perhaps including gap specialists, may eventually decline in abundance in fragments if the rate of tree mortality stabilizes, although tree mortality has remained high through the most recent samples (Laurance *et al.* 2001). Only time will reveal if species linked most closely to the structure of undisturbed forest interior will return to fragments at an increasing rate as second growth develops suitable structural characteristics, or if they remain excluded due to unsuitable structure within the fragments.

Extension to Amazonia. How can these results be extended to fragmented landscapes elsewhere in Amazonia? Before attempting any generalization, we need to emphasize that the landscape settings where we worked includes continuous forest within 100-800 m of the fragments. This forest stretches over thousands of km^2 with relatively little disturbance. Our analysis may have illustrated how matrix development drives community recovery, but forest birds in small fragments ultimately came from the continuous forest. We found little meaningful effect on capture rates due to the variation in forest cover in our landscapes, but fragments showing greater isolation would be expected to recover more slowly. Our data do not answer how recovery potential declines with loss of forest cover on a larger scale. Indeed, several datasets from fragments isolated by large areas of *Eucalyptus* or soybeans continue to lose forest species, much as predicted for the BDFFP fragments under conditions of complete isolation (Ferraz *et al.* 2003, Ribon *et al*. 2003, Anjos *et al.* 2004).

We think that our data best illustrates the low vagility of forest birds across young second growth or open pastures, as has been illustrated with several methods (Stouffer and Bierregaard 1995b, Develey and Stouffer 2001, Laurance *et al.* 2004a, Antongiovanni and Metzger 2005). At our sites one can stand on the edge of an isolated fragment, gaze across a narrow band of pasture, and see nothing but continuous forest stretching to the horizon. Yet, that isolated fragment will show declining capture rates and loss of species as long as the pasture remains in place.

Our most general conclusion is that fragments of at least 10 ha have the chance to recover something approaching their presiolation bird communities within a few decades of matrix abandonment. Our analysis through about 10 years post-isolation showed strong positive effects of *Cecropia*-dominated second growth compared to the *Vismia*-dominated scrub then growing in abandoned cattle pastures. Most of the values above the trend lines in Figure 1 come from fragments embedded in a matrix dominated by *Cecropia*, suggesting that the most rapid recovery estimates (Table 2) might be expected under these conditions. Even so, in our 2000 samples we also recorded high capture rates in fragments surrounded by second growth dominated by old *Vismia*. For example, we caught no obligate flock species in 1992 in fragment 1202, one of the fragments that had been surrounded by active pasture. By 2000, capture rate had returned to the preisolation mean, with more captures than we recorded in a fragment surrounded by 17 year old *Cecropia*. These results demonstrate that even cattle pasture can naturally recover enough for forest birds to regularly move through it within about 20 years. Again, however, we need to emphasize that the history of our site may temper this generalization. Differences in soils or intensity of pasture use would be expected to alter plant succession, in turn affecting recovery of bird communities (Mesquita *et al.* 2001, Zarin *et al*. 2001, Zarin *et al.* 2005).

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Appendix. Guild assignments of species included in our original analysis (Stouffer *et al.* 2006). See Table 1 for the guilds analyzed here. 'Insectivores' include species that eat almost no fruit; 'Frugivores' include species that sometimes eat fruit. For insectivores, 'other' includes all species that are rare in the net sample. Sequence follows Cohn-Haft et al. 1997, with taxonomy reflecting recent changes of the South American Classification Committee of the American Ornithologists' Union (http://www.museum.lsu.edu/~Remsen/SACCBaseline.html).

Species	Guild
Phaethornis superciliosus	hummingbird
Phaethornis bourcieri	hummingbird
Campylopterus largipennis	hummingbird
Florisuga mellivora	hummingbird
Thalurania furcata	hummingbird
Hylocharis sapphirina	hummingbird
Trogon rufus	frugivore- other
Momotus momota	frugivore- other
Notharchus tectus	Insectivore- other
Bucco tamatia	insectivore- other
Malacoptila fusca	insectivore- other
Galbula albirostris	insectivore- other
Dendrocincla fuliginosa	insectivore- arboreal
Dendrocincla merula	insectivore- ant follower
Deconychura longicauda	insectivore- other
Deconychura stictolaema	insectivore- flock obligate
Sittasomus griseicapillus	insectivore- other
Glyphorynchus spirurus	insectivore- flock dropout
Hylexetastes perrotii	insectivore- other
Dendrocolaptes certhia	insectivore- other
Dendrocolaptes picumnus	insectivore- other
Xiphorhynchus pardalotus	insectivore- flock dropout
Campylorhamphus procurvoides	insectivore- other
Synallaxis rutilans	insectivore- other
Philydor erythrocercum	insectivore- other
Philydor pyrrhodes	insectivore- other
Automolus infuscatus	insectivore- flock obligate
Automolus rubiginosus	insectivore- arboreal
Automolus ochrolaemus	insectivore- arboreal
Xenops minutus	insectivore- flock obligate
Sclerurus mexicanus	insectivore- other
Sclerurus rufigularis	insectivore- terrestrial
Sclerurus caudacutus	insectivore- terrestrial
Cymbilaimus lineatus	insectivore- other
Frederickena viridis	insectivore- other
Thamnophilus murinus	insectivore- other
Thamnomanes ardesiacus	insectivore- flock obligate
Thamnomanes caesius	insectivore- flock obligate
Myrmotherula guttata	insectivore- arboreal
Myrmotherula gutturalis	insectivore- flock obligate
Myrmotherula axillaris	insectivore- flock dropout
Myrmotherula longipennis	insectivore- flock obligate
Myrmotherula menetriesii	insectivore- flock obligate
Hypocnemis cantator	insectivore- gap
Percnostola rufifrons	insectivore- gap
Schistocichla leucostigma	insectivore- other
Myrmeciza ferruginea	insectivore- other
Myrmeciza atrothorax	insectivore- other
Pithys albifrons	insectivore- ant follower
Gymnopithys rufigula	insectivore- ant follower
Hylophylax naevius	insectivore- arboreal
Hylophylax poecilinotus	insectivore- arboreal
Formicarius colma	insectivore- terrestrial
Formicarius analis	insectivore- other
Myrmornis torquata	insectivore- terrestrial
Grallaria varia	insectivore- other
Hylopezus macularius	insectivore- other
Myrmothera campanisona	insectivore- other
Conopophaga aurita	insectivore- terrestrial
Mionectes macconnelli	frugivore- core
Corythopis torquatus	insectivore- terrestrial
Lophotriccus galeatus	nonforest
Hemitriccus zosterops	insectivore- other
Rhynchocyclus olivaceus	insectivore- other
Tolmomyias assimilis	insectivore- other
Platyrinchus saturatus	insectivore- arboreal
Platyrinchus coronatus	insectivore- arboreal
Platyrinchus platyrhynchos	insectivore- other
Onychorhynchus coronatus	insectivore- other
Terenotriccus erythrurus	insectivore- other
Myiobius barbatus	insectivore- flock obligate
Attila spadiceus	frugivore-other

Species	Guild
Laniocera hypopyrra	insectivore- other
Schiffornis turdina	frugivore- core
Neopipo cinnamomea	frugivore- other
Tyranneutes virescens	frugivore- other
Corapipo gutturalis	frugivore- core
Lepidothrix serena	frugivore- core
Pipra pipra	frugivore- core
Pipra erythrocephala	frugivore- core
Neochelidon tibialis	insectivore- other
Thryothorus coraya	nonforest
Troglodytes aedon	nonforest
Microcerculus bambla	insectivore- arboreal
Cyphorhinus arada	insectivore- terrestrial
Catharus fuscescens	frugivore- other
Catharus minimus	frugivore- other
Turdus albicollis	frugivore- core
Microbates collaris	insectivore- arboreal
Cyclarhis gujanensis	insectivore- other
Vireo olivaceus	frugivore- other
Hylophilus ochraceiceps	insectivore- flock obligate
Oryzoborus angolensis	nonforest
Saltator grossus	frugivore- other
Cyanocompsa cyanoides	frugivore- core
Tachyphonus surinamus	frugivore- core
Ramphocelus carbo	nonforest
Tangara chilensis	frugivore- other
Coereba flaveola	frugivore- other