

Connectivity with primary forest determines the value of secondary tropical forests for bird conservation

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Abstract

Species extinctions caused by the destruction and degradation of tropical primary forest may be at least partially mitigated by the expansion of regenerating secondary forest. However, the conservation value of secondary forest remains controversial, and potentially underestimated, since most previous studies have focused on young, single-aged, or isolated stands. Here, we use point-count surveys to compare tropical forest bird communities in 20–120-year-old secondary forest with primary forest stands in central Panama, with varying connectivity between secondary forest sites and extensive primary forest. We found that species richness and other metrics of ecological diversity, as well as the combined population density of all birds, reached a peak in younger (20-year-old) secondary forests and appeared to decline in older secondary forest stands. This counter-intuitive result can be explained by the greater connectivity between younger secondary forests and extensive primary forests at our study site, compared with older secondary forests that are either (a) more isolated or (b) connected to primary forests that are themselves small and isolated. Our results suggest that connectivity with extensive primary forest is a more important determinant of avian species richness and community structure than forest age, and highlight the vital contribution secondary forests can make in conserving tropical bird diversity, so long as extensive primary habitats are adjacent and spatially connected.

Abstract in Spanish is available with online material.

KEYWORDS

bird communities, community structure, conservation, landscape management, land-use change, Panama, secondary forest, tropical extinction crisis

1 | INTRODUCTION

Between 2010 and 2015, there was an annual loss of approximately 7.6 million ha of forest globally, with most of this deforestation occurring in the tropics (FAO 2015). Most of the world's biodiversity is found in the tropics (Dirzo & Raven, 2003), and the continued loss and degradation of tropical forests are likely to cause mass species extinctions (Dent & Wright, 2009; Wright & Muller-Landau, 2006). It has been proposed that primary forest (PF) losses may be offset

by the planting and natural regeneration of secondary forest (SF) on previously deforested land (Wright, 2005). However, the long-term conservation value of SF depends on whether these habitats can maintain similar species composition and ecosystem functions as PF (Chazdon et al., 2009; Dent & Wright, 2009).

Many studies that assess the conservation value of tropical SF have focused on birds, one of the best studied faunal groups in the tropics (e.g., Barlow, Mestres, Gardner, & Peres, 2007; Lees & Peres, 2006; Robinson, 1999; Stotz, Fitzpatrick, Parker, & Moskovits, 1996;

Willis, 1974). Birds provide important ecosystem services, such as pollination and seed dispersal (Sekercioglu, 2006; Whelan, Wenny, & Marquise, 2008), and their diverse habitat and dietary requirements often lead to species-specific responses to habitat disturbance (Hughes, Daily, Ehrlich, & Letters, 2002; Petit & Petit, 2003). Birds are also convenient indicators for ecological assessments because they are relatively easy to identify and survey.

Studies comparing avian species richness and community structure in SF and PF report inconsistent results. Some studies have found equivalent or higher species richness in SF compared to PF (Andrade & Rubio-Torgler, 1994; Blake & Loiselle, 2001; Borges, 2007; O'Dea & Whittaker, 2007; Schulze & Waltert, 2004), while other studies report reduced species richness in SF (Barlow, Mestre et al., 2007; Bowman, Woinarski, Sands, Wells, & McShane, 1990; Gibson et al., 2011; Terborgh & Weske, 1969; Tvardiková, 2010). These conflicting results may stem from three key factors: the age of SF studied, the landscape context, and the responses of different avian groups to habitat change.

In terms of SF age, most studies examining avian diversity in tropical SF have only included relatively young and single-aged stands (>35 years; e.g., Barlow, Mestre et al., 2007; Blake & Loiselle, 2001; Borges, 2007; Terborgh & Weske, 1969). With increasing forest age, SF typically develops greater structural complexity, resembling PF over time (Guariguata & Ostertag, 2001; Peña-Claros, 2003). More complex forest structure offers an increased breadth of ecological niches for forest birds (DeWalt, Maliakal, & Denslow, 2003; Zahawi et al., 2015). Thus, the structural complexity that develops over SF succession should provide habitats for increasingly diverse and complex bird communities (Casas, Darski, Ferreira, Kindel, & Müller, 2016; MacArthur & MacArthur, 1961). Studies focusing on young SF may therefore underestimate the longer-term value of SF for bird conservation. While estimates of avian species richness in young SF are often inflated by non-forest species, species composition in young tropical SF tends to differ from PF (Barlow, Gardner et al., 2007; Borges, 2007; Tvardiková, 2010). With increasing time since abandonment, both forest structure and bird communities become more similar to those of PF (Andrade & Rubio-Torgler, 1994; Borges, 2007; Raman, 1998). Thus, estimates of conservation value need to consider the recovery of forest species composition and abundance rather than richness alone.

The landscape context of SF, defined by connectivity to PF source populations and isolation within the countryside matrix, plays a critical role in determining avian community reassembly (Chazdon et al., 2009; Dent & Wright, 2009; Wolfe, Stouffer, Mokross, Powell, & Anciaes, 2015). Many tropical forest birds are highly dispersal limited with poor gap-crossing abilities and may not be able to colonize SF unless it is contiguous with PF (Lees & Peres, 2009; Moore, Robinson, Lovette, & Robinson, 2008; Tobias, Şekercioglu, & Vargas, 2013; Van Houtan, Pimm, Halley, Bierregaard, & Lovejoy, 2007). In addition, bird species occurring in isolated SF embedded within a non-forest matrix may be more sensitive to random population fluctuations and local extinction. Connectivity to PF is an important factor in SF recovery, and the

species composition of bird communities in isolated SF may never fully converge with that of PF (Jones, Bunnefeld, Jump, Peres, & Dent, 2016; Wolfe et al., 2015).

Finally, the response of bird species to forest succession may be mediated by their degree of ecological specialization. It has been suggested that generalist, migratory, or forest-edge species proliferate in SF as their wider niche breadth makes them better adapted to the conditions found in younger forest (Barlow, Mestre et al., 2007; Stotz et al., 1996). By contrast, forest specialists are likely to require foraging and nesting resources only found in more mature forest (Barlow, Mestre et al., 2007; DeWalt et al., 2003). Forest isolation has also been shown to adversely affect forest-dependent, understory insectivore species more severely than other functional groups (Barlow, Peres, Henriques, Stouffer, & Wunderle, 2006; Bradfer-Lawrence, Gardner, & Dent, 2018; Ferraz et al., 2007; Stouffer, Bierregaard, Strong, & Lovejoy, 2006). Thus, the conservation value of SF for birds is affected by species-specific responses mediated by both site and landscape factors, including habitat age, and level of isolation and connectivity to PF.

Here, we examine the species richness and composition of bird communities in central Panama across the longest SF chronosequence studied to date, spanning forest ages from 20 to 120 years, as well as PF controls (see Figure 1). Across this age gradient, we sampled forests that were either isolated from or connected to extensive PF. This landscape presents an opportunity to examine how bird communities change across both successional and isolation gradients, and to investigate the relative importance of forest age versus isolation in determining the conservation value of SF. Including forest age and landscape context introduces a new level of complexity to classical forest fragmentation studies, which arguably reflects the reality of most human-modified tropical forest landscapes.

In this context, we assessed the relative role of secondary forest age versus connectivity with primary forest in determining bird diversity—estimated as (a) bird species richness and other diversity metrics, (b) bird population density, and (c) the similarity of avian community composition to PF. In all cases, we examined the extent to which variation in bird communities is mediated by landscape context, such as isolation by water barriers.

2 | METHODS

2.1 | Study sites

We conducted field surveys in the Panama Canal Watershed, where vegetation is classified as tropical moist forest (Holdridge & Budowski, 1956). The climate is seasonal with a distinct dry season, typically from mid-December until early May, and annual rainfall of 1,900–3,600 mm (Turner, Yavitt, Harms, Garcia, & Wright, 2015; Windsor, 1990). We selected study sites in the Barro Colorado Nature Monument, Soberania National Park, and the adjacent Agua Salud Project (Figure 1). The Barro Colorado Nature Monument (5,600 ha; 9°9'N, 79°51'W) is comprised of

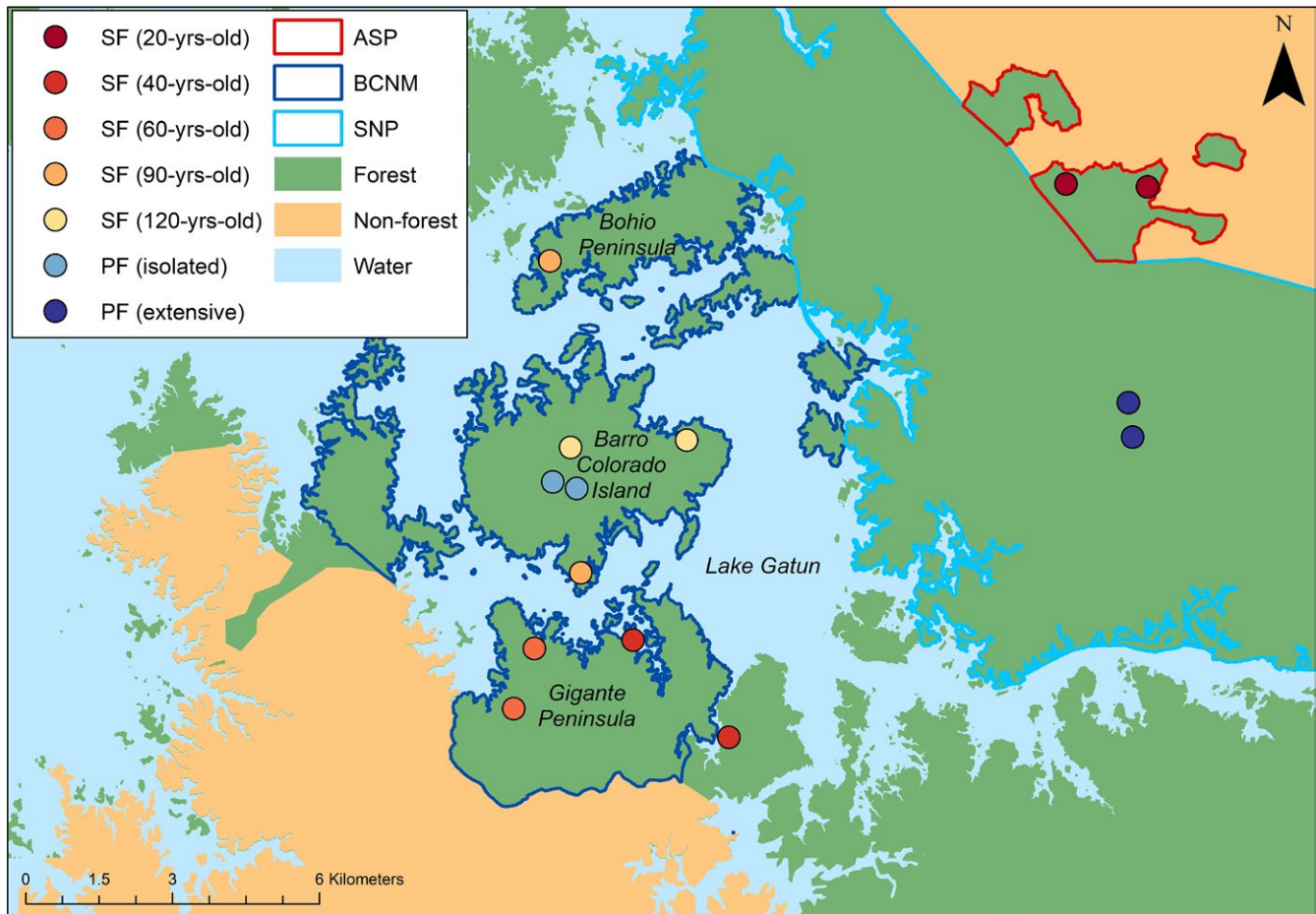


FIGURE 1 Map of the 14 study sites in central Panama. Sites are color-coded by forest age (PF: primary forest; SF: secondary forest). This area of central Panama is composed of a mosaic of contiguous forest stands of different age interspersed among a matrix of water and agricultural land. The main areas in which forest stands are embedded among other patches of forest (and therefore difficult to discretely identify) are the Barro Colorado National Monument (BCNM), including Barro Colorado Island (1,560 ha) and Gigante peninsulas (2,600 ha), Soberania National Park (SNP), and surrounding contiguous forest (22,000 ha), including the Agua Salud Project (ASP)

five peninsulas and Barro Colorado Island (BCI), all situated in Lake Gatun, which was formed in 1914 by the flooding of the Panama Canal. The Barro Colorado Nature Monument is a mosaic of PF mixed with SF stands of different ages that were used for cattle pasture or fruit production between the 1880s and the establishment of the park in 1979 (Leigh, Rand, & Windsor, 1982). Soberania National Park (22,000 ha; 9°9'N, 79°44'W) was established in 1980 and is a mix of PF and very old SF (Van Bael, Zambrano, & Hall, 2013). The Agua Salud Project research site (664 ha; 9°13'N, 79°47'W) was once predominantly cattle pasture or small-scale shifting cultivation, but, after establishment in 2008, the landscape is now predominantly SF of relatively young age (Van Breugel et al., 2013). The difference in annual rainfall between our northernmost and southernmost sites (separated by a latitudinal distance of 9.8 km) is 159 mm pa (Rompre, Robinson, Desrochers, & Angehr, 2007). As this variation is minor compared to a difference of 2,100 mm pa across the full rainfall gradient in Central Panama (Rompre et al., 2007), we treated the study area as a single climatic band (see Figure 1).

2.2 | Site selection

We selected secondary forest sites along a chronosequence of approximately 20, 40, 60, 90, and 120 year since abandonment, with two replicates per forest age. We selected sites within existing research areas having data on long-term vegetation dynamics, tree communities, and accurate age estimates compiled from historical records, aerial photographs, and interviews with residents; for details, see Denslow and Guzman (2000) and Van Breugel et al. (2013). The youngest SF in the Barro Colorado Nature Monument is 40 year old, while SF in Agua Salud is 10–34 year old (mean = 19 year old). For ease of presentation, we refer to Agua Salud sites as 20 year old. We selected four PF sites: two in a relatively small patch (c. 800 ha) of isolated PF on Barro Colorado Island (henceforth referred to as isolated PF) and two in an extensive area of mainland PF in Soberania National Park (c. 22,000 ha; henceforth referred to as extensive PF). The PF is at least 500 year old, and there is no indication that they have ever been logged or cultivated (Piperno, 1990). There is no ongoing disturbance (such as logging or hunting) in Barro Colorado Nature Monument,

whereas in Agua Salud there may be some forest clearance and disturbance in the wider landscape. Across the Barro Colorado Nature Monument chronosequence, average canopy height and structural complexity increase with SF age (DeWalt et al., 2003; Mascaro, Asner, Dent, DeWalt, & Denslow, 2012). Further details of vegetation structure and composition are available in Dent, DeWalt, and Denslow (2013), DeWalt et al. (2003), and Mascaro et al. (2012).

Habitat patch size is an important determinant of species' persistence in fragmented landscapes (Bender, Contreras, & Fahrig, 1998). However, the importance of patch size relates to the composition of the surrounding matrix. The SF sites in our study are embedded within a mixed-age forest matrix, which buffers the effects of fragment size and limits our ability to accurately calculate areas of single-aged fragments. The three forest areas in which study sites are embedded include Barro Colorado Island (1,560 ha), Gigante peninsulas (2,600 ha), and Soberania National Park and surrounding contiguous forest (22,000 ha; see Figure 1 for details). The SF and PF sites in this study experience different connectivity. The 20-year-old Agua Salud SF sites form part of a large forest network connected to extensive PF in Soberania National Park, while both island and peninsula SF sites are smaller, isolated areas of forest surrounded by water. Island SF sites (90–120 year old) are connected only to isolated PF and are separated from extensive mainland PF by water. Secondary forest on the Gigante Peninsula is more extensive and contains older patches (>200 year old) interspersed with patches of 40–60-year-old SF, but is separated from extensive PF by either water or agriculture. We sampled PF sites on both island and mainland settings to examine the effects of different types and extents of forest isolation, and to provide a baseline for studying the effects of SF age on bird communities. Due to the restrictions of available PF and SF in the study landscape, it was not possible to replicate within categories (e.g., isolation type \times isolation extent \times forest type), and even where replicates were possible, the sampling design is weakened because some sites are embedded within the same geographic feature (e.g., BCI) and therefore to some extent non-independent. We take these factors into account in our analyses (see below) and emphasize that the study landscape has distinct advantages—not least the comparison across different levels of isolation, and the availability of background data on the history of forest regeneration—which provide a unique opportunity to understand secondary forests in a spatial and temporal context.

2.3 | Bird survey methods

At each of the 14 sites, we established nine point-counts with each point separated by a minimum of 100 m from other points and by at least 50 m from forest of a different age (Robinson, Brawn, & Robinson, 2000; Van Bael et al., 2013). Two trained observers surveyed one site per morning, with the first count beginning ten mins before sunrise and the last completed by 10:30 hr. All nine stations at a site were sampled once during a survey visit, with a minimum

of 3 days between surveys; no surveys were conducted on days with heavy rain or strong wind because these limit bird activity and detectability.

Point-counts were 10 min in duration, and all birds seen or heard within a 50 m radius were identified, following previous studies (De Bonilla, León-Cortés, & Rangel-Salazar, 2012; Martin & Blackburn, 2014; O'Dea & Whittaker, 2007; Raman & Sukumar, 2002). Limiting counts to a 50 m radius can help to reduce the differences in detectability of birds among habitat types due to vegetation structure, and minimizes biases and errors in species identification and distance estimates (Petit, Petit, Saab, & Martin, 1995). For each bird seen or heard, observers used a laser range-finder to estimate the Euclidean distance from the center of the point-count to the bird (Buckland, Marsden, & Green, 2008). Distance estimates to birds detected only by ear are likely to be less consistent than estimates based on visual detections, but in most cases, the location of calling birds can be judged reasonably accurately. Birds flying above the canopy were excluded from the survey. Along with the point-count data, we kept a list of additional species encountered as we walked between the point-count stations during a survey. We conducted surveys over 3 years: July to October 2014 (wet season), January 2015, and January to March 2016 (dry season). Each site was surveyed a total of ten times over the 3 years, five times in the wet season and five times in the dry season, giving a total of 1,260 point-counts.

Observers had considerable ornithological field experience, including in tropical forest habitats. Two observers were Panamanian, with many years' experience identifying local avifauna. All observers received training before data collection began, including detection tests to check for any bias in identification ability and for consistency in estimations of distance. Recordings of calls and songs were used intensively to improve identification skills and check identifications based on vocalizations.

2.4 | Data analysis

Prior to analysis, we removed unidentified birds from the dataset (1.8% of total number of detections). We conducted all analyses both on the remaining bird species (henceforth, all birds) and on a dataset restricted to birds with a higher dependency on forest habitats (henceforth, forest specialists). We defined forest specialists as species characteristic of the interior of undisturbed forest, breeding almost invariably within forests, occurring less often away from forest interior and rarely seen in non-forest habitats, even though they may persist in secondary forest and forest patches if their particular ecological requirements are met (BirdLife International 2018, Buchanan, Donald, & Butchart, 2011). We note that classification of forest dependency in birds is potentially subjective, partly because species vary in their habitat selection geographically. We used the most recent classification of forest specialism (BirdLife International 2018) because it is global in focus, comprehensive, and widely accessible. We found results to be very similar when we used alternative, geographically restricted classifications of forest dependency, including

published descriptions by Ridgely and Gwynne (1989), habitat codes of Stotz et al. (1996), and habitat scores of Tobias et al. (2016).

We calculated rarefaction curves to compare rates of species accumulation among forest age classes for all birds and forest specialists. When scaled by the number of samples, curves reached or approached the asymptote for all forest ages and species sets, suggesting survey effort was adequate (Supporting Information Figures S1 and S2). However, curves did not reach asymptotes for some forest ages and species sets when scaled by individuals, suggesting some sites were under-sampled (Supporting Information Figures S1 and S2). To identify species that were missing from the extensive PF dataset, we compared our dataset to the species list reported in a previous survey of the same extensive PF forest (Robinson et al., 2000). This long-term study used intensive survey methods to describe the species composition of the extensive PF site and so provides a complete picture of the species present at this locality.

We calculated species richness and the percentage of PF species present in SF by combining both the point-count data and the additional species encounters. All other analyses used data from point-counts only. We conducted analyses using R (version 3.4.1, R Core Team 2017).

2.5 | Species richness, diversity, and dominance

We compared species richness, Shannon–Weiner diversity indices, and dominance across forest ages using data from all surveys combined. We calculated dominance as the percentage of individual birds represented by the five most common species in each site.

2.6 | Bird population density

We used the R package “Distance” (Laake, Borchers, Thomas, David, & Bishop, 2015) to estimate bird community population density among forest ages pooled over the 1,260 point-counts, following methods described in Buckland, Rexstad, Marques, and Oedekoven (2015). We pooled visual and audial detections, and stratified analyses by forest age to allow for differences in detectability among habitats. Using the function “ds” (“Distance” R package; Laake et al. (2015), we fitted 36 detection functions with various combinations of covariates (year, season, detection method, and observer) per forest age and used AIC model selection to choose the best-fit models (Burnham, Anderson, & Huyvaert, 2011). The detection functions provided an estimation of bird population density (number of individuals per hectare) in each of the forest ages. The function “ds” requires a minimum of 80 observations within a category to give reliable estimates per species; thus, we did not calculate detection functions for individual species, since only 4–9 bird species in each forest age category had more than 80 detections. Our results should be interpreted with caution since pooling community detectability data assumes that each species is equally detectable across each of the 14 sites.

2.7 | Species composition and similarity to primary forest

We calculated the percentage of bird species detected in PF that were also detected in SF separately for isolated PF and extensive PF sites by pooling data for each forest age category.

We used the Morisita–Horn abundance-based similarity index (S_{MH}) to compare species composition between pairs of assemblages. The S_{MH} is robust to uneven and insufficient sampling and thus suited to determine whether reassembly of PF communities occurs in SF in terms of relative abundance (Chao, Chazdon, Colwell, & Shen, 2006). We examined whether species composition of SF converged with either isolated PF or extensive PF over time by comparing the similarity in composition (S_{MH}) of each SF forest site to each of the PF sites. We examined similarity to isolated and extensive PF sites separately because isolation-related extirpations have altered the island bird communities (Robinson, 1999). Similarity values were produced using the function “vegdist” (“vegan” R package; Oksanen et al., 2016).

To determine whether forest age or geographic location explained patterns in species composition across sites, we performed Mantel tests on three matrices of pairwise distances among sites: Euclidean geographic distance, difference in forest age, and dissimilarity in species composition ($1-S_{MH}$). We assigned PF sites a nominal age of 500 year to include these sites in the distance matrix for forest age. Mantel tests were performed using the function “mantel” (“vegan” R package; Oksanen et al., 2016).

We explored qualitative similarities in species composition among sites with non-metric multidimensional scaling (NMDS; Anderson et al., 2011). This approach uses rank order, rather than absolute abundances of species, to represent the original position of communities in multidimensional space as accurately as possible using a reduced number of dimensions. We used similarity matrices generated from both the S_{MH} abundance-based and Jaccard incidence-based similarity values (S_j). We included the S_j similarity values to investigate whether PF species were present in SF, even if patterns of relative abundance were different from those in PF. Ordinations were performed using the function “metaMDS” (“vegan” R package; Oksanen et al., 2016).

To assess the significance of observed differences in species composition as related to SF age, isolation level (isolated or connected), forest type (SF or PF), and distance to extensive PF, we conducted a series of permutational MANOVAs, an analysis of variance using distance matrices. This analysis uses pseudo- F values to compare among-group to within-group similarity and assesses significance by permutation. We also investigated the effect of season (wet or dry) on species composition by conducting a permutational MANOVA at survey level. Permutational MANOVAs were produced using the function “adonis” (“vegan” R package; Oksanen et al., 2016).

We calculated the mean number of migratory bird detections in different forest age categories based on count data with no distance corrections. This gives a relative abundance of migratory birds in habitats for those species with similar detection probabilities. We

also used the point-count data to list the five most abundant species per forest age and classified these species using diet and habitat information from Ridgely and Gwynne (1989) and Wilman et al. (2014).

3 | RESULTS

Our surveys recorded a total of 183 bird species from 42 families, of which 55 species from 24 families were forest specialists (Supporting Information Table S1). We detected 13,894 individual birds in fixed-radius point-counts, of which 5,256 were forest specialists (BirdLife International 2018).

3.1 | Patterns of species richness, diversity, and dominance

No clear relationship was found between species richness and forest age (Table 1). The youngest SF (20 year old) had higher species richness than all other sites and a species richness of forest specialists similar to extensive PF (Table 1). The oldest SF (120 year old) had the lowest species richness for all birds and forest specialists. These counter-intuitive patterns of species richness appear to be influenced by differences in connectivity among sites, with higher species richness found in sites that were connected to extensive PF (Figure 2). Compared with extensive mainland PF sites, the isolated PF sites had lower species richness for both datasets. Species diversity (Shannon–Weiner index) showed similar patterns across sites, while dominance values were highest in isolated sites and lowest in connected sites (Table 1).

3.2 | Bird population density

There was no clear pattern in bird community population density estimates across the different forest ages or levels of isolation. For all birds, the 20-year-old SF had the greatest density of birds, estimated at 29 individual birds/ha (95% CI: 26, 31; Figure 3). This compares with the lowest density estimate of 17 individual birds/ha (95% CI: 16, 19) in the 120-year-old SF. Qualitatively similar patterns were found for forest specialists.

3.3 | Similarity to primary forest

Focusing on all birds, we found no clear relationship between SF age and the percentage of PF bird species detected in SF sites (as estimated by our surveys), but there was a relationship between isolation and percentage of PF species present in SF. Percentage of PF species present was consistently highest in connected sites and lower in isolated sites. When comparing SF ages, we found that the highest percentage of PF species occurred in the 20-year-old connected SF (86% when compared with extensive PF sites as estimated by our surveys; Figure 4). Surprisingly, the 120-year-old isolated SF had the lowest percentage of PF species present, with only 72 percent in common with isolated PF and 57% in common with extensive PF. This is likely due to shifts in species richness driven by isolation effects in the island PF, where we detected just 62% of the species that we found in extensive mainland PF.

For all birds, compositional similarity to isolated (but not extensive) PF increased with forest age (Figure 5). The highest similarity in species composition between PF and SF was recorded on BCI where

TABLE 1 Approximate forest age, level of isolation, species richness, Shannon–Weiner diversity index, and dominance statistics for bird communities of ten secondary forest and four primary forest sites in central Panama, for both forest specialists and all bird species

Site	Age (years)	Level of isolation	All birds			Forest specialists ^a		
			Species richness	Shannon–Wiener index	Dominance (%)	Species richness	Shannon–Wiener index	Dominance (%)
1	20	Connected	117	3.97	29.86	40	3.07	46.19
2	20	Connected	113	4.03	27.65	37	3.01	49.22
3	40	Isolated	84	3.63	36.75	26	2.72	54.55
4	40	Isolated	90	3.73	38.01	25	2.75	53.67
5	60	Isolated	76	3.61	37.16	25	2.83	50.00
6	60	Isolated	89	3.73	34.35	30	2.93	45.21
7	90	Connected	95	4.04	22.32	34	3.19	40.05
8	90	Isolated	83	3.77	32.12	26	2.77	54.25
9	120	Isolated	63	3.27	48.37	22	2.45	66.57
10	120	Isolated	62	3.37	46.42	23	2.49	63.84
11	Primary	Isolated	74	3.63	36.89	27	2.78	54.77
12	Primary	Isolated	75	3.64	35.94	28	2.79	54.17
13	Primary	Extensive	99	4.11	21.02	39	3.41	28.74
14	Primary	Extensive	96	3.95	25.13	38	3.20	39.87

^aForest specialists: species that are scored as having high forest dependence (BirdLife International 2018).

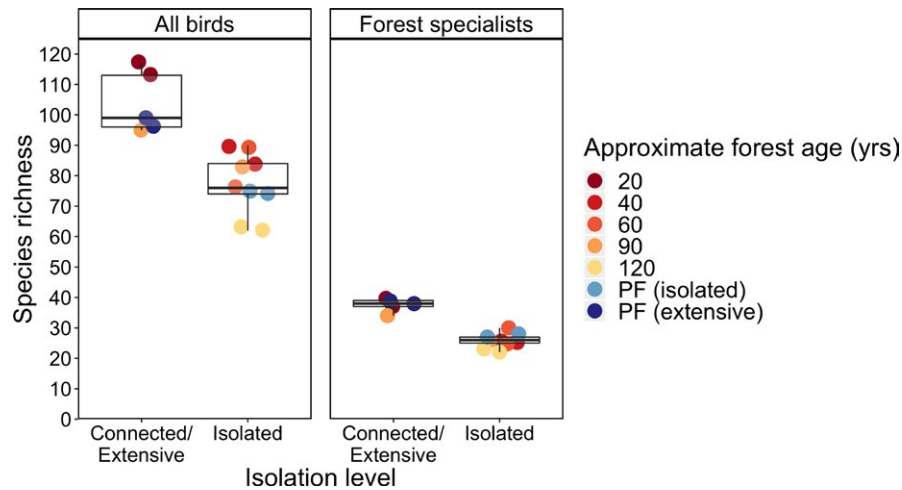


FIGURE 2 Bird species richness by forest age, forest type, and degree of isolation from extensive PF. “Forest Specialists” are species that are scored as having high forest dependence (BirdLife International 2018)

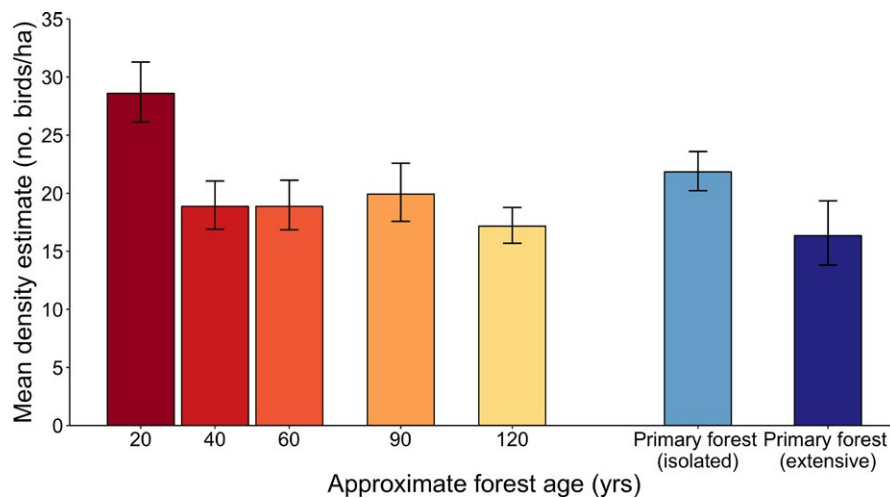


FIGURE 3 Population density estimates and 95% confidence intervals for all bird species (number of birds per hectare) using distance corrections. Species data have been pooled for the two sites in each of seven forest age categories

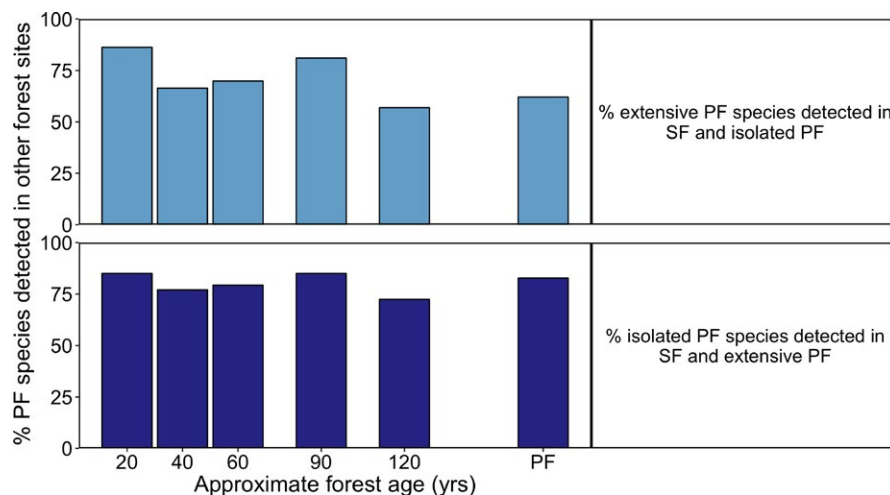


FIGURE 4 Percentage of bird species detected in primary forest (PF) that were also detected in secondary forest (SF) in five SF age categories for isolated PF sites and extensive PF sites. Species data have been pooled for the two sites in each of seven forest age categories

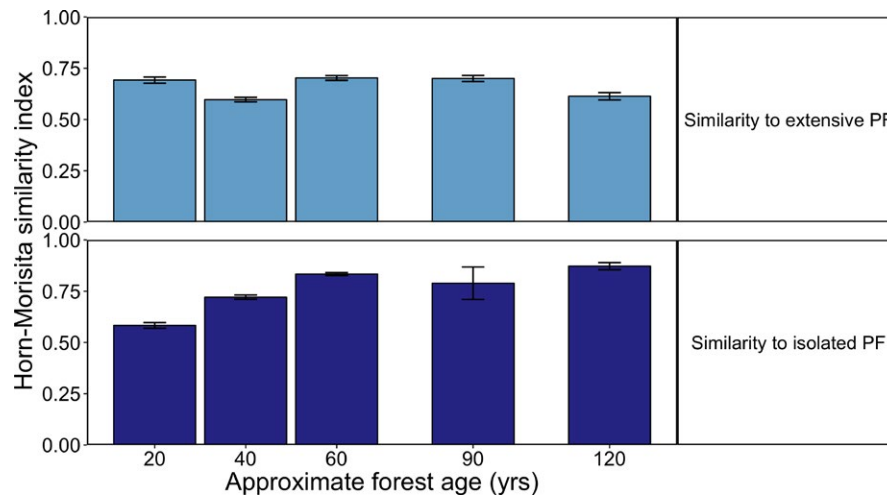


FIGURE 5 Similarity (Morista-Horn) between secondary forest sites (SF) and both isolated and extensive primary forest (PF). Each bar represents the mean similarity index (± 1 SE) between the two SF sites in each age category (20, 40, 60, 90, and 120 years old) and the PF sites. Calculated using the all-bird dataset

the community composition of the oldest isolated SF (120 year old; $n = 2$ sites) was very similar to isolated PF ($n = 2$ sites; similarity index [S_{MH}]: 0.87 ± 0.03). By contrast, the lowest similarity was between the 20-year-old SF and the isolated PF (0.58 ± 0.03); these sites span the widest range in both isolation level (mainland vs. island) and age (20-year vs. PF). Similarity was higher between extensive PF sites and 20-year-old SF (0.69 ± 0.03) than between extensive PF sites and the older, isolated 120-year-old SF (0.61 ± 0.04). Mantel tests indicated that geographic distance among sites ($R^2 = 0.74$, $p = <0.001$) explained a greater proportion of variation in species composition than forest age ($R^2 = 0.30$, $p = <0.05$). Similar patterns were found for forest specialist species, except forest age was not a significant predictor of species composition (geographic distance: $R^2 = 0.66$, $p = <0.01$; forest age: $R^2 = 0.21$, $p = 0.06$).

The NMDS of abundance-based species composition (S_{MH}) across all bird species showed a separation of sites in relation to both forest

age and isolation level (Figure 6). Sites displayed a clear split along Axis 1 that related to site location (connected or isolated), while the age of forest sites tended to increase along Axis 2. The NMDS comparisons for forest specialists showed very similar patterns as those seen for all birds, as did the NMDS results for both datasets using S_J , although the effect of forest age became less apparent when restricting analyses to species presence/absence data (Figure 6).

The permutational MANOVA using S_{MH} indicated that forest isolation level explained a greater portion of the variation in community composition of all bird species than forest age or forest type (SF vs. PF; Table 2). Distance to extensive PF was not a significant predictor of community composition. The permutational MANOVA using S_J for all birds showed very similar results (Table 2). Season had a significant effect on community composition, but it did not change the patterns observed for forest isolation, forest age, or forest type,

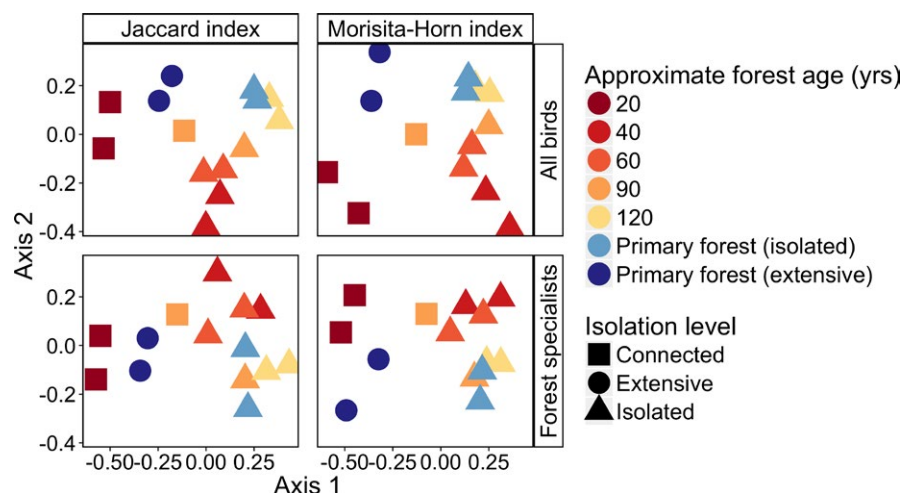


FIGURE 6 Non-metric multidimensional scaling (NMDS) plots of bird communities in two forest sites in each of five secondary forest (SF) age categories (20, 40, 60, 90, and 120 year old), and isolated primary forest (PF) and extensive PF. NMDS were generated using the Morisita-Horn index (all birds stress = 0.07; forest specialists stress = 0.08) and Jaccard index (all birds stress = 0.07; forest specialists stress = 0.06). Isolation levels are represented by different symbols. “Forest Specialists” are species that are scored as having high forest dependence (BirdLife International 2018)

TABLE 2 Permutational MANOVA results assessing species composition using community similarity matrices generated with both Morisita-Horn abundance-based similarity index (S_{MH}) and Jaccard incidence-based similarity index (S_J). We tested observed differences between forest age, isolation level (isolated or connected), forest type (SF or PF), and geographic distance to extensive mainland PF. We also investigated the effect of season (wet or dry) on species composition by conducting a PERMANOVA at survey level

	All birds				Forest specialists ^a			
	R^2	F	df	p	R^2	F	df	p
S_{MH}								
Forest isolation	0.15	9.12	1	<0.01	0.18	6.28	1	<0.05
Forest age	0.13	7.80	1	<0.01	0.02	0.84	1	ns
Forest type (SF vs. PF)	0.08	5.10	1	<0.01	0.01	0.51	1	ns
Distance to extensive PF	0.02	1.35	1	ns	0.04	1.31	1	ns
S_J								
Forest isolation	0.10	2.19	1	<0.05	0.11	2.18	1	<0.05
Forest age	0.11	2.42	1	<0.05	0.07	1.37	1	ns
Forest type (SF vs. PF)	0.09	1.93	1	<0.05	0.06	1.14	1	ns
Distance to extensive PF	0.06	1.29	1	ns	0.06	1.17	1	ns
S_{MH}^b								
Season (wet vs. dry)	0.05	11.69	1	<0.01	0.04	8.84	1	<0.01
Forest isolation	0.03	7.45	1	<0.01	0.05	9.38	1	<0.01
Forest age	0.05	10.29	1	<0.01	0.04	7.15	1	<0.01
Forest type (SF vs. PF)	0.03	6.30	1	<0.01	0.02	5.35	1	<0.01
Distance to extensive PF	0.03	5.69	1	<0.01	0.02	3.56	1	<0.05

^aForest specialists: species that are scored as having high forest dependence (BirdLife International 2018). ^bData analyzed at survey level, with season included.

although distance to extensive PF became significant (Table 2). Community composition of forest-dependent species (using S_{MH} or S_J) was largely dictated by forest connectivity. The same patterns were found for forest specialists as the all-bird dataset when season was taken in to account (Table 2).

3.4 | Compositional changes

The composition of the five most abundant bird species differed across forest ages (Supporting Information Table S2). Only one species, Black-crowned Antshrike (*Thamnophilus atrinucha*), was consistently abundant across all sites. Southern Bentbill (*Oncostoma olivaceum*) was among the top five most abundant species in the youngest forest sites (20-, 40-, and 60-year-old SF), while Red-lored Amazon (*Amazona autumnalis*) appeared in the top five for both the isolated and extensive PF, as well as the 90-year-old SF. The five most abundant species in the isolated and extensive PF, and the 90-year-old SF exhibited a greater diversity of feeding guilds and foraging strata than those found in the younger SF sites (Supporting Information Table S2).

We detected 15 species in isolated PF that we did not see in extensive PF, including species such as Crested Guan (*Penelope purpurascens*) that are susceptible to hunting and therefore extirpated from most mainland localities. By contrast, 44 species were detected in extensive PF that were not seen in isolated PF. These were predominantly understory, insectivorous species, many of which have become extinct on BCI since its isolation (Robinson, 1999; Willis, 1974).

The number of migratory birds detected per point-count was highest in the 20-year-old SF (0.533 ± 0.091) and declined with increasing SF age to only 0.078 ± 0.032 migrants detected per point-count in the 120-year-old SF (Supporting Information Figure S3). The number of migrants detected in PF sites was about half the number detected in the 20-year-old SF (island PF: 0.27 ± 0.07 ; mainland PF: 0.29 ± 0.06).

4 | DISCUSSION

Our survey data, sampled across tropical SF of varying ages and isolation levels, revealed that variation in avian species richness was best explained by connectivity to extensive PF, rather than forest age. We found the highest species richness in the youngest SF sites, which were adjacent to extensive PF. Similarly, connectivity, rather than the forest age, was the strongest predictor of community composition. Finally, the highest bird population density was also found in younger SF, although broader patterns in density did not appear to be driven by either forest age or connectivity.

4.1 | Species richness, diversity, and dominance

High species richness and abundance of birds in SF or successional areas have been documented in many studies (Blake & Loiselle, 2001; Johns, 1991; Karr, 1976; Petit & Petit, 2003), supporting the hypothesis that intermediate levels of disturbance may lead to

high species richness (Connel, 1978). In general, species richness in younger SF is boosted by an influx of non-forest, open habitat, and generalist species, although it also may contain an important component of forest species (Barlow, Mestre et al., 2007; Dunn & Romdal, 2005). Most studies report that species richness and community structure of tropical secondary forests progressively approach that of PF over time, and tend to track the increasing structural complexity of secondary forests (Dent & Wright, 2009; Raman, 1998). In our study, however, species richness and abundance did not increase with forest age and were instead highest in the youngest SF even when non-forest bird species were removed. We also found that species richness and abundance both increased with greater connectivity to extensive PF, suggesting that high species richness in the 20-year-old SF is driven by proximity to extensive PF in adjacent Soberania National Park.

Proximity to undisturbed habitats has been shown to increase the diversity of bird communities in degraded sites (Johns, 1991; Terborgh & Weske, 1969; Waltert, Mardiasuti, & Muhlenberg, 2004). In La Selva, Costa Rica, PF was the primary habitat and source population for many of the bird species found in SF (Blake & Loiselle, 2001). This pattern is supported by our findings, in which a greater number of forest specialists were found in well-connected 20-year-old SF, than in isolated PF. In a landscape of mixed ages of SF and varying connectivity among forest patches, our findings suggest that the key factor determining avian diversity is connectivity to extensive PF, rather than forest age. Extinction and colonization dynamics shape the avifaunas of forests within this landscape, with potentially lower colonization rates in isolated forest sites, and greater colonization rates in regenerating forests that are sufficiently well-connected to PF (Bradfer-Lawrence et al., 2018; Robinson, 1999).

4.2 | Bird population density

The density of birds in SF and PF varied across sites, with the highest density estimates in the youngest SF, matching patterns previously reported for the Neotropics (Blake & Loiselle, 2001; Johns, 1991; Karr, 1976; Petit & Petit, 2003). Earlier studies in Soberania National Park have reported densities 2–3 times higher than our PF estimates (Robinson et al., 2000; Van Bael et al., 2013). The disparity in figures may result from differing methodologies, particularly the spot mapping and smaller point-count radius used by previous studies. By contrast, previous population density estimates for young SF (5–6 year old) from Agua Salud were about 45 percent lower than estimated population densities from our surveys (20 year old), but comparable with our estimates from older SF (Van Bael et al., 2013). Higher population density in younger forest may in part reflect increased detectability of some species, particularly those associated with the forest canopy, which is harder to survey in PF (Robinson, Lees, & Blake, 2018). Our results may also reflect the increased resource availability of both fruit and insects often found in younger SF (Blake & Loiselle, 1991; Levey, 1988; Martin, 1985), which may encourage birds from PF to use adjacent SF for foraging.

4.3 | Similarity to primary forest

Most studies comparing the similarity of avian species composition between SF and PF report increasing similarity to PF with SF age (Borges, 2007; Dent & Wright, 2009; Raman, 1998). All our SF sites had high levels of compositional similarity to PF, and upper figures were within the range of similarity found in extensive PF. In line with our hypothesis, SF community composition became increasingly similar to that of isolated PF across the chronosequence. However, SF community composition did not converge on that of extensive mainland PF sites with increasing SF age. Similarly, there was no relationship between SF age and the percentage of PF species detected: The highest percentage of PF species was found in the youngest SF that, critically, was also the least isolated and most well-connected to extensive PF.

Based on our findings, isolation plays a greater role than forest age in determining the reassembly of bird communities in SF. Despite the persistence of high-stature PF forest on BCI, many species have disappeared from the local community since it was isolated by the inundation of Lake Gatun (Robinson, 1999; Willis, 1974). While habitat size effects and isolation by water have influenced patterns local extinction, they do not appear to drive our results since peninsula sites have similar bird communities to the island PF, with relatively low species richness. By contrast, bird communities in extensive mainland PF sites include forest specialists that have been lost from both BCI and peninsula sites, and are unlikely to recolonize SF unless it is contiguous with PF that harbors these species. In summary, SF avian communities are at least partially dependent on contiguous PF source populations. If connected PF populations have low species richness, then SF will likely never develop the bird communities associated with extensive PF forest stands (Ferraz et al., 2007; Jones et al., 2016; Stouffer et al., 2006). However, if SF sites are adjacent to extensive PF, forest specialists may recolonize relatively rapidly. For example, understory insectivores increased in abundance just 10 years after SF was abandoned adjacent to PF in Amazonia (Andrade & Rubio-Torgler, 1994). Our findings highlight that connectivity is critical for reassembly of avian communities in regenerating tropical forests (Barlow et al., 2006; Lees & Peres, 2009).

4.4 | Compositional changes

Despite the key role of connectivity in determining avian composition, forest age may still influence bird community reassembly, as demonstrated by the increasing similarity of communities in older isolated SF to that of isolated PF. However, six forest species present in isolated PF on BCI were missing from the adjacent 120-year-old SF, including the forest specialists Long-billed Gnatwren (*Ramphocaenus melanurus*), Rufous Mourner (*Rhytipterna holerythra*), Scaly-throated Leaf-tosser (*Sclerurus guatemalensis*), Semiplumbeous Hawk (*Leucopternis semiplumbeus*), Spot-crowned Antvireo (*Dysithamnus puncticeps*), and Wood Thrush (*Hylocichla mustelina*). Conversely, there were no forest specialists detected in the 120-year-old SF that were not also

present in the isolated PF. Although several studies report a high representation of PF species present in SF (>70% of PF species), SF communities often lack rare species, or those with highly specialized dietary or habitat requirements (Chazdon et al., 2009; Dent & Wright, 2009).

The loss of forest species from isolated sites across this landscape is striking and is especially evident when comparing isolated PF with extensive PF. BCI is a relatively large forest fragment (1,560 ha), but it has been isolated for >100 years, and during this time, numerous avian extinctions have been documented (Chapman, 1938; Eisenmann, 1952; Karr, 1982, 1990; Robinson, 1999; Willis & Eisenmann, 1979); 65 species have been lost from the island, including 30 forest species and 35 edge species (Robinson, 1999). Many of the forest species missing from the PF sites on BCI are understory insectivores such as Dusky Antbird (*Cercomacroides tyrannina*), Ocellated Antbird (*Phaenostictus mcleannani*), and Black-faced Antthrush (*Formicarius analis*). In addition, we only detected two of the ten species identified by Robinson (1999) as forest birds that are close to extirpation on BCI: Black-tailed Trogon (*Trogon melanurus*) and Rufous Piha (*Lipaugus unirufus*). The isolation of BCI within a large waterbody makes recolonization by many forest species unlikely as they are poorly adapted to sustained flight, and unwilling or incapable of dispersing across open water (Moore et al., 2008; Tobias et al., 2013).

Species richness and relative abundance of migratory birds were highest in younger SF, with numbers decreasing with increasing SF forest age. Similarly, Van Bael et al. (2013) found more migrant species in SF (5–6 year old) than PF sites in central Panama (0.5 and 0.2 birds/point-count for SF and PF, respectively). Migrant birds may occupy degraded and open habitats because they are excluded from optimal habitats by resident species, or because they are better able to adapt to the resources offered by SF (Greenberg, Ortiz, & Caballero, 1994; Willis, 1980; Wunderle & Latta, 1996). Our results add to a growing body of evidence confirming that secondary and degraded tropical forests are important habitats for migrant bird species (Greenberg, Bichier, Angon, & Reitsma, 1997; Greenberg et al., 1994; Van Bael, Bichier, Ochoa, & Greenberg, 2007; Wunderle & Latta, 1996).

It is possible that other aspects of community structure, such as functional and phylogenetic composition, may be affected by forest age and connectivity (Bregman et al., 2016; Pigot, Trisos, & Tobias, 2016). For example, if SF provides a simplified range of structural and dietary resources for roosting and foraging birds, then young forests may not be able to support as many closely related or functionally similar species, resulting in functional and phylogenetic over-dispersion (Bregman et al., 2016). In addition, isolation may increase functional and phylogenetic clustering as certain groups are selected against due to their inability to cross gaps between forest fragments (Bregman et al., 2016). Further studies are needed to clarify how forest successional status and connectivity across the wider landscape interact to shape bird community composition.

4.5 | Caveats

Our study design is limited by the historical and geographic features of the study landscape, making it impossible to establish a fully replicated study within the different levels of isolation and forest age (Denslow & Guzman, 2000). Thus, some of the patterns detected may be specific to the local context of water barriers associated with the Panama Canal. Nonetheless, while further studies are now required to assess how far our conclusions can be generalized to other tropical landscapes, we argue that the water barriers and detailed history of forest regeneration in central Panama provide a valuable setting for testing the relative effects of isolation and forest age on the conservation value of SF.

Effectively surveying birds across differing habitats remains a methodological challenge for studies such as ours (Buckland et al., 2008). We standardized survey effort at all sites at the risk of generating spurious differences in bird communities due to variation in detectability (Bregman et al., 2016; Robinson et al., 2018). For example, it is possible that estimates of species richness and population density in younger SF are inflated because (a) individual birds tend to be more detectable at forest edges and in lower-stature forests (Barlow, Mestre et al., 2007; Buckland et al., 2008; Ruiz-Gutiérrez, Zipkin, & Dhondt, 2010) and (b) PF bird species may have been missed by our surveys because they are relatively quiet, inactive, and inconspicuous or occur at low population densities (Robinson et al., 2018; Terborgh, Robinson, Parker, Munn, & Pierpont, 1990). To explore how detectability may have affected our results, we compared our species counts to a dataset from a previous study surveying the same extensive PF site with more intensive survey methods (including mist-netting), over a far longer survey period, and across an expanded set of species (Robinson et al., 2000). Overall, Robinson et al. (2000) reported an additional 132 species in the community. However, the majority (65%) of these were either unavoidably or deliberately excluded from our study because they fall into one of three categories: (a) nocturnal, vagrant, or migratory species which are not core components of the diurnal communities we studied (45%); (b) aerial species (e.g., swifts and raptors) (15%); and (c) birds associated with aquatic landscape features (5%). Because of our study aims, we did not survey species in the second and third categories, and indeed discounted all individual birds detected on waterbodies or in flight passing over the forest. Excluding these species, 46 species from Robinson et al. (2000) were not observed, most of which are rare or difficult to detect. While the absence of these 46 species from our censuses may underestimate the importance of PF for conservation in our analysis, we note that this is a relatively minor component of overall biodiversity and represents a small number of individual birds. Moreover, increased surveying and mist-netting of our SF sites would no doubt also increase species richness in SF by an unknown amount; thus, we do not believe our main conclusions would be altered by further surveying.

A separate issue relates to the breeding status or viability of populations of forest birds in younger SF. It has been hypothesized that populations of many PF bird species in SF may be non-viable,

and therefore less important to conservation, because they are largely made up of (a) transient individuals or (b) temporary territories with infrequent breeding and low breeding success (Tobias et al., 2013). We cannot rule out this possibility based on our results, and more research is needed to clarify population demography and viability in SF. However, the relatively high population density of primary forest bird species in younger SF suggests that, at a minimum, SF can greatly increase the population carrying capacity of adjacent PF, thus increasing its importance for conservation.

5 | CONCLUSIONS

Our results suggest that the link between tropical bird communities and successional trajectories differs between isolated and non-isolated SF sites; in isolated sites, bird communities converge with isolated PF over time, whereas highly connected SF sites converge rapidly with extensive PF. In addition, we find evidence that SF, even when relatively young, can support dense populations of PF species, so long as forests are connected to extensive PF. Crucially, even if these populations are transitory, SF may theoretically increase the population carrying capacity of PF, reducing the risk of local extinction. The importance of habitat connectivity highlighted by our results is specifically relevant to tropical forests as species at higher latitudes are often better adapted for survival in SFs or dispersal between patches of PF (Stratford & Robinson, 2005). These findings emphasize the importance of reforestation and maintaining existing SF at the borders of extensive tropical forest and highlight the need for improved protection of SF in protected area buffer zones throughout the tropics.

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DATA AVAILABILITY

Data available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.77m6100> (Mayhew, Tobias, Bunnefeld, & Dent, 2019).

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SUPPORTING INFORMATION

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