BIOTROPICA
THE JOURNAL OF THE ASSOCIATION FOR TROPICAL BIOLOGY AND CONSERVATION

BIOTROPICA 47(6): 723–732 2015 10.1111/btp.12253

Changes in Habitat Use at Rain Forest Edges Through Succession: a Case Study of Understory Birds in the Brazilian Amazon

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ABSTRACT

Primary tropical rain forests are being rapidly perforated with new edges via roads, logging, and pastures, and vast areas of secondary forest accumulate following abandonment of agricultural lands. To determine how insectivorous Amazonian understory birds respond to edges between primary rain forest and three age classes of secondary forest, we radio-tracked two woodcreepers (*Glyphorynchus spirurus*, $N = 17$; *Xiphorhynchus pardalotus*, $N = 18$) and a terrestrial antthrush (*Formicarius colma*, $N = 19$). We modeled species-specific response to distance to forest edge (a continuous variable) based on observations at varying distances from the primary-secondary forest interface. All species avoided 8–14-yr-old secondary forest. *Glyphorynchus spirurus* and *F. colma* mostly remained within primary forest <100 m from the young edge. Young *F. colma* rarely penetrated >100 m into secondary forest 27–31 yr old. Young *Formicarius colma* and most *G. spirurus* showed a unimodal response to 8–14-yr-old secondary forest, with relative activity concentrated just inside primary forest. After land abandonment, *G. spirurus* was the first to recover to the point where there was no detectable edge response (after 11–14 yr), whereas *X. pardalotus* was intermediate (15–20 yr), and *F. colma* last (28–30 yr +). Given the relatively quick recovery by our woodcreeper species, new legislation on protection of secondary forests > 20-yr old in Brazil's Pará state may represent a new opportunity for conservation and management; however, secondary forest must mature to at least 30 yr before the full compliment of rain forest-dependent species can use secondary forest without adverse edge effects.

Abstract in Portuguese is available with online material.

Key words: antthrush; continuous edge response; fragmentation; Neotropical birds; secondary forest; terrestrial insectivores; woodcreeper.

Habitat loss often leads to fragmentation, isolation of remnant habitat and heterogeneous landscapes rich in edges. For example, in a 1.2 million km^2 area of the Brazilian Amazon, deforestation and logging generated ~70,000 km of new forest edges from 1999 to 2002 (Broadbent *et al.* 2008). Although both annual deforestation rates and the number of new large-scale clearings have slowed recently in the Brazilian Amazon (INPE 2013), the number of new small forest clearings (<50 ha) has remained consistent (Rosa *et al.* 2012); thus, there is now an enormous and ever growing matrix of roadways and small clearings along with an associated network of forest edges much greater than would be created by an equivalent area of large clearings. Edge effects are one of the principal drivers of both species- and community-level response to fragmentation (Laurance *et al.* 2002, Ries and Sisk, 2004).

Most resident insectivorous birds of the tropical rain forest understory are especially edge-averse, even more so than their temperate and frugivorous counterparts (Lindell *et al.* 2007). There are several likely reasons for this edge sensitivity of tropical insectivores, including dietary specialization (Rosenberg 1990, Marra & Remsen 1997), differences in insect community composition between edge and interior (Didham *et al.* 1998), the behavioral reticence of the guild to cross gaps (Lees & Peres 2009, Ibarra-Macias *et al.* 2011), and the relative abundance of fruit and nectar favored by frugivores and nectarivores along edges due to increased light (Stiles 1975, Levey 1988, Rodewald & Brittingham 2004). At our study site, the Biological Dynamics of Forest Fragments Project (BDFFP), Laurance *et al.* (2004) found that five of eight foraging guilds of understory insectivorous birds had lower

Received 13 October 2014; revision accepted 1 May 2015.

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capture rates within 70 m of forest road edges, including all 14 species of terrestrial insectivore examined.

In addition to the creation of new edges, timber management and abandonment of agricultural areas creates a complex landscape that includes primary forest, selectively logged forest, agricultural areas and secondary forest in different stages of regeneration. Secondary forests now constitute 4.5 million km^2 of humid tropical forests worldwide (Asner *et al.* 2009) and in the Brazilian Amazon, the area of secondary forest increased from 29,000 to 161,000 km^2 from 1978–2002 alone (Neeff *et al.* 2006) —about two thirds the size of the United Kingdom. Borges (2007), working in Jaú National Park, Brazil, found that sites in primary forest were richer in insectivorous mixed-species flock species than sites in secondary forest. However, given enough time for forest succession, secondary forest can recover the majority of species present in primary forest (Moura *et al.* 2013) and can likely serve as an effective corridor between and buffer of primary forest patches (Chazdon *et al.* 2009). The details of forest recovery remain poorly understood, in part because the time scale for recovery of forest biodiversity in secondary forest is poorly calibrated (Wright & Muller-Landau 2006). Prior research has made it clear that: (1) edges are not static in time; (2) edges influence communities within forest fragments; and (3) edges and secondary forest composition influence the community at the landscape scale (Porensky 2011).

As we continue to lose tropical forest and the remaining patches of primary forest continue to be fragmented by roads, agricultural fields, secondary forests etc., it becomes increasingly important to understand how animals respond to those edges between habitats across space and time. Because edges are the first barrier for a dispersing animal to cross if it is to move among forest fragments, hard edges at the landscape scale can reduce functional connectivity among forest fragments (Porensky 2011), which isolates populations and elevates extinction risk (Laurance 2000). Few studies have tracked edge responses of tropical birds in both directions from the edge (*i.e.*, not just 'inside' the primary forest), or quantified distance to edge as continuous in space (Ewers & Didham 2006, but see Zurita *et al.* 2012); none have tracked the dynamics of avian edge responses across age classes of secondary forest.

Here we present what we believe is a realistic and practically applicable approach for studying the spatiotemporal effect of edges on Amazonian birds with respect to secondary forest. Our main objectives were twofold: (1) to quantify and compare the edge responses of three common understory insectivores with different patterns of space use among primary forest and three age classes of secondary forest; and (2) to estimate the minimum time after land abandonment at which there is no avian edge response (*i.e.*, 'recovery' of secondary forest). Given known differences in natural histories among our three study species (see Methods: Study species), we predicted that edge avoidance would gradually decrease with age of secondary growth adjacent to primary forest, and that *Glyphorynchus spirurus*, a versatile woodcreeper, would recover first, whereas *Formicarius colma*, a terrestrial antthrush, would recover last.

METHODS

Study area.—We conducted fieldwork during the June to October 'dry' seasons of 2009, 2010, and 2011 at the BDFFP, which is located approximately 80 km north of Manaus, Amazonas, Brazil (2°30′ S, 60° W; for site details, see Bierregaard & Gascon 2001, Laurance *et al.* 2011). The ~140-km^2 experimental forest within the BDFFP (Fig. 1) is embedded within a vast area of continuous primary rain forest to the north, east and west, with increasing anthropogenic influence toward Manaus in the south. The BDFFP presents a landscape context distinct from that of other research performed in severely fragmented tracts of Pará and Rondônia (Brazilian National Space Research Institute [INPE] 2010).

The BDFFP consists of 11 experimentally isolated forest fragments (five 1 ha, four 10 ha and two 100 ha; Fig. 1) within a matrix that is primarily secondary forest of various ages, but also includes pasture and forest roads. We pooled secondary forest into three age classes based on the natural breaks in age distributions that arose from the temporal pattern of cutting and abandonment at the BDFFP: 'young' (8–14-yr old; mean canopy height ~6 m), 'intermediate' (15–24; ~17 m tall) and 'old' (27–31; ~19 m tall). Primary forest at the BDFFP in areas used by our focal birds averaged about 23 m tall with occasional emergent trees up to 55 m (Gascon & Bierregaard 2001). Mean canopy heights listed here are from areas used by radio-tagged birds and were estimated from a LiDAR canopy height model from 2007 (M. Lefsky and S. Saleska, unpubl. data).

Study species.—We selected three common species that were catchable enough for us to obtain a reasonable sample size and varied in their natural histories and abundances in secondary forest. *Glyphorynchus spirurus* is an abundant small woodcreeper that can forage independently or as part of mixed-species flocks; it is found in primary forest, edges, and secondary forest (Cohn-Haft *et al.* 1997). *Xiphorhynchus pardalotus* is a medium-sized woodcreeper that is typically part of the core of understory mixed-species foraging flocks. The species is common in primary forest, but has also been reported in secondary forest (Marantz *et al.* 2003). *Formicarius colma* is a medium-sized solitary terrestrial antthrush that forages by walking along the forest floor alone or in pairs, picking invertebrates from leaf litter and flipping leaves as it goes (Krabbe & Schulenberg 2003). The species is rare or absent in secondary forest (Cohn-Haft *et al.*1997, Krabbe & Schulenberg 2003, Barlow *et al.* 2007), and movement by the *F. colma* was strongly impeded by 20-yr-old edges created by forest road clearings at the BDFFP (Laurance *et al.* 2004). See Appendix S1 for more detail on the study site and focal species.

Captures.—We captured and radio-tagged birds throughout the BDFFP, including within nine of the 11 forest fragments, spacing captures such that there was little home range overlap between individuals of the same species (Fig. 1). We tagged both adult and young *F. colma* (see Supporting information), but the woodcreepers could not be reliably aged in the hand after their skulls

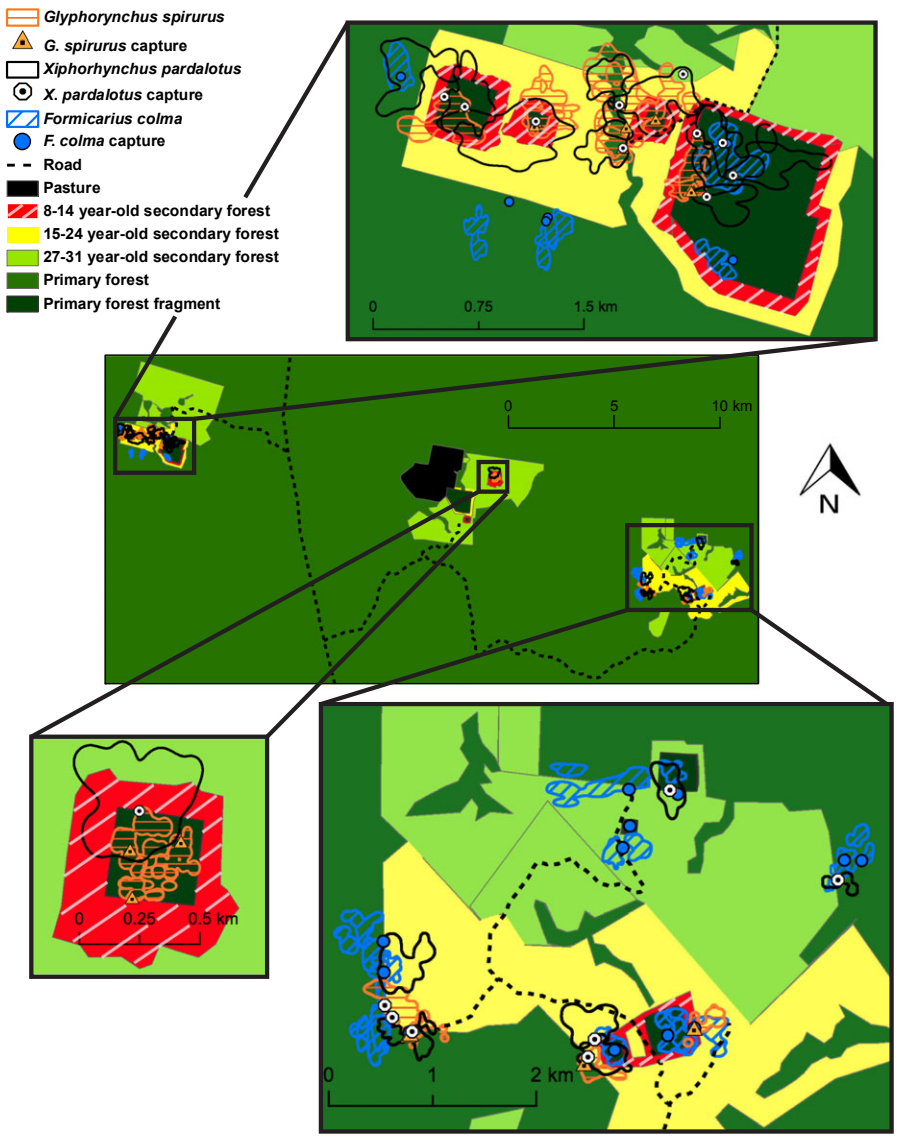

FIGURE 1. Distribution of home ranges and capture locations of radio-tagged *Glyphorynchus spirurus* (*N* = 17), *Xiphorhynchus pardalotus* (*N* = 18), and *Formicarius colma* (*N* = 19) tracked for analysis of edge response at the Biological Dynamics of Forest Fragments Project. The entire experimental forest is pictured at center with three insets identified by thick black outlines.

ossified, so we radio-tagged only 'adult' woodcreepers with ossified skulls. We fitted each bird with a radio transmitter (<5% of body weight) from Holohil Systems Ltd. (Carp, ON, Canada; model BD-2) using a 0.8-mm-diameter elastic thread harness (modified from Rappole & Tipton 1991).

We captured using both passive netting and target netting with conspecific playback. We sought to capture the individuals holding conspecific territories closest to edges and to evaluate variation in edge activity by birds using multiple forest ages. We started with 12-m mist nets on edges, capturing 21 (six *G. spirurus*, eight *X. pardalotus*, and seven *F. colma*) of 54 focal birds directly along edges. If we failed to capture any individuals along the edge on the initial attempt, we gradually placed target nets further into primary or secondary forest until we caught a bird holding the territory closest to the edge. All else equal, this approach allowed us to assume that focal birds had free access to both primary and adjacent secondary forest, and that no other conspecific territory was between the focal territory and the edge. Because of the relative rarity of our focal species in (particularly the youngest) secondary forest and the capture strategy, we caught most birds just within primary forest. Mean distance from capture location to secondary forest (*i.e.*, the edge) was 25 m (±15 SE) for *G. spirurus*, 39 m (±29 SE) for *X. pardalotus* and 24 m (±19 SE) for *F. colma* (Fig. 1).

RADIO TRACKING.—All species could easily cross their home ranges in 15 min, so we used this interval as the minimum time between relocations that allowed 'biological independence' among

locations (Lair 1987: 1099). We stratified the daylight hours into four equal time blocks, collecting at least five locations within each time block to control for diurnal patterns in bird activity. We triangulated bearings with Location of a Signal (LOAS) v. 4.0.3.3 (Biotas™ 2004), and excluded locations for which the error ellipse was > 40 percent of the home range size. We tracked individuals as over a period lasting an average of 23.6 (±3.0 SE) days. This approach resulted in a mean of 37 ± 2.4 SE locations per *G. spirurus,* 39 ± 3.0 SE for *X. pardalotus* and 42 ± 3.2 SE for *F. colma*. The resulting dataset was very similar to that used in Powell *et al.* (2015) for a study of movement rates among habitats.

Data analysis.—To evaluate habitat-specific edge response, we employed the approach used by both Ewers and Didham (2006) and Zurita *et al.* (2012), which continuously quantifies distance inside and outside of the primary-secondary forest interface. We defined three secondary forest age classes (see Methods: study area). Similar to the analysis of Zurita *et al.* (2012), we estimated the relative activity of each species in secondary forest relative to primary forest along eight distance belts, with distance belts placed with increasing distance to the interface between habitats (*i.e.*, the edge). We selected the scale of distance belts (0–19.9 m, 20.0–49.9, 50.0–99.9, 100.0–149.9, 150.0–199.9, 200.0–400) because they fall within the scale of the mean home range size of target species: 299 m for *G. spirurus*, 413 m for *X. pardalotus,* and 316 m for *F. colma*. Figure S1 provides an example of distance belts, and our calculation of habitat availability and relative activity. Home range estimates were calculated with the 95 percent kernel density estimator and taken from Powell (2013). Relative activity is an index of the number of telemetry records per distance belt. We performed a correction on relative activity to account for habitat availability within each distance belt. We defined 'available' habitat as everything contained in a buffered region around the birds' capture location, with the diameter of the buffer equal to the diameter of the mean species home range (Zurita *et al.* 2012). For example, in a given distance belt, if young secondary forest represented only 20 percent of the total habitat cover inside the buffer, we weighed the relative activity for each species in this habitat by 0.2. With this approach we minimize the effects of under or over estimating relative activity as a consequence of the availability of different habitat cover.

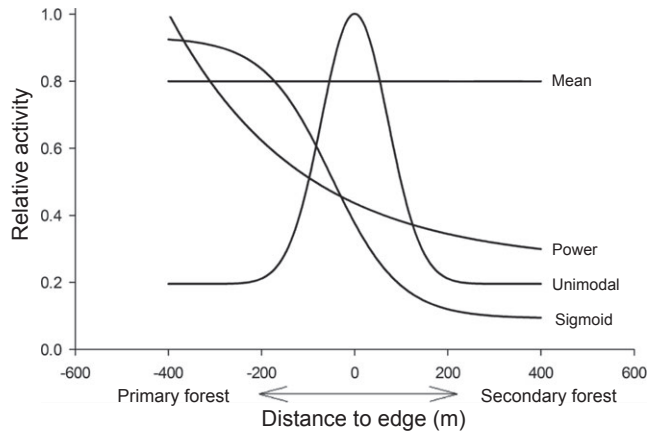

FIGURE 2. Theoretical response of birds to the edge between primary and secondary forest. Linear model (not shown for clarity) is a non-horizontal straight line. See supporting information for more detail on these models, including formulas.

ence (increased relative activity near the edge) or no edge response (relative activity not quantifiably different on either side of edge). We used relative activity of each species per distance belt as the dependent variable and the distance to the primary-secondary forest edge (binned) as the independent variable. We denoted distances inside primary forest as negative values on the *x*-axis, whereas distances inside secondary forest were positive (zero is the edge). Using an iterative regression procedure, we fitted each species to all models, and then used Akaike's Information Criterion with a correction for small sample size (AIC_c) to compare among five models (Fig. 2, Table S1; see Ewers & Didham 2006, & Zurita *et al.* 2012 for more detail). We used the best-fit models based on AIC_c in subsequent analyses as well as to visualize edge response (Figs. 3–5).

To quantify the progression of each species' edge response as secondary forest matured, we first estimated the magnitude of the edge effect, which we calculated using percent difference between the lower and upper asymptote of the sigmoid function (Y_{min} and Y_{max}), or in the case of a unimodal response, the lower and upper asymptote of the power functions. To quantify habitat use in three age classes of secondary forest relative to primary forest, we divided relative activity in primary forest (Y_{max}) by relative activity on secondary forest (Y_{min}), where a coefficient greater than one

$$\text{Relative activity on distance belt X and habitat Y} = \frac{\text{Number of telemetry records in X}}{\text{Area of X} \times \text{Proportional cover of Y}}. \quad (1)$$

We used a series of theoretical models (mean, lineal, power, sigmoid, and unimodal) to quantify the relative activity of each species at increasing distances inside and outside the edge (Fig. 2). More detail describing models, including their formulas, may be found in Supporting Information. Birds may show edge avoidance (decreased relative activity near the edge), edge prefer-

indicates greater use in secondary forest and a coefficient less than one indicates lower use relative to primary forest. To visualize the recovery paths, we used three theoretical functions to describe the relationship between primary/secondary forest use and forest age: lineal, exponential, or sigmoid. Because the number of independent secondary forest ages (3) was too small to perform a regression

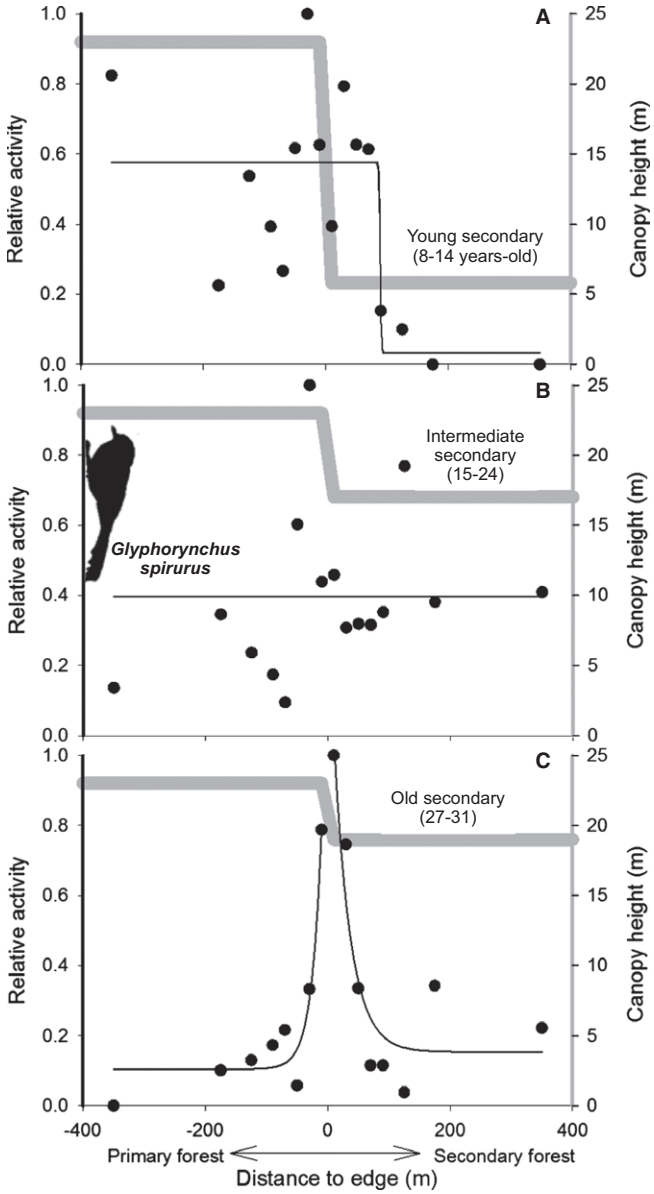

FIGURE 3. Response of radio-tagged *Glyphorynchus spirurus* to edges between primary forest and young (A; 8–14-yr old), intermediate (B; 15–24-yr old) and old (C; 27–31-yr old) secondary forest in the Brazilian Amazon. Gray line represents canopy height.

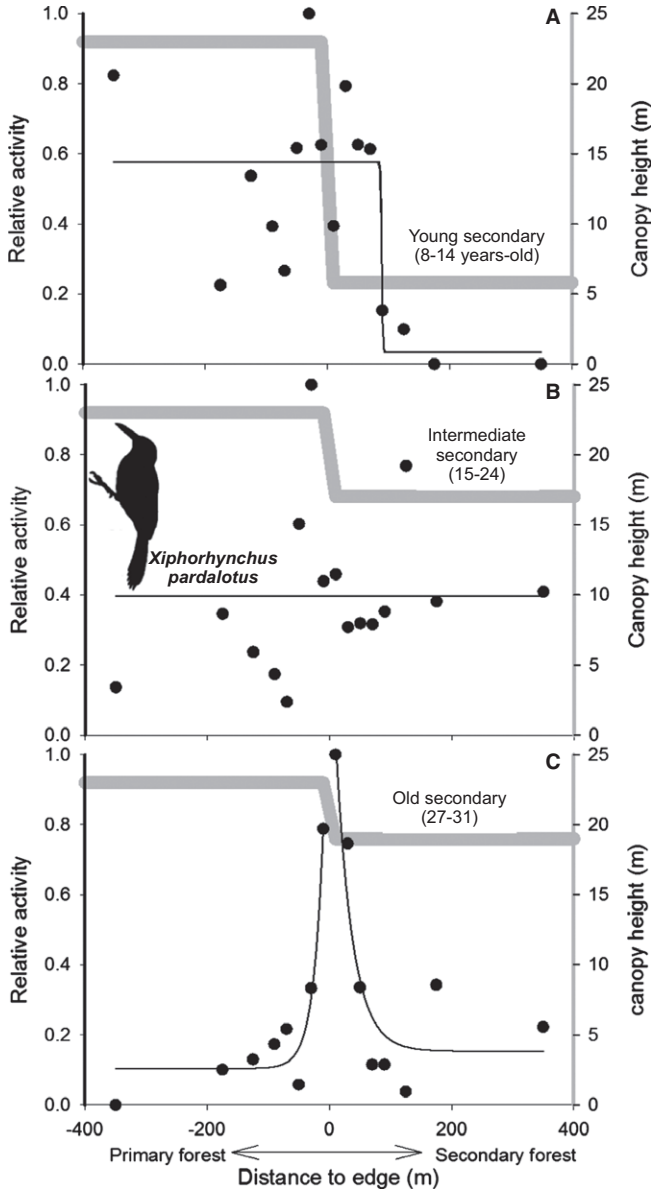

FIGURE 4. Response of radio-tagged *Xiphorhynchus pardalotus* to edges between primary forest and young (A; 8–14-yr old), intermediate (B; 15–24-yr old) and old (C; 27–31-yr old) secondary forest in the Brazilian Amazon. Gray line represents relative canopy height.

analysis, we only performed non-parametric correlations and a visual exploration of the area covered by the three potential functions; the intersection between this area and a line at $y = 1$ represented the forest age at which there was no detectable edge effect, *i.e.*, the point of recovery. Of our focal species, only *F. colma* could be sexed in the hand, but sex was not considered in the analyses as we worked during the species' non-breeding season, so we had no *a priori* reason to suspect that sex had an effect on edge response. We used SigmaPlot v. 11.0 (Systat Software, Inc., San Jose California USA, www.sigmaplot.com) for all analyses and graphs.

RESULTS

We radio-tracked 17 *G. spirurus* (387 locations in primary forest; 257 in secondary forest), 18 *X. pardalotus* (398 primary; 257 secondary) and 19 *F. colma* (612 primary; 188 secondary). The 19 *F. colma* included seven young, 11 adults, and one bird of unknown age (see supporting information for definitions of 'young' and 'adult'). *Glyphorynchus spirurus* showed a strong unimodal edge response, with highest relative activity levels along the edge of primary and young secondary forest. Relative

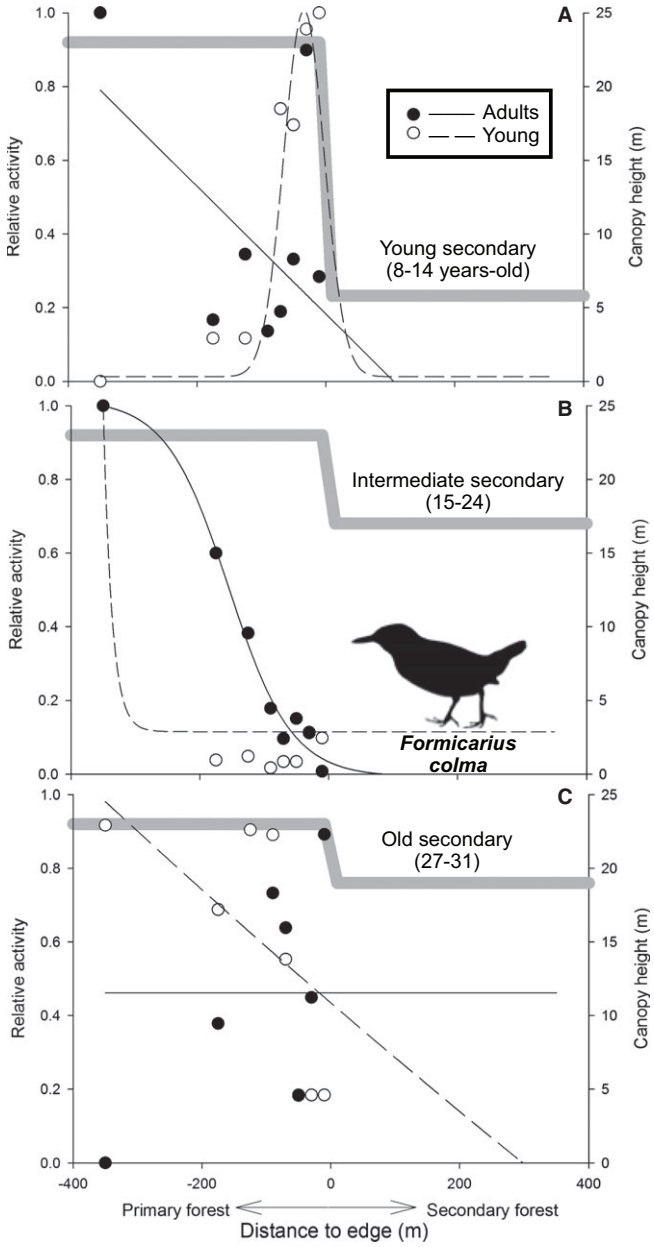

FIGURE 5. Response of radio-tagged juvenile and adult *Formicarius colma* to edges between primary forest and young (A; 8–14-yr old), intermediate (B; 15–24-yr old) and old (C; 27–31-yr old) secondary forest in the Brazilian Amazon. Filled circles and solid lines represent adults; open circles and dashed lines represent juveniles, and the gray line represents canopy height. Note that a datapoint for juveniles is concealed under an adult datapoint in the top left of (B).

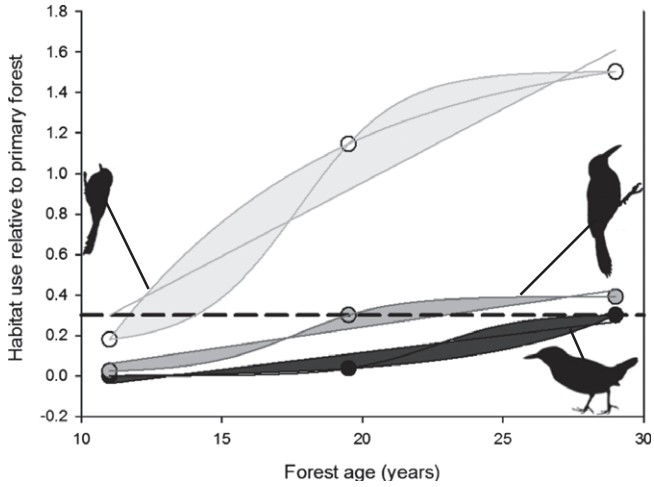

FIGURE 6. Relationship between relative activity levels in primary vs. secondary forest for three species of understory insectivores at the Biological Dynamics of Fragments Project near Manaus, Brazil. Open circles represent *Glyphorynchus spirurus,* filled gray circles is *Xiphorhynchus pardalotus* and black circles represent *Formicarius colma*; lines connecting circles represent linear, exponential and sigmoidal regressions. For each species, the point of intersection between regression lines and the dashed line (representing primary forest) is the age at which relative activity in primary and secondary forest is equivalent. For *X. pardalotus*, only two regression lines are visible because linear and exponential functions overlap.

activity was highest within 100 m of the primary forest side of the edge (Fig. 3A). Intermediate and old secondary forest had increasingly higher relative activity than primary forest for *G. spirurus,* as represented by the sigmoidal response curves (Figs. 3B and C).

Xiphorhynchus pardalotus showed a strong sigmoidal edge response to young secondary forest with relative activity dropping off sharply 100 m into secondary forest (Fig. 4A). The species showed no response to intermediate secondary forest edges (Fig. 4B), but a strong unimodal response at edges of primary forest and old secondary forest, with relative activity concentrated precisely along the edge (Fig. 4C).

In young secondary forest, young, *F. colma* showed a unimodal response, clustering relative activity about 50 m inside primary forest, whereas adult birds showed a linear trend with relative activity increasing with distance inside primary forest (Fig. 5A). In intermediate secondary forest, both young and adult birds showed a sigmoidal response with higher relative activity within primary forest; adults avoided intermediate secondary forest entirely, whereas young birds penetrated into intermediate secondary forest more frequently (Fig. 5B). When primary forest formed an edge with old secondary forest, adult *F. colma* showed no edge response—both habitats were used equally; however, young birds showed a linear response, with practically no relative activity >100 m outside primary forest (Fig. 5C).

When calculating 'recovery' of secondary forest—the point of no detectable edge response—we found that as predicted, edge effect diminished with increasing age of secondary growth (Fig. 6), and that *G. spirurus* was the first species to recover to the point of no edge effect (after 11–14 yr). *Xiphorhynchus pardalotus* took second longest to recover (15–20 yr), and *F. colma* took the longest (28–30 yr or more; Fig. 6).

DISCUSSION

All three understory rain forest species showed a unimodal spike of relative activity at or near the edge in at least one age of secondary growth (Figs. 1A, 2C, and 3A). For forest birds, edge effects along hard edges are generally thought to be negative (*sensu* Gates & Gysel 1978, but see Zurita *et al.* 2012, Lenz *et al.* 2014), and the BDFFP is no exception (Laurance *et al.* 2002). However, due to land abandonment at the BDFFP, edges have become softer over time, and now appear to provide resources for these three rain forest species—two of which, *X. pardalotus* and *F. colma*, are typically defined as forest interior rather than edge species (Cohn-Haft *et al.* 1997, Krabbe & Schulenberg 2003, Marantz *et al.* 2003). Unlike *G. spirurus*, *X. pardalotus* did not concentrate relative activity along edges of young secondary forest; rather, relative activity was equally high in primary forest and along the edge, and then dropped off sharply after about 100 m into the secondary forest. We suspect differences between the two woodcreepers can be explained by their foraging strategies and willingness to leave mixed-species flocks. *Xiphorhynchus pardalotus* is typically much more closely associated with mixed-species flocks than *G. spirurus* (Cohn-Haft *et al.* 1997), so it may simply join other flock members along edges to reap the benefits of increased vigilance in searching for predators such as *Micrastur* forest falcons (Thiollay & Jullien 1998).

Pattern of edge response to young secondary forest.—Young *F. colma* showed a peak of relative activity about 50 m inside young secondary forest edges, whereas adults simply showed a linear trend with relative activity increasing with increasing distance inside primary forest. Adult *F. colma* occupy year-round territories that they defend against conspecifics (Stouffer 1997), so dominant adult territory holders appear to exclude subordinate young, pushing them into marginal habitats (*i.e.*, edges alongside young secondary forest), as Johnson (2011) found in small fragments at the BDFFP. Young secondary forest may offer few resources for terrestrial insectivores such as *F. colma*, as the understory is dry, bright, and has a thick leaf litter, which is generally avoided by terrestrial insectivores (Stratford & Stouffer 2013, 2015).

In the only other study using the same statistical approach we used here, Zurita *et al.* (2012) analyzed the edge responses of three Atlantic rain forest birds in Brazil. The terrestrial leaftosser *Sclerurus scansor* was the only species that showed a unimodal response to edges between ~80-yr-old and ~20–50-yr-old secondary forest; this response was nearly identical to that of *F. colma* in this study, with the peak of relative activity concentrated about 30 m inside the edge of primary forest (forest ages from M. Hansbauer, pers. comm.). By estimating that *G. spirurus* and young *F. colma* congregate just inside primary forest when it abuts young secondary forest, we present a similar, but subtly different description of the predicted edge response than that described in Ries and Sisk's (2004) conceptual model. Ries and Sisk (2004) predict that when one habitat is of higher quality than the other and resources are complimentary (*i.e.*, divided between habitats), then abundance will peak right at the edge. For both *F. colma* and *G. spirurus*, however, we did find a peak in activity along young secondary forest edges, but relative activity was concentrated *just inside* primary forest, not immediately on the edge as the conceptual model predicts.

Pattern of edge response to intermediate and old secondary forest.—All three species showed a fundamentally different pattern of relative activity along the edges of intermediate secondary forest compared to young secondary forest. *Glyphorynchus spirurus* showed considerably higher relative activity levels in intermediate secondary forest relative to primary forest, suggesting that at this point the species had passed the point of recovery (where activity levels are indistinguishable to those in primary forest, *i.e.*, no detectable edge effect). One possible explanation is the virtual absence of other small woodcreepers from younger secondary forest (Cohn-Haft *et al.* 1997, Barlow *et al.* 2007), which may allow *G. spirurus* to exploit foraging niches not available in relatively species-rich primary forest (*i.e.*, release from competition, Powell 2013). *Xiphorhynchus pardalotus* showed no edge response at the intermediate age class, suggesting that this was the point of recovery to no edge effect for the species. *Formicarius colma* showed a more gradual negative response to intermediate secondary forest; relative activity levels were highest >200 m into primary forest, suggesting that negative edge effects extend a considerable distance into the primary forest. Young *F. colma* were more likely to venture out into intermediate secondary forest than adults. The most likely mechanism to explain this pattern is that rather than restricting *F. colma* to within forest fragments as appears to occur alongside pasture and edges of young secondary forest (*i.e.*, hard edges), the conditions in intermediate secondary forest soften, allowing young birds to wander away from edges of primary forest. Further, adult birds likely hold territories in much of the primary forest habitat, whereas young birds may have more access to nearby sub-par, yet unoccupied intermediate secondary forest. Stratford and Stouffer (2013) found that at the BDFFP, terrestrial insectivores were associated with thinner leaf litter, more large trees, and fewer small trees than expected; those conditions are not likely to arise until secondary forest matures beyond intermediate age. The dense understory that develops early in forest succession may be less useful for terrestrial insectivores like *F. colma*; this may be particularly evident when land is burned after cutting, as it tends to develop into a dense *Vismia*- rather than thin *Cecropia*-dominated understory (Mesquita *et al.* 2001, Powell *et al.* 2013).

Responses to old secondary forest edges were fundamentally different from responses to younger secondary forest. *Glyphorynchus spirurus* showed considerably higher relative activity levels in old secondary forest relative to primary forest, which probably a explanation to that described above for intermediate forest. *Xiphorhynchus pardalotus* showed a strong unimodal edge response when the oldest secondary forest abutted primary forest, with relative activity concentrated precisely along the edge,

perhaps due to the species' participation in mixed-species flocks, which often show increased relative activity levels along edges (K. Mokross, pers. comm). *Formicarius colma* adults showed no response to edges along the oldest secondary growth; however, young birds showed a linear trend with the highest relative activity levels were in primary forest with very little relative activity >100 m into old secondary forest. This suggests that even 30 yr after abandonment of deforested areas, resources may still be suboptimal for young *F. colma* far from primary forest. We caution that due to the challenge in capturing any *F. colma* near or within secondary forest, we tracked only two young *F. colma* near old secondary forest. Although both of these young *F. colma* had several kilometers of old secondary forest available to them (Fig. 1; bottom right inset), any results based on $N = 2$ should be interpreted with caution. Future work on the effect of secondary growth on juvenile dispersal should help us understand connectivity in heterogeneous landscapes at a larger spatial scale.

'Recovery' of secondary forest to the point of no edge effect.—As predicted, *G. spirurus* was the first to recover relative activity levels in secondary forest (11–14 yr after abandonment), followed by *X. pardalotus* (15–20 yr) and as predicted, *F. colma* (28–30 yr or longer) was last. In analysis of capture rates of the guild 'mixed-species flock dropouts' (*G. spirurus, X. pardalotus* and the antwren *Myrmotherula axillaris*) along edges of primary forest and secondary growth from 1991–2011 at the BDFFP (Powell *et al.* 2013), recovery to capture rates in primary forest took 10–21 yr after abandonment, remarkably similar to the species-level telemetry estimates of recovery time presented here. Comparatively, in Jari, Brazil, Barlow *et al.* (2007) had reduced detections of both *G. spirurus* and *X. pardalotus* in 14–19-yr-old secondary forest compared to primary forest. For *F. colma,* we estimated a return to no edge response about 28–30 yr after abandonment (possibly longer for young birds), somewhat less than a previous estimate of recovery time for capture rates of terrestrial insectivores at the BDFFP (45–88 yr; Powell *et al.* 2013, 12 species including *F. colma*). Our results concur with those of Powell *et al.* (2015) who using a very similar dataset, showed reduced movement of *F. colma* from primary forest to ~30-yr-old secondary forest. Although *F. colma* was the last to recover in our analysis, the species may actually be among the *least* sensitive terrestrial insectivores at the BDFFP; six species in Powell *et al.* (2013) were never captured along the edge with secondary forest of any age. See supporting information for additional discussion on interpreting recovery estimates.

Conservation and management.—Given that once vast, homogeneous blocks of tropical rain forest are being rapidly perforated by new edges, it is essential that we understand the dynamics of how sensitive species respond to those newly variable landscapes. Sensitive species and guilds (*e.g.*, terrestrial insectivores) can be especially useful as indicators of habitat quality as landscape change takes place. This study adds to a growing body of research concluding that terrestrial insectivores of tropical rain forests are among the first guilds to disappear when forests are fragmented, and among the last to recover after secondary growth is abandoned (Stratford & Stouffer 1999, 2012; Canaday & Rivadeneyra 2001, Peh *et al.* 2005, Waltert *et al.* 2005, Stouffer *et al.* 2011, Powell *et al.* 2013).

For rain forest birds, crossing the primary forest edge is the first step toward maintaining connectivity and gene flow across the landscape, thus larger models of functional connectivity can be parameterized by smaller models of species response to edges (Castellón & Sieving 2007), such as the ones we present here. Specifically, this study shows that given enough time for forest succession, formerly hard edges gradually transition to soft, and then to functionally non-existent. For example, after only 15–24 yr, both woodcreepers recovered to primary forest-like edge effects, so intermediate-aged secondary forest has real value for birds moving across heterogeneous landscapes (Chazdon *et al.* 2009, Powell *et al.* 2013, Chazdon 2014).

Pará state, Amazonia's eastern neighbor, which contains 40 percent of the Amazon's secondary forests, recently became the only Amazonian state in Brazil to implement legislation defining stages of secondary forest (Vieira *et al.* 2014). This new legislation recommends protection of secondary forests >20-yr old as quantified by satellite imagery, but creation of similar legislation in other Brazilian states remains uncertain. Thus, 20+ yr-old secondary forests can now be identified remotely and afforded protection, which can be a valuable tool for land managers seeking to maximize connectivity for understory birds. On the other hand, young *F. colma* show very little relative activity in 27–31-yr-old secondary forest (Powell *et al.* 2015), and *F. colma* is among the least sensitive of the terrestrial insectivores (Powell *et al.* 2013), so managers will likely have to wait for secondary forest to mature beyond 30 yr for the full compliment of rain forest-dependent species to secondary forest without adverse edge effects.

ACKNOWLEDGMENTS

We thank Paul Des Brisay, Marconi Cerqueira, Elizabeth Condon, Camila Duarte, Gilberto Fernandez Arellano, Jairo Lopes, Alercio Marajo de Reis, Rachelle McLaughlin, Karl Mokross, Osmaildo, Aída Rodrigues, and Tatiana Straatmann for their contributions in the field. The LSU 'Bird Lunch' group, Kristina Cockle, Kyle Harms, Michael Kaller, Curtis Marantz, James Nichols, Stefan Woltmann, and J. Van Remsen contributed insightful reviews and advice on data analyses. We thank the following funding sources: US National Science Foundation (LTREB 0545491), AOU's Research Award, the Frank M. Chapman Award, the Paul A. Stewart Award, and the Lewis & Clark Fund. We conducted this research under LSU IACUC approval and under applicable Brazilian permits. This is publication number 668 in the BDFFP technical series and number 39 in the Amazonian ornithology technical series. This manuscript was approved for publication by the Director of the Louisiana Agricultural Experimental Station as manuscript number 2015-241-22456.

SUPPORTING INFORMATION

Additional Supporting Information may be found with online material:

APPENDIX S1. Study site details.

FIGURE S1. Depiction of analytical procedure used to calculate relative activity of species in different distance belts and habitats.

TABLE S1. *Model selection results for five models describing edge effect in secondary forest of three different age classes adjacent to primary forest.*

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