Recovery of Understory Bird Movement Across the Interface of Primary and Secondary Amazon Rainforest

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RECOVERY OF UNDERSTORY BIRD MOVEMENT ACROSS THE INTERFACE OF PRIMARY AND SECONDARY AMAZON RAINFOREST

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Abstract.—Amazonia now contains vast areas of secondary forest because of widespread regeneration following timber harvests, yet the value of secondary forest to wildlife remains poorly understood. Secondary forest becomes structurally similar to primary forest after abandonment, and therefore we predicted that avian movement across the interface of primary and secondary forest (hereafter "the interface") would gradually increase with time since abandonment until recovery to pre-isolation levels. From 1992 to 2011, we captured 2,773 understory birds of 10 foraging guilds along the interface of primary forest fragments and zero- to 30-year-old secondary forest at the Biological Dynamics of Forest Fragments Project near Manaus, Brazil. Our objectives were to understand the differences in land-use history that affect cross-interface movement and to determine how long it takes each guild to recover to pre-isolation capture rates. Across guilds, age of secondary forest within 100 m of the interface was the most important explanatory variable affecting capture rates; rates increased with age of secondary forest for all guilds except non-forest species. Mean recovery to pre-isolation was 26 years (asymmetric SE = 13 years below and 16 years above estimate) after secondary forest abandonment and 9 of 10 guilds recovered within 13 to 34 years. In the slowest guild to recover, terrestrial insectivores, 6 of 12 species were never caught along the interface, and we projected that this guild would recover in ~60 years. Our recovery estimates quantify the dynamic permeability of the interface and contribute to a better understanding of the value of secondary forests as corridors among primary forest fragments. *Received 26 October 2012, accepted 19 May 2013.*

Key words: bird communities, edges, fragmentation, landscape effects, Neotropical birds, secondary forest, terrestrial insectivores.

Recuperação Do Movimento De Pássaros Sub-Bosque Em Toda A Interface Do Primário E Secundário Da Amazônia

Resumo.—Atualmente, a Amazônia possui extensas áreas de florestas secundárias devido à regeneração generalizada de áreas desflorestadas; no entanto, o valor da floresta secundária para a vida selvagem ainda é pouco conhecido. As florestas secundárias tornam-se estruturalmente similares às florestas primárias após o abandono da área desmatada, e portanto, nós prevemos que o movimentos das aves entre a interface da floresta primária e floresta secundária (doravante denominada "interface") aumentaria gradualmente com o tempo desde o abandono até a recuperação a níveis de pré-isolamento. De 1992 a 2011, nós capturamos 2,773 aves de sub-bosque pertencentes a 10 diferentes guildas ao longo da interface de fragmentos de floresta primária e de florestas secundárias de zero até 30 anos no Projeto Dinâmica Biológica de Fragmentos Florestas, próximo à Manaus, Brasil. Os nossos objetivos foram entender quais diferenças no histórico de uso da terra afetam o movimento entre a interface; e determinar quanto tempo cada guilda leva para recuperar as taxas de recaptura do pré-isolamento. Entre guildas, a idade da floresta secundária dentro de 100 m da interface foi a variável explanatória mais importante a afetar as taxas de captura; as taxas aumentaram com a idade da floresta secundária para todas as guildas, com exceção das espécies não florestais. A média da recuperação a nível de pré-isolamento foi de 26 anos (estimativa assimétrica de EP = 13 anos abaixo e 16 anos acima) após o abandono da floresta secundária, e 9 das 10 guildas recuperaram-se entre de 13 a 34 anos. A guilda com recuperação mais lenta, insetívoros terrestres, teve 6 de 12 espécies que nunca foram capturadas ao longo da interface, nós projetamos que esse grupo deve recuperar-se em aproximadamente 60 anos. As nossas estimativas de recuperação quantificaram a permeabilidade dinâmica da interface, e contribuem para um melhor entendimento do valor das florestas secundárias como corredores entre os fragmentos de floresta primária.

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Over the past 20 years, timber harvests and agricultural expansion have removed >328,000 km^2 of the Brazilian Amazon—an area larger than Poland (Brazilian National Space Research Institute [INPE] 2010). Although deforestation rates have slowed since 2005, the Brazilian Amazon continues to lose 7,000 km^2 year^{-1} (INPE 2010). Further, changes to the Brazil Forest Code may expose an additional 220,000 km^2 of forest to legal clearing (Sparovek et al. 2010, Nazareno et al. 2012). In contrast to much of the southern Amazon, where clearcuts often produce long-term pasturelands, in eastern and central Amazonia, clearcut areas are typically abandoned within 5 years after conversion to cattle pasture (Fearnside 2005). In the Brazilian Amazon, the area of secondary forest increased from 29,000 to 161,000 km^2 from 1978 to 2002 alone (Neeff et al. 2006). These vast expanses of secondary forest will inevitably become a necessary element of conservation planning, particularly given that growth of secondary forests from abandoned pastures represents a significant way to offset carbon lost to deforestation in the Amazon (Nepstad et al. 2009, Asner et al. 2010).

Despite the pervasiveness of secondary forests in the tropics, our understanding of them is poor and their conservation value is still debated (Brook et al. 2006; Wright and Muller-Landau 2006a, b), in part because few empirical studies exist. Despite their perceived mobility, tropical birds do not appear to be as tolerant of secondary forest as other taxa. For instance, records of 16 taxonomic groups studied in the Jari forest landscape of the northeastern Amazon showed that in 14- to 19-year-old secondary forest, only grasshoppers had a lower proportion of primary-forest species than birds; only 38% of all the primary-forest bird species were present (data from C. A. Peres, J. Barlow, T. A. Gardner, and the Jari Forest Project database; for further details, see Barlow et al. 2007). In 9- to 13-year-old secondary forest at our study site, the Biological Dynamics of Forest Fragments Project (BDFFP), Stouffer and Borges (2001) found two-, five-, and eight-fold reductions in capture rates of ant-followers, terrestrial insectivores, and mixed-species flock obligates, respectively. Stratford and Stouffer (1999), also working in young secondary forest at the BDFFP, speculated that the terrestrial insectivores would be the last to recover as secondary forest matures. Using data from 10 studies (7 from the Neotropics), Dunn (2004) concluded that avian richness in tropical secondary forests may take only 20 years to recover to levels seen in primary forest, although contemporary bird distributions at the BDFFP, where some secondary forest is now 30 years old, suggest otherwise. The effects of fragmentation and isolation are now well known at the BDFFP (Laurance et al. 2011); however, few have studied the effect of secondary forest on birds: Stouffer and Borges (2001) and Borges and Stouffer (1999) studied understory birds in young secondary forest, and Sberze et al. (2009) studied the nocturnal bird community. Older secondary forests are even more poorly studied than young secondary forests (Chazdon et al. 2009). Consequently, research in the now more than 30-year-old secondary forests of the BDFFP represents a much-needed opportunity to quantify the conservation value of older secondary forest.

Primary forest in Amazonia is becoming increasingly fragmented because of high levels of forest loss and subsequent regeneration of secondary forest, with a staggering 53,000 km of forest edges created each year (Numata et al. 2011). This boundary between primary and secondary forest (hereafter "the interface") may present a barrier to movement, but propensity to cross a barrier likely varies widely among species and foraging guilds. Understanding how animals perceive the permeability of the interface can lead to a quantification of the value of secondary forest as a corridor among primary forest patches. For individuals moving across a fragmented landscape, the interface is the first step toward movement among remnant patches of primary forest; this process is fundamental to understanding source–sink and metapopulation dynamics (Brawn and Robinson 1996), gene flow and genetic structuring (Bates et al. 2004), and species' persistence in isolated forest fragments (Ferraz et al. 2007).

We formulated a conceptual model to describe the spatiotemporal dynamics of understory bird movement during forest fragmentation and regrowth of secondary forests. The overarching assumption of the model is that as secondary forests regrow following clearcutting and abandonment, the permeability of the interface increases for understory birds, eventually reaching a point of "recovery" at which bird movement across the interface is essentially identical to what was observed pre-isolation (i.e., prior to clearcutting continuous primary forest). The model proceeds as follows: (1) as continuous forest is initially clearcut, rainforest birds are entirely excluded from the recently cut (and often burned) area and essentially imprisoned within forest fragments. At this point, territory boundaries are aligned along the interface, birds are excluded from fragments too small to sustain their territories (Stouffer and Bierregaard 1995b), and capture rates along the interface are effectively zero. During early regrowth, (2) vertical structure of the young secondary forest permits some movement (i.e., dispersal) across secondary forest—a few individuals may occasionally use small fragments (Stouffer and Bierregaard 1995b). As secondary forest ages and begins to recover resources, (3) birds begin to expand their territories into secondary forest and into small fragments (Borges and Stouffer 1999, Stouffer et al. 2011), showing increased rates of movement across the interface. At the point of recovery, (4) bird territory boundaries and cross-interface movements are indistinguishable from those in primary forest, regardless of fragment size.

We used mist-net captures to study the dynamics of recovery of movement along the interface, with particular interest in quantifying how movement (i.e., capture rate) changes as secondary forest matures. Specifically, we sought to answer two questions about the system. (1) What land-use history characteristics affect recovery of movement along the interface? And (2) how long does it take for understory avian guilds to recover to pre-isolation movement across the interface?

Methods

We conducted field work from October 1992 to September 2011 at the BDFFP, located ~80 km north of Manaus, Amazonas, Brazil (2°30′S, 60°W). The BDFFP consists of 11 forest fragments (5 of 1 ha, 4 of 10 ha, and 2 of 100 ha). After pre-isolation sampling, initial isolation started in 1980. Most forest fragments were periodically re-isolated along borders that were not maintained by cattle pastures by cutting 100-m bands around their perimeters (hereafter "the border"). Forest fragments are embedded in a variable inter-fragment matrix (non-primary-forest areas beyond the border, hereafter "the matrix"), which has included active cattle pasture, zero- to 30-year-old secondary-growth forest, and unpaved forest roads. Early in the succession of secondary forest, the clearing process produced two major types of vegetation: a *Cecropia*-dominated forest community

that regenerated in the absence of fire, and a *Vismia*-dominated community that regenerated after burning (Mesquita et al. 2001). Thirty-year-old secondary forest averages ~19 m tall at the BDFFP (K. Mokross pers. comm.). By contrast, primary forest is thought to be 30 to 37 m tall (Gascon and Bierregaard 2001). The BDFFP receives ~2,500 mm of rain per year, with a pronounced wet season from January to April and a dry season from June through September (Stouffer and Bierregaard 1993). The 140-km^2 experimental forest within the BDFFP is embedded within a vast area of primary rainforest to the north, east, and west, with increasing anthropogenic influence to the south (for detailed descriptions of the site, see Bierregaard et al. 2001, Laurance et al. 2011).

Sampling.—Post-isolation mist netting took place in June to October during three time blocks: 1992–1993, 2000–2001, and 2007–2011. We ran mist nets (NEBBA type ATX, 36-mm mesh, 12 × 2 m) along the interface on approximately 1-m-wide trails with the bottom of nets set at ground level. Post-isolation nets were run in lanes of four consecutive nets, with one lane per side of each of 11 square forest fragments. We assumed that samples in different time blocks were independent given that the generation time of many small tropical birds is <6 years and species turnover within fragments at the BDFFP is high among 6-year intervals (Stouffer et al. 2011). We netted each lane for 1 day at a time, beginning at 0600 hours and continuing until 1400 hours, unless heavy rains forced us to close the nets. Within time blocks, we generally sampled lanes at intervals of ≥6 weeks. From 1992–1993, 2000–2001, and 2007–2011, we sampled along the interface of secondary-forest and primary-forest fragments.

Because our site exhibited the typical tropical pattern of high richness but low abundance, we pooled species into guild assignments modified from Stouffer et al. (2006; Table S1). We defined guilds as follows: non-forest species included any understory species typically absent inside but present outside unbroken forest; edge species frequented edges or tree fall gaps; core frugivores were common and primarily frugivorous; ant-followers foraged only by following insects fleeing from army ant swarms; sallying insectivores were solitary sallying species; bark insectivores were woodcreepers that were solitary and not professional ant followers; flock dropouts were facultative mixed-species flock participants; flock obligates were obligate mixed-species flock participants; near-ground insectivores foraged in the lowest stratum of the forest, but rarely on the ground; and terrestrial insectivores foraged by walking along the forest floor (Cohn-Haft et al. 1997). We excluded canopy species, raptors, kingfishers, and large ground omnivores, such as tinamous and cracids, because they are rare or cannot be reliably sampled with mist nets. We excluded hummingbirds because previous work on this system showed that matrix and border age have little effect on hummingbird movement (Stouffer and Bierregaard 1995a). Finally, we excluded species never caught in forest fragments (and that were thus unavailable to be caught along the interface) or that did not fit guild assignments.

Our measure of bird movement along the interface was capture rate per 1,000 mist-net hours. We acknowledge that capture rate is an imperfect metric of movement, because structural differences among habitats may affect capture rate (Remsen and Good 1996). Capture rate conveniently normalizes unequal sampling effort among samples. We estimated time to recovery (see below) based on a single pre-isolation capture rate for each guild across fragments (mean [± SE] fragment^{-1} = 2,678 ± 1,088 net-hours

before isolation). Pre-isolation nets were arranged in 8- or 16-net lanes in reserve (soon to be fragment) interiors as summarized below; more detail is provided in Stouffer and Bierregaard (1995b).

We had to consider the possibility that avian abundance within fragments affected capture rate along the interface. Therefore, we summarized post-isolation capture rates from fragment interiors during each time block and used those values as an index of avian abundance in fragment interiors, which we then included as a variable in our candidate model set. In interiors, post-isolation nets were in single lanes of 8 (in 1-ha fragments) or 16 nets (in 10-ha fragments); these interior nets were run on the same days as the nets along the interface. In 100-ha forest fragments, two or three 16-net lanes were separated by ≥200 m. Because 100-ha fragments had >1 interior net lane, we calculated capture rate separately for each interior net lane, and then used those values to represent interior capture rate for the nearest interface net lane.

Because of concerns about the independence of interface net lanes only 70 m apart along 1-ha fragments, we pooled the four net lanes along the interface of each 1-ha fragment, creating a single sample for each 1-ha fragment during each time block. We assumed that net lanes along the sides of 10- and 100-ha fragments, all separated by ≥220 m, were spatially independent (sensu Hill and Hamer 2004), so we did not pool those lanes. To ensure that we had a large enough sample of the oldest secondary forest, we added four four-net samples along the interface of continuous primary forest and 27- to 30-year-old secondary forest in 2011—these were the only locations not sampled prior to isolation. This gave us a total of 91 samples, each with at least 63 net-hours (mean = 282; maximum = 1,175).

Model selection.—To normalize residuals and meet the assumptions of parametric statistics, we log-transformed the response variable, capture rate along the interface. During exploratory analyses, we attempted to fit asymptotic models (i.e., models in which the capture rate curve reaches an asymptote when capture rate stabilizes), but these models fit poorly because in most cases we had few data with which to model the tail of the asymptote. In other words, if recovery to pre-isolation occurred at 27 years, asymptotic models probably fit poorly because the oldest secondary forest at the BDFFP was only 30 years old, so there were few data with which to fit the asymptotic part of the curve. We therefore used log-transformed linear models, which appeared to fit the data well on the basis of residual plots. Even so, we focused on the trajectory toward recovery and ignored the exponential path of the curve after it crossed the pre-isolation capture rate.

We used an information-theoretic framework (Burnham and Anderson 2002) to model capture rates as a function of land-use history around forest fragments. We formed *a priori* candidate model sets for each of the 10 avian guilds, representing combinations of land-use history characteristics hypothesized to affect capture rate (Table S2); global models for each guild are provided in Table 1. Variable definitions are as follows: BorderYrs (age of secondary growth along primary–secondary forest interface), Area (area of primary forest fragment adjacent to the interface), MatrixYrs (age of initial cut of the entire ranch in which fragments are embedded), BorderUnburned (whether secondary forest adjacent to the interface was left unburned), MatrixUnburned (whether the ranch was left unburned when it was intially cut), CF800 (area of continuous forest [CF = unbroken primary rainforest, excluding forest fragments] within 800 m of the sample location, as estimated

using LANDSAT imagery and project records), and InteriorCap-Rate (guild-specific capture rate in the forest fragment interior). We determined the age of secondary growth through examination of BDFFP monthly reports, interviews with project directors (G. Ferraz unpubl. data) and LANDSAT imagery. Candidate model sets were based on our knowledge of the species' behavior as well as previous work at the BDFFP on landscape effects on recovery rates of avian guilds within forest fragments (Stouffer et al. 2006, Stouffer and Bierregaard 2007). In selecting candidate models, we included only what we believed to be biologically plausible combinations of variables (Burnham and Anderson 2002). For example, Stouffer and Bierregaard (2007) found that the amount of continuous forest within 700 m of fragments affected recovery of capture rates of frugivores within fragments, so we included that variable in our candidate set of models affecting interface capture rates of frugivores. Preliminary analyses suggested that for three guilds less dependent on large patches of primary forest (i.e., flock dropouts, edge species, and core frugivores), capture rates along the interface were highest when secondary forest was of intermediate age (5–15 years old). For these three guilds, we included two models with a quadratic effect of border age, which would allow the trend in capture rate to be highest (or lowest) at intermediate border age. For several guilds, we included models with interaction terms between BorderYrs and Area as well as BorderYrs and BorderUnburned

because we suspected that the effects of Area and BorderUnburned on capture rates would decrease considerably as secondary forest along the border matured (Table 1). BorderUnburned and Matrix-Unburned were the only highly correlated variables (Spearman's $\varrho = 0.61$), so we avoided including those two variables together in the same model. Finally, we had no reason to suspect that fragment size affected capture rates of edge species or non-forest species along the interface, so we did not include this variable in the candidate set for these guilds. For the four samples from 2011 along the interface of secondary forest and primary continuous forest, we took a simplistic approach to area, using 1,000 ha as the area for those samples. We used PROC MIXED in SAS, version 9.2 (SAS Institute, Cary, North Carolina), to calculate Akaike's information criterion corrected for small sample size (AIC_c) for each model in the candidate and considered models, with $\Delta AIC_c < 2$ as those with substantial support (Burnham and Anderson 2002).

Time to recovery.—We considered "recovery" to be the age of the border at which capture rate reached the pre-isolation capture rate for a guild. We calculated pre-isolation capture rate for each forest fragment and then used those calculations along with the best-fit model for each guild to calculate the time to recovery. To maximize parsimony via exclusion of parameters with little predictive power, we did not include parameters in the model that we used to calculate time to recovery if the parameter ± SE in the

TABLE 1. Complete list of all *a priori* candidate sets of models describing capture rates along the primary–secondary forest interface for 10 avian guilds at the Biological Dynamics of Forest Fragmentation Project, 1991–2011. Checkmarks indicate that the model was included in the candidate set for a given guild. The global model for each guild is a saturated model including all variables and interactive effects listed for the guild.

Candidate model [a]	Flock dropouts	Edge species	Non-forest	Core frugivores	Six remaining guilds [b]
BorderYrs	✔	✔	✔	✔	✔
BorderYrs²	✔	✔		✔	
Area	✔			✔	✔
Area MatrixYrs	✔			✔	✔
BorderYrs Area	✔			✔	✔
BorderYrs * Area [c]	✔			✔	✔
BorderYrs BorderUnburned	✔	✔	✔		✔
BorderYrs * BorderUnburned	✔	✔	✔		✔
BorderYrs MatrixUnburned	✔	✔	✔		✔
BorderYrs MatrixYrs	✔	✔	✔	✔	✔
BorderYrs MatrixYrs BorderUnburned	✔	✔	✔		✔
BorderYrs MatrixYrs MatrixUnburned	✔	✔	✔		✔
MatrixYrs MatrixUnburned	✔	✔	✔		✔
BorderYrs² MatrixYrs	✔	✔		✔	
BorderYrs Area CF800				✔	
BorderYrs * Area CF800				✔	
BorderYrs CF800				✔	
Area CF800				✔	
InteriorCapRate	✔	✔	✔	✔	✔
InteriorCapRate BorderYrs	✔	✔	✔	✔	✔
InteriorCapRate BorderYrs Area	✔			✔	✔
NULL	✔	✔	✔	✔	✔

[a] BorderYrs = age of secondary growth along primary–secondary forest interface; Area = area of primary forest fragment adjacent to secondary forest; MatrixYrs = age of initial cut of the entire ranch in which fragments are embedded; BorderUnburned = whether secondary forest adjacent to the interface was left unburned; MatrixUnburned = whether the ranch was left unburned when it was intially cut; CF800 = area of continuous forest within 800 m of sample; and InteriorCapRate = guild-specific capture rate in the forest fragment interior.
[b] Remaining guilds: obligate ant-followers, sallying insectivores, bark-foraging insectivores, obligate mixed flock species, near-ground insectivores, and terrestrial insectivores.
[c] Interactive models also include additive effects.

best-fit model overlapped zero. To calculate an estimate of error in the recovery calculation, we used the intersections of the SE curves for interface capture rate and pre-isolation capture rate; this produced asymmetrical SEs. Finally, we were particularly interested in terrestrial insectivores, but capture rates were too low to model species-specific recovery rates, so we used bar graphs to examine species-specific capture rates over time for this guild.

RESULTS

In >25,928 net-hours, we recorded 3,735 captures along the interface, 2,773 of which we assigned to 1 of the 10 avian guilds for which we modeled capture rates.

Model selection.—For each of 10 guilds, the best-fit model performed substantially better than a null model (mean ΔAIC_c of null model = 31.7). Residual plots of best-fit models generally showed little skew and normal distributions. BorderYrs was included in the best-fit model of all 10 avian guilds (Table 2 and Tables S2–S11) and, as expected, the parameter estimate for BorderYrs was positive for all guilds except non-forest species. In other words, increasingly old secondary forest along the interface was associated with higher capture rates of all guilds except non-forest species, which we caught more often along the interface when secondary forest was young. Other land-use-history variables were generally less influential than BorderYrs, in that BorderUnburned, MatrixYrs, MatrixUnburned, and Area occurred in best-fit models for 3, 2, 2, and 2 guilds, respectively. CF800 had little effect on the capture rate of core frugivores, in that the best-fit model including that variable received essentially no support (ΔAIC_c = 17.7). InteriorCapRate was included in the best-fit model for core frugivores, ant-followers, and near-ground insectivores but had little effect on other guilds.

Time to recovery.—Mean time to recovery to pre-isolation capture rates across all 10 guilds was 26 years (asymmetric SE = 13 years below and 16 years above estimate; Fig. 1). Nine of 10 guilds showed a recovery to pre-isolation capture rates between 13 and 34 years; our model projects that terrestrial insectivores will take considerably longer at 54 years (with unburned borders) or 67 years (with burned borders; Fig. 2). Area appeared to be an important driver of capture rates of flock obligates along the interface, in that it was included in the best-fit model for the guild and showed an interaction with BorderYrs (Table 2). Although Area had a strong effect on capture rates of flock obligates in the early years after abandonment, the interaction term in the best-fit model suggested that Area had little effect in later years; recovery time was similar among 1-, 10-, and 100-ha fragments at 22.2 years (SE = 5.3 years below and 8.3 years above), 20.9 years (8.2 years below and 18.2 years above), and 17.9 years (12.2 years below and 82.3 years above), respectively. Guilds that we suspected to be among the least sensitive to young secondary forest predictably took the least time to recover: edge species (13 years with border burned; 17 years with border unburned), core frugivores (13 years), and flock dropouts (14 years with burned matrix; 21 years with unburned matrix).

TABLE 2. Details of best-fit models predicting capture rates for each of 10 avian guilds along the primary–secondary forest interface at the Biological Dynamics of Forest Fragments Project, 1991–2011.

Guild	Parameter(s) in best-fit model [a]	$\hat{\beta}$	SE	Number of models [b]
Non-forest species	BorderYrs	−0.11	0.03	11
	BorderUnburned	−1.49	0.42	
	BorderYrs*BorderUnburned	0.09	0.04	
Edge species	BorderYrs	0.08	0.03	13
	BorderUnburned	1.59	0.44	
	BorderYrs*BorderUnburned	−0.11	0.04	
Core frugivores	BorderYrs	0.03	0.01	16
	InteriorCapRate	0.02	0.00	
Ant-followers	BorderYrs	0.12	0.02	16
	InteriorCapRate	0.02	0.01	
Sallying insectivores	BorderYrs	0.10	0.02	16
	MatrixUnburned	−1.15	0.39	
Bark-foragers	BorderYrs	0.07	0.02	16
	MatrixYrs	−0.01	0.00	
Flock dropouts	BorderYrs	0.12	0.02	18
	MatrixUnburned	−0.75	0.38	
Flock obligates	BorderYrs	0.17	0.03	16
	Area	0.50	0.12	
	BorderYrs*Area	−0.02	0.01	
Near-ground insectivores	BorderYrs	0.09	0.02	16
	InteriorCapRate	0.03	0.01	
	Area	−0.13	0.08	
Terrestrial insectivores	BorderYrs	0.06	0.02	16
	BorderUnburned	0.50	0.19	
	MatrixYrs	0.00	0.00	

[a] Intercept parameter not shown.
[b] Total number of *a priori* models run in the candidate set for the guild, including the null model. See Table 1 footnote for variable definitions. Complete model selection results can be found in Tables S2–S11.
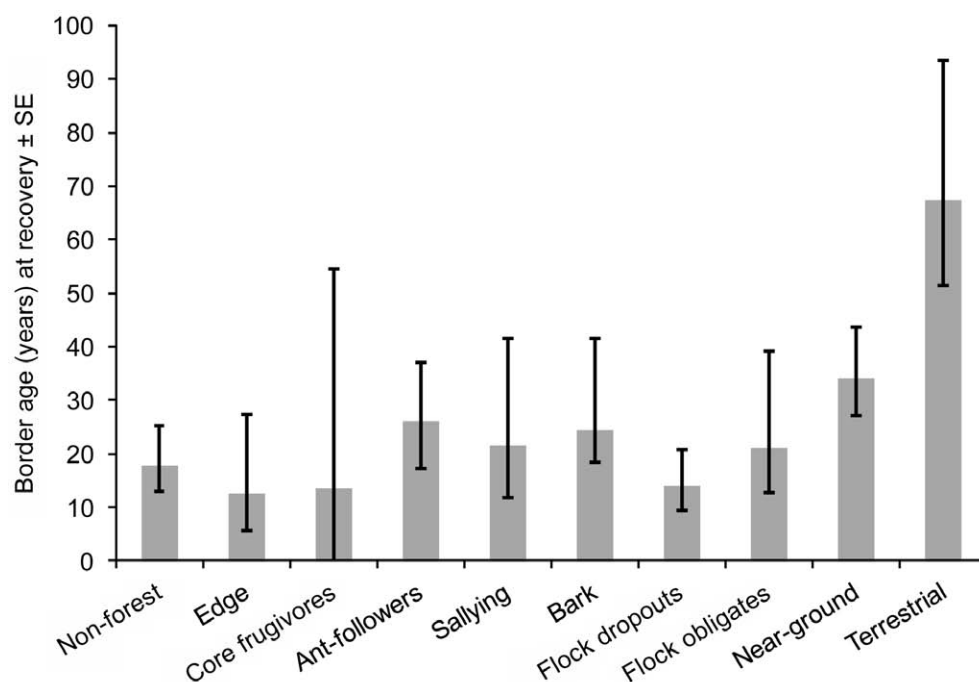
FIG. 1. Estimated time to recovery of capture rates along primary–secondary forest interface to pre-isolation capture rates. For 9 of 10 guilds, capture rates were low along the interface when borders were young, then recovered to pre-isolation capture rates in time. Conversely, capture rates of non-forest species were high along the interface when borders were young, then took ~19 years to decrease to pre-isolation levels. To simplify visualization of recovery for guilds with best-fit models including variable(s) other than border age, values shown represent estimates for burned border (non-forest, edge, terrestrial), burned matrix (sallying, flock dropouts), 10-ha fragments (flock obligates) or mean capture rate in fragment interiors (core frugivores, ant-followers, near-ground). Guilds to the right of core frugivores are insectivorous. This same simplification was also used to calculate mean recovery time for all guilds (see text).
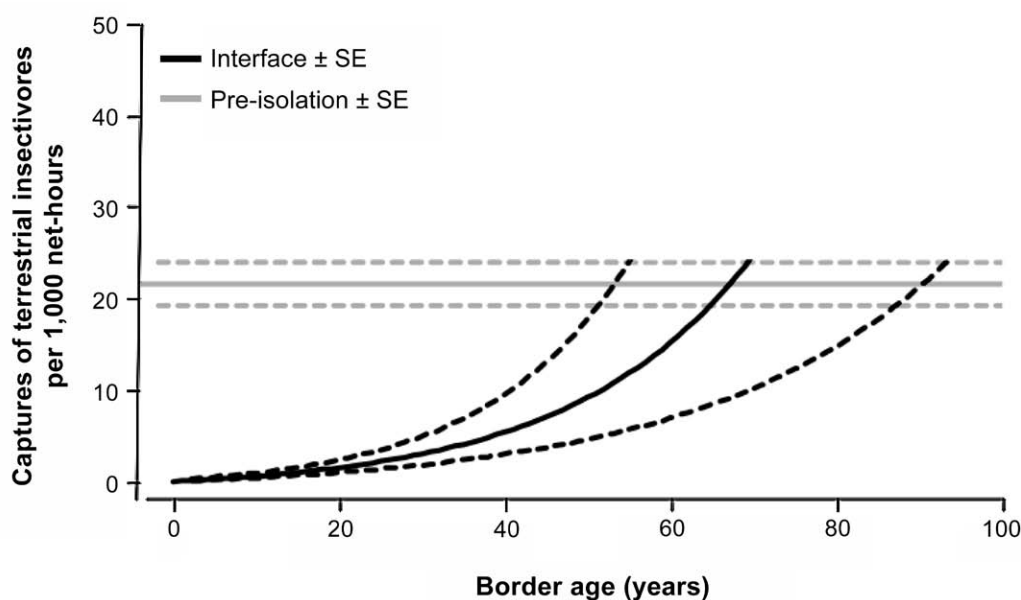

FIG. 2. Curve for the best-fit model predicting capture rate of terrestrial insectivores along the interface of primary forest and secondary forest at the Biological Dynamics of Forest Fragments Project, 1992–2011. The oldest secondary forest sampled was 30 years old, so beyond 30 years, the curve is a projection. The curve shown represents samples with borders burned at least once. The curve stops above the pre-isolation value because we were only interested in modeling recovery up to the pre-isolation capture rates, not beyond.
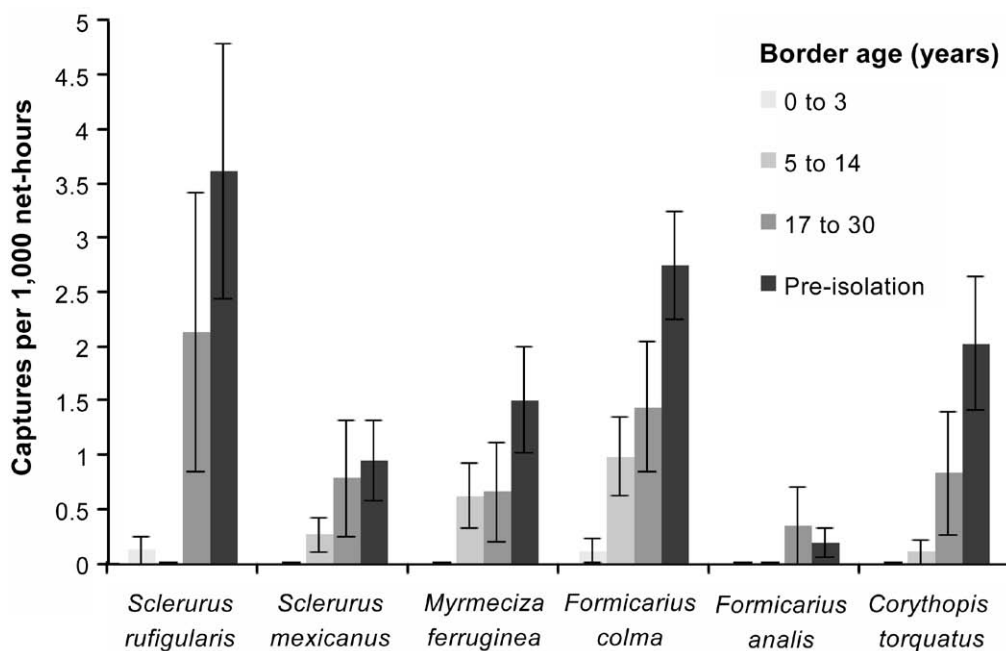
Fig. 3. Capture rates of six terrestrial insectivore species along the primary–secondary forest interface, grouped by age of the secondary forest along the border. The six other terrestrial insectivore species in the guild (*Myrmornis torquata, Grallaria varia, Hylopezus macularius, Conopophaga aurita, Corythopis torquatus,* and *Cyphorhinus arada*) were never captured along the interface.

Terrestrial insectivores.—Of the 12 species of terrestrial insectivores, 6 were never captured along the interface: *Myrmornis torquata*, *Grallaria varia*, *Hylopezus macularius*, *Conopophaga aurita*, *Sclerurus caudacutus*, and *Cyphorhinus arada*. Each of these six species was captured at least once within post-isolation forest fragments, indicating that they were available for capture along the interface but were not caught. We caught 45 individuals from the remaining six terrestrial insectivore species: *Formicarius colma* (*n* = 19), *Myrmeciza ferruginea* (11), *S. rufigularis* (6), *S. mexicanus* (5), *Corythopis torquatus* (3), and *F. analis* (1). When borders were young (1–3 years), we caught only two terrestrial insectivores in 9,858 net-hours: one *S. rufigularis* and one *F. colma*. Capture rates of the six terrestrial insectivores we captured along the interface increased with increasing border age, but only *S. mexicanus* appeared to reach pre-isolation capture rates by 17 to 30 years (Fig. 3). *Sclerurus rufigularis* was conspicuously absent when borders were <14 years old—we caught one in 22,576 net-hours.

Discussion

Although secondary forest is now an important component of the Amazonian landscape, we have few data with which to determine how secondary forest management and distribution affect animal movements. We found that border age had a pervasive influence on capture rates along the interface and that 9 of 10 guilds showed recovery of pre-isolation capture rates along the interface with borders between 13 and 34 years old—terrestrial insectivores should take ~60 years. Border age was included in the best-fit model for all guilds, with a strong positive effect—except for non-forest species, for which the effect was predictably negative (Table 2). The relative importance of other land-use-history characteristics varied, with no other variable

appearing in more than three best-fit models. This importance of border age strongly suggests that management along the interface, specifically age since last cut, is the most important factor driving interface permeability. In other words, birds regain the ability to cross the interface primarily because of secondary forest regrowth in that immediate location; fragment size, burn history, and matrix effects are generally less important. Two previous studies at the BDFFP (Stouffer et al. 2006, Stouffer and Bierregaard 2007) also showed pervasive effects of border age, but on capture rates in forest fragment interiors. Border age thus appears to drive not only colonization–extinction dynamics within forest fragments, but also the permeability of the interface along the edges of forest fragments.

For most guilds in our study, the variation in border age encapsulated most of the variation in interface capture rates without the addition of interior capture rate to the best-fit model. This weak effect of interior capture rate suggests that when birds recolonize fragments following isolation (Stouffer et al. 2011), many likely cross the interface once (e.g., during dispersal), then remain to live within forest-fragment interiors. This pattern may be particularly prevalent with terrestrial insectivores because 6 of 12 species in the guild were captured at least once in forest-fragment interiors but were never captured along the interface. Area, so important in driving capture rates in fragment interiors (Stouffer et al. 2006, Ferraz et al. 2007), was included in the best-fit model for only near-ground insectivores and flock obligates, which suggests that for most guilds, the age of the border drives capture rates along the interface, regardless of fragment size. Given the similarity of recovery times in different fragment sizes for flock obligates and the importance of the interaction term between Area and BorderYrs, area effects may be more important early in recovery, then less important as borders mature; this fits with our conceptual model.

The effect of burning was variable among guilds but clearly had a negative effect on terrestrial insectivores. When burned plots were essentially scorched earth, we did not catch terrestrial insectivores, but the effect appeared to weaken as borders matured, with the recovery time of the guild only marginally different between burned (67 years; SE = 16 years below and 26 years above estimate) and unburned (54 years; SE = 16 years below and 27 years above estimate) treatments. Both floral and avian communities are radically affected by burning following postclearcut abandonment at the BDFFP (Borges and Stouffer 1999, Mesquita et al. 2001). Over time, the dichotomy between secondary forests dominated by tall, fast-growing *Cecropia* (unburned) and short, dense *Vismia* (burned) decreases considerably, with both becoming more similar to primary forest (Norden et al. 2011). Chronosequesces at the BDFFP show that basal area in *Cecropia*-dominated plots was ~3 times that found in *Vismia* plots 5 years after abandonment, but those values converge to 35 m² ha⁻¹ after ~22 years (G. B. Williamson unpubl. data). Structural convergence toward primary forest-like vegetation probably has a profound effect on decisions made by moving birds.

Recovery of structural complexity over time.—Mean recovery to pre-isolation capture rates was 26 years (SE = 13 years below and 16 years above estimate), roughly consistent with Dunn's (2004) estimate of recovery of tropical avian species richness in 20 years. Not surprisingly, edge species and flock dropouts, among the first guilds to colonize young secondary forest, were among the first to recover, ~14 years after cutting and abandoning the border. Stouffer and Bierregaard (2007) estimated that in the interiors of 1- and 10-ha fragments at the BDFFP, flock dropouts recovered 21 years after border abandonment and core frugivores 15 years after. Flock obligates, thought to be among the most sensitive guilds, were surprisingly quick to recover, at ~21 years, consistent with Stouffer and Bierregaard's (2007) estimate of fragment interior recovery for the guild (16 years). As Stratford and Stouffer (1999) envisioned, terrestrial insectivores indeed took the longest to recover (mean 61 years), nearly tripling Dunn's (2004) recovery estimate. Even along the interface with the oldest secondary forest at the BDFFP, individual species of terrestrial insectivores were remarkably consistent in providing little evidence of recovery (Fig. 3), but we caution that our estimate of recovery for this guild is a projection beyond 30 years—only time will tell precisely how long terrestrial insectivores take to recover. It seems unlikely that the vulnerability within terrestrial insectivores is due to phylogenetic effect, because the 12 species are members of seven different families; conversely, 10 of 12 species are found within the suboscine infraorder Furnariides (i.e., tracheophones). Curiously, near-ground insectivores (a guild in which the sample is dominated by *Willisornis poecilinotus*) had the second-longest recovery time, 34 years. From the rainforests of Peninsular Malaysia, to the Ecuadorian Amazon, several studies have also found that ground-dwelling species are most vulnerable to disturbance (Canaday and Rivadeneyra 2001, Peh et al. 2005, M. Zakaria Hussin unpubl. data), which suggests that the structure of secondary forest near the ground may drive movement rates and/ or occupancy, so these forest floor guilds could potentially be used as indicators of the quality of tropical secondary forests worldwide. Aside from vegetation structure itself, mechanism(s) driving the absence of terrestrial insectivores from secondary forests may include lack of resources (e.g., food, nest sites), light or heat aversion, or elevated predation risk (Wright et al. 1994, Raheem et al. 2009).

The structural complexity of the understory converges with primary forest over time since abandonment (Norden et al. 2011), which likely helps drive the recovery of bird movement. Five years after abandonment, basal area of trees at the BDFFP is dominated by a monoculture of *Vismia* (cut and burned; dominance = 0.90) or *Cecropia* trees (cut only; dominance = 0.79); monogeneric dominance is reduced to 0.35 after 22 years in *Vismia* plots, and to 0.05 after 26 years in *Cecropia* plots (G. B. Williamson unpubl. data). Further, linear regressions predict that tree species at the BDFFP increase from only 10 species per 500 m² after 5 years (*Cecropia* and *Vismia* plots) to approximately 50 and 117 species after 26 years for *Vismia* and *Cecropia* plots, respectively (Williamson et al. 2013). Thus, at the mean recovery time of 26 years post-abandonment for all avian guilds in the present study, secondary forest trees are 5 to 12 times more diverse than after only 5 years, providing direct benefits to frugivores (e.g., availability of new fruit species) and indirect benefits to insectivores (habitat for new species of arthropods).

Caveats.—Our study focused on quantifying recovery of avian movement but is not an attempt to document demographic patterns, measures of fitness, or site fidelity. For example, movement rates may recover, but secondary forest or small fragments of primary forest could be occupied by less competitive or young birds that are less productive (Johnson 2011) or in poorer condition (Stratford and Stouffer 2001). We therefore advocate the further development of aging techniques for tropical birds (Johnson et al. 2011, E. I. Johnson unpubl. banding guide) so that underlying demographic patterns can be understood. Further, estimates of survival would certainly be meaningful predictors of recovery, but even long-term capture data sets like that of the BDFFP suffer from sampling issues that make the estimation of survival challenging (Ruiz-Gutiérrez et al. 2012). Ultimately, a complete understanding of the dynamics of secondary forest recovery will depend on researchers' ability to integrate measures of movement, demography, and fitness, building toward a comprehensive model of (meta)population movement and population viability in variable landscapes.

Finally, our study provides a robust framework for studying avian movement along the primary–secondary forest interface, but the landscape context of the BDFFP likely makes our recovery estimates optimistic in relation to heavily fragmented landscapes. The landscape context of the secondary forest has a considerable influence on recovery (Chazdon et al. 2009), with mostly primary forest landscapes recovering faster than degraded landscapes (Dent and Wright 2009). Landscapes under heavy deforestation pressure such as vast tracts of Pará and Rondônia likely present fewer opportunities for bird colonization of forest fragments than more remote, intact areas of Amazonia (INPE 2010). Further, agricultural expansion in fragmented areas results in less clearcut abandonment, more burning, and, thus, less forest succession (Fearnside 2005). The hundreds of square kilometers of unbroken primary rainforest that surround the BDFFP provide opportunities for (re)colonization of forest fragments isolated by dozens to hundreds of meters. Our estimates can be interpreted positively, in that 9 of 10 guilds recovered in <34 years. However, without the opportunities for recolonization from large tracts of primary rainforest nearby, recovery times will be much longer (and infinite as species become extinct on the landscape).

Conservation implications.—Even with heavy deforestation over the past few decades, most of the Amazon rainforest remains unbroken within vast continuous blocks; 54% of Amazonia is set

aside in protected areas (Soares-Filho et al. 2010). Thus, the majority of Amazonian second growth is quite similar to the BDFFP—surrounded by mostly continuous primary forest—so our estimates of recovery time should apply broadly. Amazonia now contains vast areas of secondary forest that are not a substitute for primary forest (Gibson et al. 2011) but could at least serve as buffers of, or corridors among patches of primary forest. We clearly show that secondary growth has value for understory birds: 34-year-old secondary forest is not a barrier to 9 of 10 avian guilds, and by ~60 years, even most terrestrial insectivores will likely view the interface as entirely permeable. For a more complete understanding of the conservation value of secondary forest as a corridor, we must combine our knowledge of area and isolation with an understanding of how animals move (and disperse) among forest fragments imbedded in a matrix of roads, agricultural land, and variable secondary forest.

Supporting Information

Guild assignments (Table S1) and complete model selection results for each guild (Tables S2–S11) are available online at dx.doi.org/10.1525/auk.2013.12202. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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