ABSTRACT
For decades, ecologists have studied fundamental questions of how Amazonian biodiversity is maintained, and whether that diversity can persist following deforestation. The long history of avian research at the Biological Dynamics of Forest Fragments Project, near Manaus, Brazil, has helped advance this understanding in the context of a broader research program focused on rainforest fragments embedded in a dynamic matrix. By sampling birds beginning before fragments were isolated, in the late 1970s, and continuing the protocol to the present, our work has revealed community dynamics driven not just by area and isolation, but also by larger landscape patterns, particularly second growth recovery over decadal scales. Fragments permanently lose some bird species, but their communities need not follow a trajectory toward catastrophic change. Our challenge now is to determine under what conditions remnant patches and developing second growth can support not just the rich diversity of Amazonian rainforest species but also their population processes and emergent community properties.

Keywords: Amazonia, bird communities, Brazil, deforestation, forest fragmentation, island biogeography, landscape ecology, rainforest, second growth

INTRODUCTION
In 1976, the idea that eventually became the Biological Dynamics of Forest Fragments Project (BDFFP)—the longest-running experimental study of tropical forest fragments—emerged to Thomas Lovejoy, then the vice-president for science at the World Wildlife Fund–US. Following a tortuous logistical path, the project began on the ground in Amazonian Brazil in 1979 (Figure 1; Bierregaard and Gascon 2001). An important strength of the project was that sampling began before fragments were isolated. This unique design allowed researchers to monitor changes, such as loss of species, as they unfolded (Lovejoy et al. 1986). For some taxa, particularly understory birds sampled with mist nets, sampling has continued to the present following the same protocol, providing unrivalled data continuity. Results from the BDFFP have revealed important patterns and processes central to our understanding of effects of rainforest fragmentation (Laurance et al. 2002, 2011, 2018). Here we synthesize some of the most important results from birds, emphasizing the value of long-term standardized data collection, even as the
First, it addressed a goal of maintaining the integrity of the entire ecosystem. In the 1970s, rainforests of the central Amazon were vast and generally intact, making this a meaningful objective. Second, it derived its theoretical context from the species/area relationship and island biogeography, particularly MacArthur and Wilson’s equilibrium model, which emphasized the twin roles of distance and area in determining the number of species on an island (MacArthur and Wilson 1967). Front and center at the project’s inception was the objective of addressing whether biodiversity would be better maintained in a single large fragment or an equivalent area of smaller fragments (the SLOSS debate, e.g., Simberloff 1988).

Sampling began in 1979, the first fragments were isolated in 1980, and the project’s original design and objectives had to be reconciled with the reality of what could be accomplished on the ground. The hard work of removing
primary forest to create the BDFFP fragments was meant to be done by ranchers preparing cattle pastures on 3 adjacent ranches. The fragments would then be included in rainforest set-asides required under Brazilian law at the time. Going into the 1980s, it was not clear what form the larger landscape around the BDFFP fragments would eventually take, as it would depend on market forces and government incentives influencing decisions by ranch managers (Bierregaard and Gascon 2001). As Brazil’s economy faltered through the 1980s, pasture creation slowed, in turn affecting the BDFFP design. The largest planned fragments (1,000 and 10,000 ha) were never isolated, and replication of 1-, 10-, and 100-ha fragments did not reach expectations. By the end of the 1980s, the fragments within the study area reached their final numbers, with five 1-ha fragments, four 10-ha fragments, and two 100-ha fragments. The reduced pace of deforestation in the 3 ranches and beyond produced the landscape that would be central to interpreting our results up to the present: the BDFFP fragments are surrounded by vast areas of undisturbed primary rainforest that have not changed appreciably in the past 30 yr (Figure 1).

KEY RESULTS

Fragment Isolation Drives Dramatic Changes in Bird Communities

Longitudinal bird sampling with mist nets began as soon as the potential fragments were delineated, beginning in 1979, and has continued in the same plots following the same protocol up to 2017 (e.g., Hernández-Palma and Stouffer 2018, Rutt et al. 2019a). Early results, which accompanied the process of fragment isolation through the first few years after isolation, revealed several important patterns. Bird species disappeared from mist net samples following fragment isolation (Bierregaard and Lovejoy 1989). Despite limited replication, these early results were among the first to track the process of avian community change from intact forest to isolated fragment. This initial change following isolation paralleled striking results for trees at the BDFFP, which showed a significant pulse in mortality immediately after isolation (Laurance et al. 2011). At about the same time, a flurry of studies began to appear from outside the BDFFP quantifying area effects on communities in habitat fragments (reviewed in Debinski and Holt 2000). This topic, generally drawing inference based on short-term (“snapshot”) sampling in fragments of unknown age, paralleled the development of landscape ecology as a discipline. These researchers were working from a fundamental premise of island biogeography: fragments are discrete islands of habitat in a sea of unsuitable matrix. Fragments, such as woodlots surrounded by agricultural fields or chaparral patches in an urban matrix, were modeled as if they were oceanic islands (e.g., Soulé et al. 1988, Blake 1991).

Temporal sequences from the BDFFP fragments also revealed an interesting pattern that did not emerge from studies based on snapshot samples of fragments sampled long after their isolation. Immediately following isolation, the number of individuals and species in fragments increased, and 1-ha fragments gained proportionately more than 10-ha fragments (Bierregaard and Lovejoy 1989). Presumably, this crowding effect was due to forest interior birds fleeing deforestation and finding temporary refuge in fragments. Crowding persisted for about a year following isolation, followed by a steep decline in abundance to below pre-isolation levels. The ultimate fate of individual birds crowded into fragments remains unknown, but the result was that the number of species or individuals in fragments was not a simple decline following isolation. This result parallels hyperdynamism in butterfly and tree communities that played out at different time scales in the BDFFP fragments (Laurance et al. 2011).

The crowding effect was more than a quirk in the data; it meant that communities and social organization, such as complex mixed-species flocks, were altered considerably by the process of fragmentation and did not simply deteriorate from the pre-isolation state (Mokross 2014). A crowding effect leading to restructured communities that vary idiosyncratically among replicates for a few years after isolation may be typical for dispersal-limited systems (Stouffer and Bierregaard 1995a; see also Terborgh et al. 1997), although it contrasts with the highly predictable nested communities that were identified by snapshot sampling of more mobile birds in older fragments in the temperate zone (e.g., Blake 1991, Bolger et al. 1991).

Fractions Are Not Invaded by Non-forest Birds

In the first few years after clearing began at the BDFFP, many species associated with non-forest habitats appeared at the ranches (Stotz and Bierregaard 1989). Despite their persistence in pastures, young second growth, roadides, and even fragment edges, these species were never significant contributors to mist net samples in fragment interiors or continuous forest (e.g., Stotz and Bierregaard 1995a, 1995b; Stotz and Borges 2001, Johnson et al. 2011). A longer view has shown that most generalist and open area species colonized the landscape within the first decade following deforestation, but their numbers have decreased as secondary forest has replaced pasture (Rutt et al. 2017, 2019b). As in other studies (e.g., Sullivan et al. 2016), biotic homogenization from increased numbers of generalists occurred at the broad spatial scale of the 3 ranches and their associated landscapes, but the effect varied strongly among landscape elements, with even small forest patches used
almost exclusively by forest birds, even when the patch was bordered by pastures and young scrub full of thriving generalists (Stouffer and Borges 2001).

**Matrix Regrowth Facilitates Recolonization**

The original plan to follow forest islands isolated by a sea of static cattle pastures changed together with the Brazilian...
economy within a few years after the fragments were isolated. As cattle pastures were abandoned, second growth regenerated around some fragments, and bird communities in fragments began to reveal not just area effects but also the influence of the adjacent matrix. We determined that fragments surrounded by *Cecropia sciadophylla*, the dominant tree in regrowth when forest is cut but not burned, were more readily recolonized by birds than were fragments surrounded by *Vismia* spp. scrub growing in burned pastures (Stouffer and Bierregaard 1995a). This effect was particularly striking for obligate army-ant-following birds, which disappeared completely following isolation but returned to fragments surrounded by >5-yr-old *Cecropia* (Figures 2B and 3). Other bird guilds responded differently. For example, terrestrial insectivores often went locally extinct in fragments and generally did not recolonize, showing isolation and area effects 5–15 yr after isolation (Stratford and Stouffer 1999). At the other extreme, understory hummingbirds were essentially unaffected by fragment area or matrix regeneration (Stouffer and Bierregaard 1995b; Figure 2D). Variation among bird species in response to matrix can combine with area effects to drive nonrandom patterns of occurrence in fragments. A similar effect has also been observed in small mammals and frogs at the BDFFP; capacity to use second growth is a key predictor of which species occurred in small fragments (Gascon et al. 1999).

Many studies at the BDFFP have now integrated fragment processes not just with temporal changes inside the fragment, but also with matrix dynamics (reviewed in Laurance et al. 2002, 2011, 2018). Our interest in how land cover affects birds paralleled ongoing research by BDFFP plant ecologists on succession in *Visnia* vs. *Cecropia* second growth (Mesquita et al. 2001, Longworth et al. 2014, Mesquita et al. 2015). The idea of extrinsic factors (matrix dynamics) affecting processes within fragments has now become an integral part of most studies of habitat patches (e.g., Barbosa et al. 2017, Boesing et al. 2018, Freeman et al. 2018a). Not considering these factors probably explains poor performance of the species/area relationship in some

**FIGURE 2.** Four common species at the BDFFP. (A) Ferruginous-backed Antbird (*Myrmoderus ferrugineus*) is a terrestrial insectivore. This is one of the least sensitive species in this guild, but it did disappear from small fragments after isolation. (B) White-plumed Antbirds (*Pithys albifrons*) forage exclusively at army ant swarms. They have territories >100 ha that they use to track multiple ant swarms. Because of these large area requirements and their reluctance to cross open areas, they disappeared from isolated fragments. They readily move through second growth, however, so they now occur throughout the BDFFP landscape. (C) Female (above) and male Long-winged Antwrens (*Myrmotherula longipennis*) are core flock members, living permanently in mixed-species understory flocks (Figure 5). (D) The most common hummingbird at the BDFFP, Long-tailed Hermit (*Phaethornis superciliosus*), showed no decline in abundance due to forest fragmentation.
Narrow Deforested Openings Reduce Bird Movements

Most fragments were periodically re-isolated beginning in 1991. In some cases, this was associated with activities on the farms, but most clearing was conducted by the BDFFP. This gave us the opportunity to observe isolation effects on fragment communities multiple times, and also to couch the re-isolation into broader analyses that included more landscape factors, such as age of fragment borders, age and composition of the larger second growth matrix, and distance to continuous forest. Doing so, this time with a 20-yr time series, revealed that the single most important factor determining bird abundance in a fragment was the age of the narrow strip of vegetation bordering the fragment (Stouffer et al. 2006). Clearing a 50- to 100-m border reduced understory bird activity by as much as 95% for some guilds in small fragments (Stouffer et al. 2006). This dramatic effect of a narrow clearing, driven by unwillingness of birds to cross narrow openings, paralleled our earlier results and observations from other tropical forest isolates (Willis 1974, Develey and Stouffer 2001, Lees and Peres 2009). Unwillingness to cross open areas represents one of a suite of important differences between tropical and temperate forest birds that research at the BDFFP helped reveal (Stratford and Robinson 2005).

The older the second growth forest became, the better it was for bird movements into fragments. The difference between burned and unburned matrix (i.e. between Cecropia- and Vismia-dominated second growth), a critical factor in the early years after forest clearing (Stouffer and Bierregaard 1995a), lessened with time; eventually, age of the second growth became more important than the initial treatment of burning or not (Stouffer et al. 2006, Powell et al. 2013). Distance to continuous forest, which only varied by a few hundred meters, was not important for most guilds. The implication was that many birds are able to move around the landscape and find forest fragments provided they do not need to cross open areas, a result supported by later work comparing the BDFFP fragments with actual islands at the Balbina reservoir ~70 km north of the BDFFP (Wolfe et al. 2015). Actual ~100-ha islands were depauperate in insectivorous flocking species and terrestrial insectivores, including species that successfully recolonized even 10-ha fragments at the BDFFP (Wolfe et al. 2015; see also Aurelio-Silva et al. 2016).

Researchers looked more closely at the role of narrow openings on bird movements by taking advantage of the narrow road that bisects the BDFFP. Second growth along the roadsides was cut to allow sunlight penetration to the road surface, leading to a linear opening 20–40 m wide. Sampling along roads and in the adjacent landscape revealed that understory mixed-species flocks used forest up to the edge of the road, but their movements were impeded by the narrow linear canopy interruption (Develey and Stouffer 2001). Other bird species showed both impeded movement and avoidance of edges adjacent to the road, although most at least occasionally crossed the road (Laurance et al. 2004). Open pastures 250 m wide were not crossed by translocated birds (Laurance and Gomez 2005). Other taxa showed similar results at the BDFFP. Narrow openings reduced movements for forest-dependent herbivorous insects, eupllostine bees, dung beetles, and lichen spores (reviewed in Laurance et al. 2011, 2018).

Fragment Communities Are Dynamic Because of Both Extinction and Colonization

Our long-term mist net sampling has the benefit of replication, standardization, and little observer error, but it suffers from a problem inherent in most animal sampling: some birds are present but not detected (Nichols et al. 1998). Thus, a species could be considered to have disappeared from a fragment when it was really present. Addressing this problem from our long-term data, using both improved survey tools (Box 1) and more sophisticated analyses, allowed us to estimate the actual number of understory species (species at least occasionally captured in ground-level mist nets) present in a fragment at a given time. This estimate, in turn, allowed us to address the trajectory of species loss in the fragments (Ferraz et al. 2003, 2007;
was an important process at the BDFFP (Figure 3). These early as the 1990s, when it was clear that recolonization do not match BDFFP data. This result was anticipated as models that assume ongoing loss of species in patches dynamism calls into question the idea of extinction debt; in fragments, especially 1- and 10-ha fragments. This process of extinction occurring over the long term has been referred to with 2 seemingly incongruous euphemisms. Based on islands that lose species when seas rise, biogeographers came up with the term “relaxation” (Diamond 1972). Conservation biologists, on the other hand, call the process “extinction debt” in habitat patches (Tilman et al. 1994).

Determining how extinction debt is paid requires time-series data, so few studies can address it directly. Longitudinal data from the BDFFP provided an opportunity to look at the temporal pattern of bird extinctions. Data from the early years at the BDFFP were extrapolated with an extinction-only model (i.e. no recolonization was included; a species could either persist or go extinct in a given fragment) to predict extinctions over time, leading to the estimate that 50% of bird species would go extinct in a 100-ha fragment in <20 yr (Ferraz et al. 2003). With additional sampling, however, it was apparent that these predicted extinctions did not occur (Stouffer et al. 2009, 2011); empirical data conformed better to a model that allowed recolonization (Ferraz et al. 2003). As additional time-series data were acquired, permitting analysis of extinction and colonization in each fragment over multiple time intervals, we saw that bird communities represented a near balance of some species going locally extinct and others recolonizing (Figure 4). Some groups, such as terrestrial insectivores, continued to lose species over as much as 20 yr, but species in other guilds appeared and disappeared in fragments, especially 1- and 10-ha fragments. This dynamism calls into question the idea of extinction debt; models that assume ongoing loss of species in patches do not match BDFFP data. This result was anticipated as early as the 1990s, when it was clear that recolonization was an important process at the BDFFP (Figure 3). These recolonization processes also drive occurrence patterns for other taxa in the fragments, including monkeys and a variety of arthropods (Laurance et al. 2011, 2018). Whether this failure to consider recolonization is a general weakness of predictions of extinction debt remains to be seen; in some systems extinction “credits” have been identified as matrix conditions improve (Lira et al. 2012, Latta et al. 2017). Undoubtedly, however, some systems are so area-limited and isolated from potential colonists that colonization is unlikely to save small populations (e.g., Canale et al. 2012). On the other hand, processes identified in the dynamic landscapes of the BDFFP, created by actual forces leading to on-the-ground deforestation, may be more representative than the dramatic extinctions that have been described for atypical, worst-case scenario systems like reservoir islands (Terborgh et al. 1997, Gibson et al. 2013). Even if the setting of the BDFFP makes our results a best-case scenario, we have demonstrated that small and old remnants of forest can be used by many forest birds.

Recent advances in our ability to determine the age of birds (Box 1) have revealed some of the mechanisms leading to the dynamic distributions we see in the landscape. For some species (e.g., army ant followers Pithys albifrons and Gymnopithys rufigula), birds can reach high abundance in fragments, but most of the birds in small fragments are young, and can be shown through mark–recapture analysis to be transients who do not establish territories in fragments (Johnson 2011). Army ant swarms use second growth, providing foraging opportunities that connect fragments to continuous forest (Roberts et al. 2000). Vocalizations from obligate ant followers attract

![FIGURE 4. Extinction and colonization parameter estimates from 10-ha fragments (Stouffer et al. 2011). Each set of pairs of points of the same shape refers to an individual fragment, with the open symbol representing extinction and the filled symbol representing colonization for that interval. Note that both extinction and colonization decreased over time after fragment isolation, and that colonization often matched extinction, reflecting turnover, not net loss of species. “Pre” refers to pre-isolation (continuous forest) samples. One fragment was sampled in 2 time intervals before isolation, providing estimates of colonization and extinction within continuous forest (pre-pre).](https://academic.oup.com/condor/article/122/3/duaa005/5816446)
opportunistic species, an emergent process that enhances local-scale bird diversity (Martinez et al. 2018). Other species caught in fragments, such as gap specialists, are represented by both adult non-transients and young birds, probably indicating successful reproduction in the fragments (Johnson 2011). A large subset of understory insectivorous species only infrequently occur in fragments, usually as young birds, suggesting that they are relatively less mobile and are also area-sensitive for breeding (Johnson 2011). An emergent property of demographic and abundance patterns in the landscape was revealed by network analysis of mixed-species flock structure; although fragment flocks may have similar species richness as intact forest flocks, interspecific interactions within networks were reduced in fragments (Figure 5; Mokross et al. 2013, 2018).

**Edge Effects Diminish with Time But Are Sometimes Subtle**

Edge effects associated with fragmentation have received explicit attention for a variety of taxa and processes at the BDFFP (Lovejoy et al. 1986, Laurance et al. 2011, 2018). We began sampling birds on fragment edges in 1991 to examine how birds used the variety of edges available at the BDFFP. At that time, the boundary was stark at some fragments, with tall forest on one side of the net and pasture on the other side. These edges were used by a combination of forest and non-forest birds (Stouffer and Borges 2001). We followed these edges as second growth aged, increasing edge use by forest birds, or was recut, reducing use and movement across edges (Rutt et al. 2020). With the long time series now available, we know that bird movement across ~25-yr-old edges does not differ appreciably from movements within forest except for terrestrial insectivores, which are on a trajectory to recover only after about 50 yr (Powell et al. 2013, 2015). As in our analysis of movement through second growth (Stouffer et al. 2006, Powell et al. 2013), bird samples on edges showed that by 25 yr after abandonment the treatment following initial deforestation (burning or not) was no longer important for birds. The pronounced difference between Cecropia and Vismia second growth had disappeared from the point of view of birds using the interface between forest and second growth, even if it persisted as an effect on vegetation (Mesquita et al. 2015).

Although birds are moving across these edges with old second growth, recent studies focused on the movements of individual birds have revealed nuanced patterns (facilitated by advances in GPS technology; Box 1). Radio-tagged birds whose territories straddled edges moved through second growth with longer and straighter movements than they did in forest, consistent with reduced foraging opportunities in second growth (Figure 6D; Powell et al. 2015, 2016). Mixed-species flocks moved parallel to edges, making limited forays across into second growth, but some flock members remained behind in taller forest (Mokross et al. 2018).

Edges mediate habitat quality within fragments depending on second growth conditions. Increasing second growth age surrounding fragments was associated

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**FIGURE 5.** An example of how flock social networks vary across the BDFFP landscape (Mokross et al. 2013). Within the 3 networks, each circle (node) represents a flock species, with the size of the node reflecting the degree of participation in the flock (for example, the large central node in each panel refers to Cinereous Antshrike [Thamnomanes caesius], which always leads flocks). Lines indicate the shared participation of pairs of species; darker, thicker lines between species mean that they usually occur in flocks together. Weaker interactions appear as transparent. Notice the dense network of interactions in primary forest compared to the 10-ha fragment, although the number of participating species did not strongly differ. Flocks in secondary forest had fewer species and reduced social organization.
with increased feather growth rates for birds within the fragments (Hernández-Palma and Stouffer 2018). Experimental creation of hard edges altered flock movements not just at the edge, but in fragment interiors as well (Rutt et al. 2020).

**Mechanisms Remain Elusive**

Although we understand the pattern of loss of species following fragment isolation and something of the process of recovery, mechanisms leading to species attrition remain poorly resolved at the BDFFP and in other rainforest systems (Stratford and Robinson 2005, Robinson and Sherry 2012, Visco et al. 2015). Part of the process is easily explained: area effects combined with unwillingness to use young second growth mean that 1- and 10-ha fragments are too small for many species to maintain normal territories (Figure 6; Stouffer 2007, Johnson et al. 2011; see also Ferraz et al. 2007). But what mechanisms, beyond

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**FIGURE 6.** Conceptual model illustrating dynamics of avian territories and movement during recovery of secondary forest following deforestation and fragmentation (Powell et al. 2016). Circles and ellipses represent resident bird territories for a hypothetical species ubiquitous in primary forest, diagonally hatched fill represents primary forest, and increasingly dark solid shading (white to dark gray) represents increasingly old secondary forest. Thick black lines representing the edges of primary forest are dashed relative to permeability of the edge. As continuous forest (A) is initially cut (B), birds are entirely excluded from the recently cut area. At this point, home range boundaries are aligned along the interface and birds are excluded from fragments too small to sustain their home ranges. During early regrowth (C), increased vertical structuring of the young secondary forest permits some movement (e.g., dispersal) across secondary forest, and some individuals may occasionally occur in small fragments. As secondary forest matures and begins to recover resources (D), birds begin to expand their territories into secondary forest and small fragments, showing increased rates of movement across the interface. At the point of recovery (E), bird territory boundaries and cross-interface movements are indistinguishable from those in primary forest, regardless of fragment size. In the close-up of (D), a higher proportion of the animal’s core area (gray ellipse) is within primary forest, whereas the overall home range (black ellipse) contains a higher proportion of secondary forest. Here individual bird movements (thin arrows) show that birds in primary forest move in short, curvy (i.e. high tortuosity) paths; conversely, movements in secondary forest are straighter (i.e. low tortuosity) and longer, so movement rate is relatively high.
stochastic attrition, lead to the loss of species that can maintain normal-sized territories in fragments? Forest structure changes in fragments (Laurance et al. 2018). This reduces preferred microhabitats for terrestrial insectivores (Stratford and Stouffer 2015) and likely affects flock movements, which are responsive to tree height (Potts et al. 2014). Some species that persist show reduced condition as measured by feather growth rates (Stratford and Stouffer 2001, Hernández-Palma and Stouffer 2018), perhaps reflecting reduced habitat quality. Microclimate sensitivity has been postulated to explain both avoidance of open areas and negative response to structural change by rainforest interior birds (Stratford and Robinson 2005, Robinson and Sherry 2012). So far, research has not shown that rainforest species vulnerable to fragmentation are especially sensitive to light (Rutt et al. 2019a) or temperature conditions (Pollock et al. 2015). Even so, seasonal variation in rainfall and temperature mean that conditions vary considerably over the course of a year, and between years due to El Niño events. Combined with the reticulated topography at the BDFFP, with deeply dissected streambeds that stay wetter than plateaus only tens of meters away, this means that birds may face considerable variation in microhabitat or microclimate suitability in space and time (V. Jirinec personal observation).

Fragment isolation and resultant microhabitat change may reduce food resources for birds, but this research path has not led to major insights. Hummingbirds and small frugivores are unlikely to respond negatively to fragmentation based solely on food availability. These groups have enhanced foraging opportunities due to flowering and fruiting on newly created edges or in gaps (e.g., Levey 1988). For insectivores, understanding the full range of foods used, and its availability, is a daunting task. Work so far does not reveal loss of food as a significant mechanism limiting insectivorous birds (Sekercioğlu et al. 2002, Mestre et al. 2010). Even so, the combination of topography and seasonality at the BDFFP may lead to periods of food stress that remain undetected.

The important processes of nest parasitism and nest predation in fragments have not been a direct research focus at the BDFFP. Nest predation may be elevated in fragmented rainforest landscapes, but unambiguously negative edge and area effects have not emerged (Robinson and Sherry 2012, Visco et al. 2015). In fact, birds along edges and in small fragments sometimes have elevated nest success (Visco et al. 2015, Angkaew et al. 2019). Unfortunately, nest data are unlikely to be generally obtainable at the BDFFP as a means of addressing comparative demography across the landscape. Individual species occur at low density, with large territories (Johnson et al. 2011), and many breed almost year-round (Stouffer et al. 2013). These factors complicate any research effort focused on natural nests. The BDFFP has a full complement of predators, so likely does not have the mesopredator or collared peccary (Pecari tajacu) release that occurs in other disturbed landscapes (Visco et al. 2015). Avian brood parasitism is not important at the BDFFP, or in the Amazon more generally (Rutt et al. 2017).

Second Growth Forest is Valuable for Forest Birds

Beginning in the 1990s, tropical ecologists began paying closer attention to the second-growth matrix as it affected fragments (e.g., Gascon et al. 1999). Eventually, second growth itself became a research focus (reviewed in Chazdon 2014). Particularly important for stimulating this interest at the BDFFP and elsewhere were analyses integrating economic and human demographic factors to predict both deforestation and subsequent abandonment of deforested areas in the tropics (Wright and Muller-Landau 2006). This process, as was played out on a small scale at the BDFFP, leads to a dynamic landscape of decreasing primary forest cover and increasing and aging second growth. With time, second growth supports more forest species. An essential question is how long it takes for second growth to be equivalent to primary forest. Put more directly, can recovering second growth save forest species by the time most primary forest is removed (Chazdon et al. 2009, Sayer et al. 2017)?

At the BDFFP, we have entered a research phase where we consider the matrix not just for its utility as a conduit for birds to move among forest elements, but also for its own habitat value. We summarized the process of how developing second growth drives our observations in fragments and second growth in a conceptual model that we used to guide our recent research (Figure 6; Powell et al. 2016). Standardized sampling at the BDFFP expanded to second-growth plots, following several short-term projects there (Borges and Stouffer 1999, Freitas 2011, Campos e Silva et al. 2012, Figueira et al. 2015). Data so far show that most terrestrial insectivore species remain rare in second growth (Rutt et al. 2019a) and terrestrial insectivores are the understory guild stalled at the earliest stage of population recovery as second growth forest ages (Figure 6); neither second growth nor small fragments presented suitable foraging microhabitats, at least through 10–15 yr (Stratford and Stouffer 2013, 2015). For species that occur in second growth, our work now focuses on determining whether second growth and fragments can sustain bird populations, or whether the birds we find there were just overflow from adjacent forest. Results so far suggest that forest insectivores are mostly represented in second growth by young birds, but that frugivores are not as limited in age classes (Wolfe 2014). Mixed-species flocks use second growth in proportion to its height (Mokross et al. 2018). Direct observation of flocks and captured birds reveal that many forest birds breed in second growth at the BDFFP.
suggesting that the age structure includes young birds produced in second growth and immigrants from continuous forest (C.L. Rutt personal observation). Determining population processes in second growth is fundamental to the debate over whether maturing second growth will maintain tropical biodiversity (e.g., Mahood et al. 2012, Şekercioğlu et al. 2019).

We addressed the potential for reproduction in second growth for a large suite of birds by quantifying the availability of cavities for the many species that nest in tree holes they do not excavate (Dantas 2015). These secondary cavity nesters take advantage of cavities resulting from both woodpecker excavation and natural decay (Cockle et al. 2011). Nesting cavities could be considered an emergent property of decay and woodpecker use of second growth. Many species in the Amazon are secondary cavity nesters, including some raptors, parrots, puffbirds, toucans, and woodcreepers. Surveying cavity availability is laborious and provides few active nests, but this sampling is critical for determining if populations are limited by a scarcity of nesting sites. Based only on cavity availability (i.e. not actual nest data), there were almost no cavities available in second growth younger than about 15 yr. After that, the number of cavities increased but, even after 35 yr, did not reach the abundance found in continuous forest (Dantas 2015).

EMERGING QUESTIONS

Collaboration, data sharing, and large-scale, synergistic analyses have become increasingly important in ecology. Within the BDFFP, some patterns based on work with birds can be linked with larger processes, such as seed dispersal, an emergent property driven by frugivore movements in the landscape (Cramer et al. 2007, Uriarte et al. 2011, Mesquita et al. 2015). Beyond the BDFFP, a major research effort is underway to address patterns of biodiversity at large spatial scales in replicated perturbed tropical forest landscapes (Ewers et al. 2011, Gardner et al. 2013, Moura et al. 2016). Synergistic effects linking deforestation, fire, and other disturbances have also become a major research focus (e.g., Michalski and Peres 2005, Moura et al. 2016), with the BDFFP contributing important comparative data (Barlow et al. 2006, Pfeifer et al. 2014, Powell et al. 2015). BDFFP data are especially valuable for global-level comparative studies because our samples include fragmentation-sensitive species that have already been removed from other systems through an overall loss of forest cover (e.g., Betts et al. 2019).

We also hope to address another important current topic that was not part of the original research plan: What has climate change done to Amazonian birds since 1979, and what does the future hold (e.g., Blake and Loiselle 2015, Brawn et al. 2017, Freeman et al. 2018b)? Our long-term banding data have several strengths for considering this question. First, we have data from many continuous forest sites for the 40-yr history of the project. Some of these sites have remained embedded in forest that has seen almost no direct anthropogenic disturbance. Second, our standardized sampling allows direct comparison of relative abundance and body condition across time. We hope to examine these metrics for birds in the context of climate change and resultant biological processes occurring across the Amazon basin (Baker et al. 2004, Brienen et al. 2015, Feldpausch et al. 2016).

Collaboration and Capacity Building in Brazil

Although this review emphasizes science related to birds, ornithological research at the BDFFP has also been important for capacity building in Brazil and for turning Manaus into a nexus of ecological research (summarized in Bierregaard and Gascon 2001, Laurence et al. 2018). Over time, the BDFFP became fully integrated within Brazil’s National Institute for Amazon Research (Instituto Nacional de Pesquisas de Amazônia- INPA), which now serves as its physical and administrative base. These connections with INPA facilitate research, education, and collaboration with INPA’s cadre of ornithologists. In the internet age, working in Manaus does not lead to the isolation from the larger scientific community that it once did. As a result of improved communication, infrastructure, and training resources developed at the BDFFP (Box 1), the BDFFP has become a leading site for ornithological training for students from Brazil, elsewhere in South America, and beyond. Over the years of the BDFFP, the number of researchers and students based in Manaus studying birds has grown to the point where these local ornithologists hosted a major international ornithological conference in 2015. Much work remains to be done at the BDFFP. We look forward to the progress that will be made by a new generation of ornithologists in the years to come.

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