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ORIGINAL ARTICLE

Partial recovery of primary rainforest bird communities in Amazonian secondary forests

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Abstract

Loss of primary rainforest imperils species, communities, and ecosystem services. Secondary forests play a role in supporting primary forest species, making it important to assess how variation in landscape composition, sample area, and secondary forest age influence their value for maintaining biodiversity. We sampled bird communities in three 16-ha sites in 31-36-year-old secondary forest (SF) and three adjacent primary forest (PF) sites at the Biological Dynamics of Forest Fragments Project near Manaus, Brazil. SF sites were surrounded by vast, minimally broken PF. Spot-map surveys revealed 204 species, with 48 found only in PF (SF estimate 117–144 species/site, PF estimate 163–180). SF communities were distinct, but composed almost entirely of PF species and overlapped PF communities in functional attributes. Cavity-nesting species were slightly underrepresented in SF. Important differences in SF included much reduced abundance of canopy, terrestrial, and insectivorous species. Vegetation structure may limit canopy species: SF had a homogeneous canopy of 20–25 m, >10 m lower than the heterogeneous PF canopy. Sensitivity of terrestrial insectivores conforms to an expected pattern, perhaps exacerbated by a lack of colonists for these regionally declining species. Relatively better recovery of midstory and understory species does not align with some studies, perhaps because our landscape facilitated their colonization. In this system, SF bird communities appear to be recovering, with frugivores, nectarivores, and granivores (including game species) already well matched to PF. Complete recovery may be slowed not just by SF habitat suitability, but also by demographic processes in PF that limit availability of colonists.

Abstract in Portuguese is available with online material.

KEYWORDS
Brazil, forest recovery, forest restoration, forest structure, habitat selection, second growth, species richness, succession

1 | INTRODUCTION

Tropical primary rainforests are lost at a rate of 2.5–6 Mha/year, with the Brazilian Amazon alone losing 27.8 Mha of humid primary forest (PF) from 2002–2021 (Hansen et al., 2013, University of Maryland and World Resources Institute, 2023). Erosion of biodiversity associated with PF loss has long been a concern, now with the additional consideration of how changes in PF carbon storage could affect global climate and regional maintenance of the rainforest biome (Boulton et al., 2022; Flores et al., 2024; Lovejoy &

Oren, 1981; Sayer & Whitmore, 1991). Variation in land use following deforestation drives both the return of biodiversity and recovery of carbon stores (Smith et al., 2021). Understanding the trajectory of forest biodiversity recovery in secondary forest (SF) under multiple scenarios provides a means to assess the potential of species, communities, and emergent processes to return to PF levels (Lennox et al., 2018; Prieto et al., 2022).

Research in tropical SF has generated considerable data on biodiversity and ecosystem properties, with local studies recently employed in broader syntheses (Arroyo-Rodriguez et al., 2023; Martin et al., 2013; Prieto et al., 2022; Smith et al., 2021). Inconsistent conclusions from small-scale studies have been interpreted as showing that SF offers limited value for maintaining biodiversity (Barlow et al., 2007; Gibson et al., 2011). Even so, it is useful to emphasize two fundamental characteristics of tropical SF. First, increasing extent of SF is inevitable as cleared areas are abandoned (Wright & Muller-Landau, 2006). Second, even poorly performing SF will have greater value for forest biodiversity than the degraded areas it replaces, and that value will increase over time if SF is allowed to develop (Chazdon, 2014; Martin et al., 2013). Some of the same factors that influence vegetation succession will drive variation in animal communities in SF, particularly time and local availability of PF to provide colonists (Bradfer-Lawrence et al., 2018; Loiselle & Blake, 1994; Mayhew et al., 2019).

In the Amazon, vast areas of PF support large populations of most bird species in communities that can be relatively homogeneous at the scale of 10s or possibly 100s of km in unbroken forest (Rutt et al., 2023). Dispersal limitation can be extreme, at both evolutionary timescales (e.g., Naka et al., 2012), and at ecological scales by low movement of some taxa across even narrow openings (Ibarra-Macias et al., 2011; Laurance & Gomez, 2005; Stouffer et al., 2006). Deforested areas carved out of PF will often be abandoned in a setting with forest taxa locally available to recolonize over the course of secondary succession (Powell et al., 2016).

In the ~1500 km^2 larger landscape that includes the Biological Dynamics of Forest Fragments Project (BDFFP), north of Manaus, Brazil, PF cover has been ~90% for >30 years (Rutt, Jirinec, et al., 2019). As occurred elsewhere in the Brazilian Amazon, a flurry of deforestation in the 1980s was followed by large-scale abandonment, resulting in additional deforestation being partially balanced by SF recovery (Bierregaard & Gascon, 2001; Laurance et al., 2018). We have a good understanding of how SF recovery facilitates movements of forest understory birds through the landscape (Powell et al., 2013; Stouffer et al., 2006), and how mixed-species flocks and understory birds use SF (Coddington et al., 2023; Powell, Zurita, et al., 2015; Rutt et al., 2020; Rutt & Stouffer, 2021). At least 40 forest species are estimated to breed in 30-35-year-old SF (Rutt et al., 2021). Only about half as many cavities are available at these sites, potentially limiting cavity-nesting birds (Dantas Oliveira et al., 2024). Although we do not know details of colonization, survival, and reproduction in SF, it appears to be suitable for a large subset of species present in adjacent PF. As such, it represents a setting for comparing bird communities in recovering SF with communities from intact PF. The larger landscape has not lost any PF bird species in the last 40 years, although bird communities have changed even in the absence of landscape effects (Stouffer et al., 2021). Modest disturbance following initial deforestation as well as juxtaposition with vast undisturbed PF make this setting a best-case scenario for passive recovery in the Amazon.

Here we use spot-map surveys to compare bird communities in replicated SF and PF sites. We begin by describing the vegetation structure of the sites to provide context for the degree of recovery in SF. For birds, our objectives are: (1) compare abundance and species richness between SF and PF; (2) assess the recovery of cavity-nesting species; (3) identify species that remain absent from SF, and species unique to SF; and (4) compare community organization, including foraging guild, stratum, and other functional attributes between SF and PF.

2 | METHODS

2.1 | Study site

We worked in six square 16-ha sites at the BDFFP, three each in PF and 31–36-year-old SF (Figure S1). All sites were embedded in either PF or SF, 700–1000 m from the alternative forest type. We used new or existing trails to establish a 100 m grid system at each site. At the time of our sampling, the larger landscape of 1500 km^2 was ~95% PF (Rutt, Jirinec, et al., 2019).

2.2 | Vegetation sampling and analysis

Our objective with vegetation sampling was to provide a basis for evaluating the extent to which SF sites had recovered PF structure. We chose simple metrics that could be easily transferred to other studies (canopy height, dbh, and vegetation profile) as well as measurements that reflected our own perceptions of systematic differences between PF and SF (palms, vines, and litter). Within each of the six sites, we randomly sampled eight of the 16 1-ha subplots. Within each chosen subplot, we randomly established an 8 m radius sampling plot, which we further divided into four quadrants. In the middle of each quadrant, we measured canopy height with a laser rangefinder, and presence or absence of live vegetation in vertical bins of 0.5–3, 3–10, and 10–20 m (representing the top of SF canopy). At the same point, we measured litter depth by counting the number of leaves perforated by a fine stake. Within each sampling plot, we also measured the tallest canopy height and the dbh of the largest live tree. We counted all trunkless palms and vines in the northeast quadrant of each sampling plot.

We analyzed the main effect of PF vs. SF with random effects of site with linear mixed-effects models using the R package "lme4." We improved normality with log transformation for all variables except litter depth. For vegetation profiles, we summed the number of times vegetation appeared within each height band for the 32 sample points within each site, which we present as a visual depiction of vertical structure.

2.3 | Bird sampling and analysis

Each site was sampled on 11 days between 26 June and 27 July 2018. We acknowledge that this level of sampling provides only a snapshot of the bird community in a one-month window, but the effort is roughly comparable to the annual effort in other studies (e.g., Blake & Loiselle, 2024). Sampling in late June and July adequately represents the BDFFP bird community, which shows little within-year variation (Cohn-Haft et al., 1997). A single observer arrived by 0520 h (sunrise was ~0605 h) and recorded all birds seen or heard until 0930 h, surveying the entire 16-ha site. On most days, three observers were working simultaneously in separate plots. Observers did not follow a prescribed route or timing; we used the trail grid to follow flocks or move to areas with greater activity. We recorded all individuals detected, mapping location to 1-ha subplots. The 1-ha mapping helped us to avoid recounting individuals in the same day. We also noted birds detected outside the 16-ha site, although they were not included in the main analysis. We excluded flyovers. We rotated three experienced observers (CLR, PCS, and Claudeir Vargas) among sites daily so that each of us surveyed every site at least three times. We made voucher tape recordings of many species, especially in SF (archived at Macaulay Library). Taxonomy follows Remsen et al. (2022).

We analyzed SF vs. PF effects on overall bird abundance based on the number of detections at each site, with each sampling day as a replicate, with ANOVA using *lmer* from the R package "lmerTest." We estimated species richness at each site with the Chao2 estimator using *specpool* in "vegan," based on the list of species detected in each of 11 surveys at a site. We performed similar analyses of detections and species richness for just cavity-nesting birds (van der Hoek et al., 2017, Billerman et al., 2022, K.L. Cockle, pers. comm.). We used hierarchical cluster analysis (*pvclust* in "vegan") to quantify the relationships among the six sites based on total detections of each species (Suzuki et al., 2019). Sites were clustered based on Bray-Curtis dissimilarity using the average linkage method and 10,000 multiscale bootstrap resamples. This method returns statistical support as approximately unbiased (AU) probabilities of 0%–100%.

To examine guild-level differences and functional diversity, we generated a pseudoabundance metric for each species at each site, based on the number of surveys (0–11) in which the species was detected (Rutt et al., 2023). This defines the same range for all species and avoids undue impact of species that are detected in monospecific flocks. Across the three sites in each treatment (PF and SF), individual species pseudoabundance scores can range from zero (never detected in the treatment) to 33 (detected in each of the 11 surveys at each of the three sites in the treatment). We then tested for treatment effects on pseudoabundance for each foraging stratum and each foraging guild with paired *t*-tests comparing species-specific pseudoabundance in PF and SF. We determined functional diversity at each site based on morphological traits and categorical ecological characteristics following the framework of Villéger et al. (2008), resulting in three metrics (see Supporting Information): functional richness (FRic; volume of functional space the community occupies), functional evenness (FEve; evenness within the volume), and functional divergence (FDiv; divergence from the center of the functional space).

3 | RESULTS

3.1 | Vegetation structure

Mean canopy height was about 7.5 m lower in SF (Figure 1a and Table S1; PF overall mean = 29.1 m, SF overall mean = 21.6 m, $F_{1,4} = 23.12$, $p = .0086$). Mean canopy height was more heterogeneous within and among sites in PF, with >5 m separating site means in PF compared to <1 m in SF. Maximum canopy height mean differed by ~10 m between PF and SF (Figure 1b and Table S1; PF overall mean = 33.2 m, SF overall mean = 23.4 m, $F_{1,4} = 24.86$, $p = .0076$). SF sites were remarkably consistent in mean height compared to PF, with almost all measurements between 20–25 m. Despite the much taller PF canopy height, vegetation profiles at 10–20 m were similar between PF and SF sites (Figure 1d). In SF, density at 3–10 m aligned with canopy density, but this level was more open in PF. The lowest 3 m were more vegetated in PF, but highly variable in SF.

Not surprisingly, maximum dbh in PF was ~15 cm larger than in SF (Figure 1c and Table S1; PF overall mean = 50.2 cm, SF overall mean = 34.8 cm, $F_{1,4} = 11.18$, $p = .029$). Even so, many SF subplot samples were well within the range of PF samples, especially compared to P3, which also had the lowest canopy of the three PF sites. We counted over twice as many palms in PF, although there was considerable variation within and among sites in both forest types (Figure S2a and Table S1; PF overall mean = 7.9, SF overall mean = 3.6, $F_{1,4} = 12.79$, $p = .023$). Mean number of vines and mean litter depth were higher in SF, but within-site variation was much greater than the treatment effect for both metrics (vines [Figure S2b and Table S1]- PF overall mean = 7.7, SF overall mean = 12.0, $F_{1,4} = 4.34$, $p = .081$; litter [Figure S2c and Table S1]- PF overall mean = 8.2, SF overall mean = 10.8, $F1,4 = 4.69$, $p = .096$).

3.2 | Bird abundance and species richness

At all sites combined, we recorded 5992 total detections of 204 species (Table S2). Detections/site/day were 22% lower in SF (Figure 2a; PF overall mean = 102.2, SF overall mean = 79.7, $F_{1,3.85} = 11.83$, $p = .028$). Combined, PF sites hosted 187 total species (139–149 species/site), compared to 149 species, 20% fewer, in SF (106–109 species/site; Figure 2b). Chao2 estimated species richness was 160–180 species/site in PF, but just 120–140 species/site in SF, with only a single SF site (S1) overlapping the estimated range of PF sites. S3 was the most depauperate, falling 45 species below the lowest estimate for a PF site. For cavity nesters, we made 1524 detections of 62 species. Detections/day were reduced by

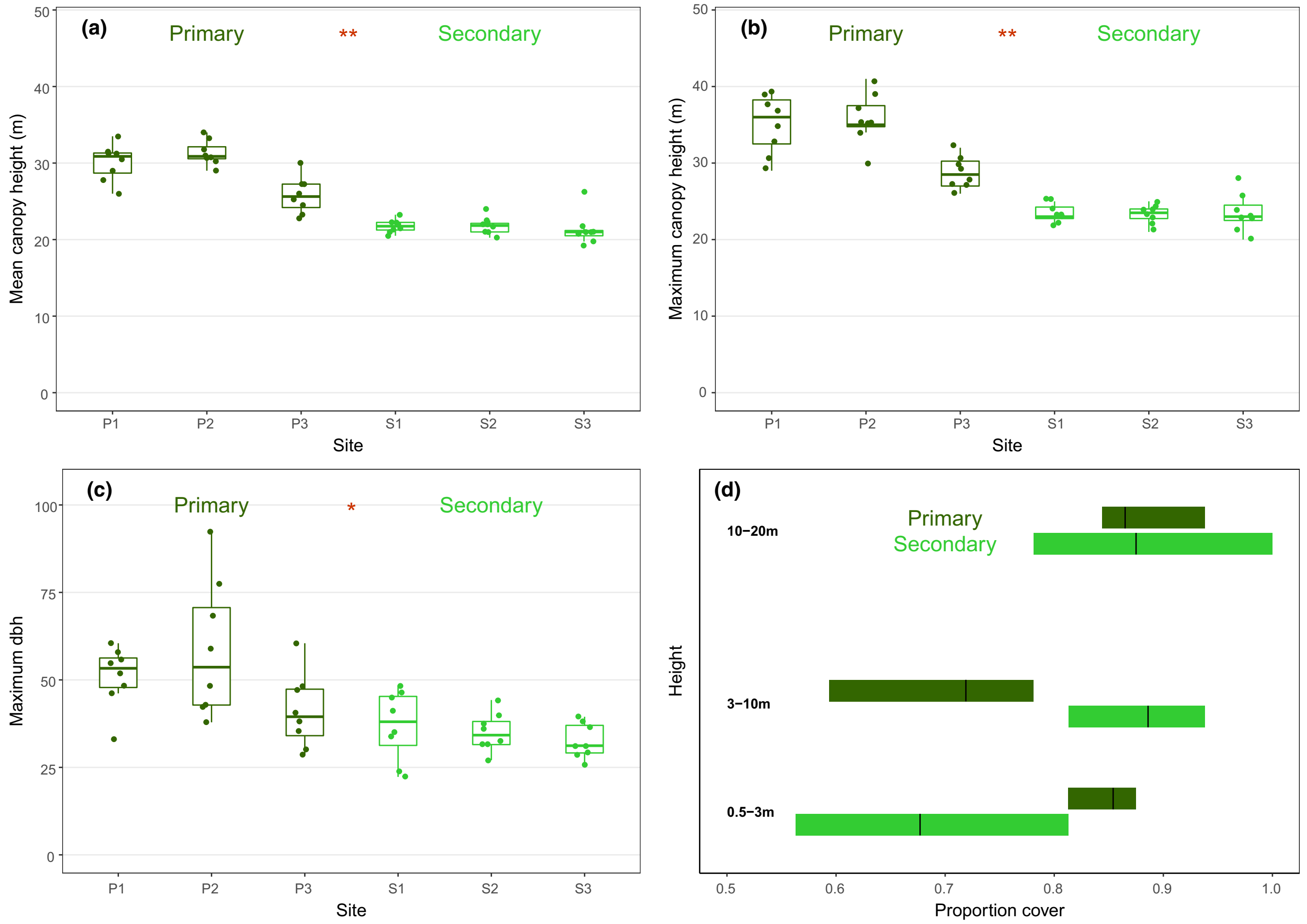


FIGURE 1 Vegetation characteristics in PF and SF sites. For a, b, and c, whiskers represent 5 and 95% percentiles, boxes 25% and 75% percentiles, and the horizontal line is the median. (a) Mean canopy height. (b) Maximum canopy height. (c) Maximum DBH. (d) Vegetation structure profiles. For (d), each bar represents the range of proportions for the three sites/forest type, with the vertical bar representing the mean. Significant treatment effects of forest type by ANOVA (see text) in a, b, and c are indicated by * ($p < .05$) or ** ($p < .01$).

27% in SF (Figure 2a; PF overall mean = 27.0, SF overall mean = 19.6, $F_{1,4} = 10.28$, $p = .033$). Even so, as a proportion of the entire community, there was only a small difference between SF and PF; cavity nesters represented 25%–27% of detections at PF sites compared to 22%–26% at SF sites. Species richness of cavity nesters showed a comparable difference between PF and SF, with 44 species in SF, 28% fewer than in PF (61). For individual sites, PF had 42–50 species/site compared to 28–35 species in SF (Figure 2b). Chao2 estimated species richness was 49–60 species/site in PF compared to 31–42 in SF. In contrast to species richness for all species, S1 and S3 showed similar results for cavity nesters (Figure 2b). S2 fell much lower, predicted to hold only 31 cavity-nesting species, barely half the estimate for P2.

3.3 | Species absent from SF

Overall, SF included 132 (71%) of the 187 species detected in PF (Table S2). The 55 species not detected in SF included species that were commonly detected at all PF sites (e.g., *Schiffornis olivacea*, *Myiopagis gaimardii*, *Tunchiornis ochraceiceps*, *Lamprospiza melanoleuca*), species that were readily detected but patchy at the scale of our sites (e.g., *Piculus chrysochloros*, *Formicarius analis*, *Hylopezus macularius*, *Corythopis torquatus*), and 18 species that were detected just one or two times in PF. Seven species that we did not record within our SF sites were recorded in SF adjacent to a sampling site. Considering only cavity-nesting species, SF included an almost identical proportion of PF species as in the comparison of all species: 44 of 61 PF species (72%).

3.4 | Species detected only in SF

We recorded 17 species in SF only (Table S2). Of these, 13 were recorded at just one site, including nine species with 1–2 records. Just two species, *Lophotriccus galeatus* and *Pheugopedius coraya*, were present in all three SF sites, with another two species, *Crypturellus soui* and *Cyclarhis gujanensis*, present at two sites. Three species detected only in SF were also detected in PF, but outside of our sampling sites.

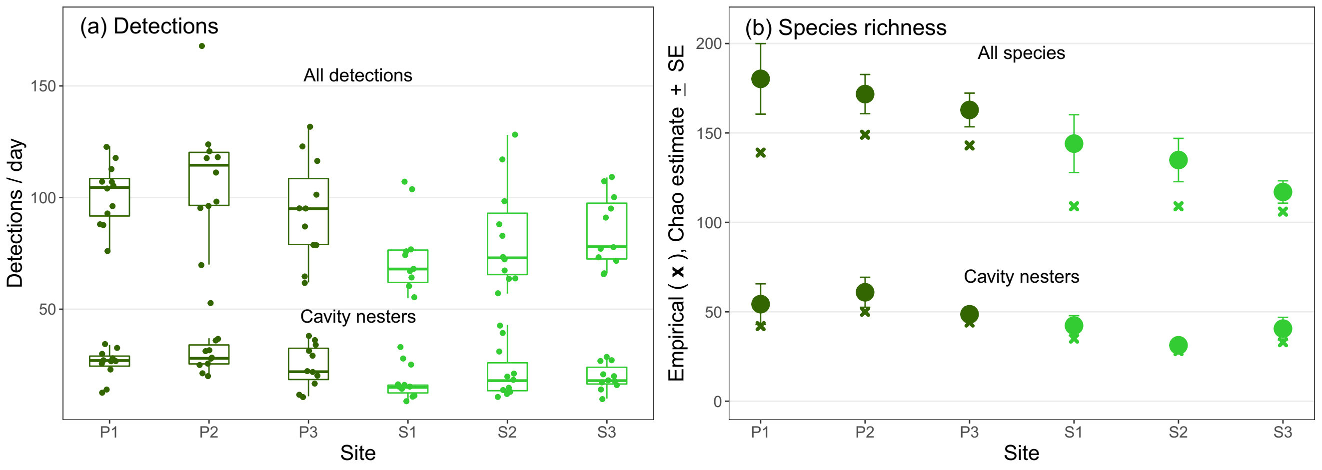
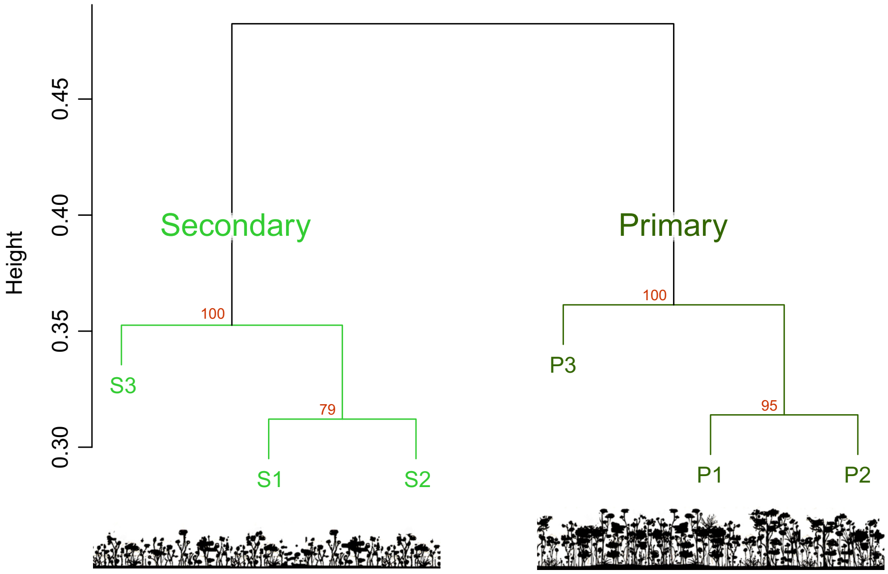


FIGURE 2 PF sites had more detections and more species than SF sites. (a) Number of detections/sampling day for all species combined and for cavity nesters. Box and whisker plots as in Figure 1. The effect of forest type was significant (ANOVA $p < 0.05$, see text) for all species as well as for cavity nesters. (b) Empirical (x) and Chao2 estimated species richness for all species combined and separately for cavity nesters.

FIGURE 3 Hierarchical cluster analysis of PF and SF bird communities among sites. AU values (red) ≥95% indicate strong support for the ensuing grouping.



3.5 | Community organization

Hierarchical cluster analysis strongly supported a division between PF and SF communities (Figure 3). Other than one pair of SF sites (S1 and S2), all other sites were significantly distinct from each other (AU values >95), with P3 and S3 the most distinct sites in PF and SF, respectively. Cluster grouping did not reflect geographic proximity for PF sites, but did for SF.

We plotted PF and SF pseudoabundance and stratum associations on a log scale to visualize the low pseudoabundance values of many species (Figure 4). This required adding 1 to each pseudoabundance value. The representation shows pseudoabundance in PF as the distance along the x-axis, pseudoabundance in SF as the distance along the y-axis, and difference between PF and SF as distance from the solid diagonal line. Most species were more common in PF than in SF, as indicated by more points below the solid diagonal line. Even so, many species were present in PF and SF in roughly comparable abundance (points near the solid diagonal line). This is particularly obvious for a cluster of species common in both PF and SF at the upper end of the solid diagonal line. Paired *t*-tests revealed significantly higher pseudoabundance in PF for canopy species ($t_{96} = 4.17$, $p < .001$) and terrestrial species ($t_{16} = 2.40$, $p = .029$), marginally significant differences for midstory species ($t_{50} = 1.79$, $p = .079$), but no difference for understory species ($t_{23} = 1.55$, $p = .134$) and near-ground species ($t_{13} = 1.59$, $p = .135$). Other than the species absent from PF (PF pseudoabundance +1 = 1), only one species, *Nonnula rubecula*, had pseudoabundance >5x higher in SF (point above the upper dashed diagonal line), compared to many species with >5x higher pseudoabundance in PF (points below the lower dashed diagonal line).

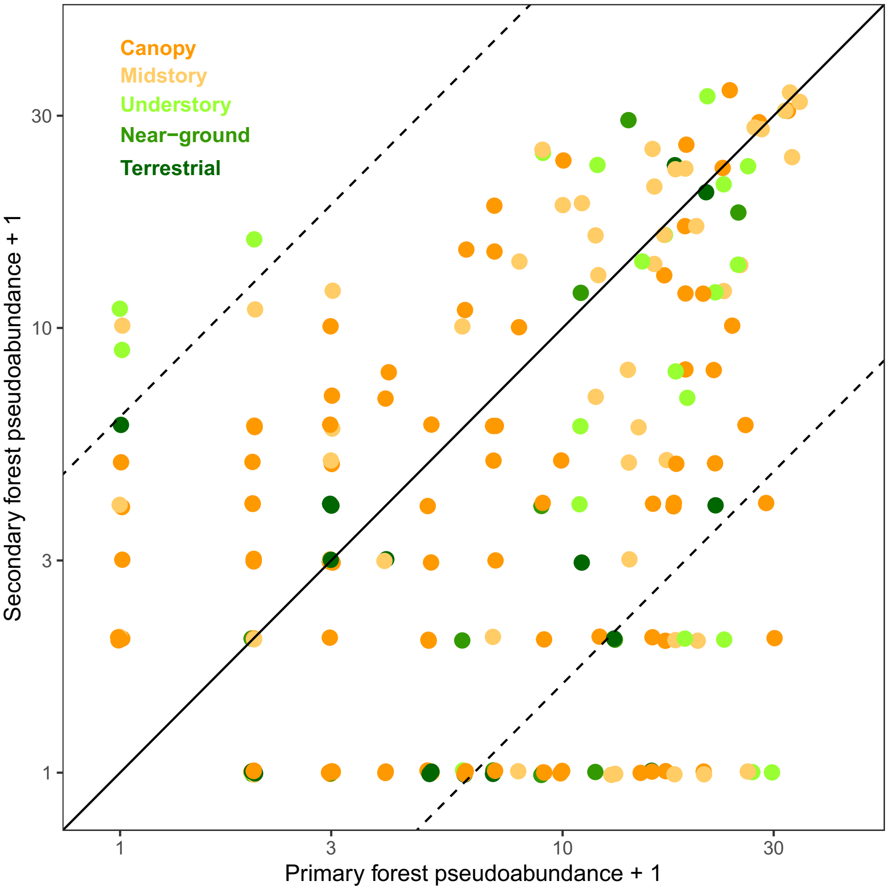


FIGURE 4 Abundance of each species in PF and SF, based on summed pseudoabundance across 11 samples of three sites for each forest type (range 0–33 in each forest type). The solid diagonal line (1:1) designates equal pseudoabundance in both forest types; the dashed lines represent ~5× higher pseudoabundance in SF (upper line) or PF (lower line).

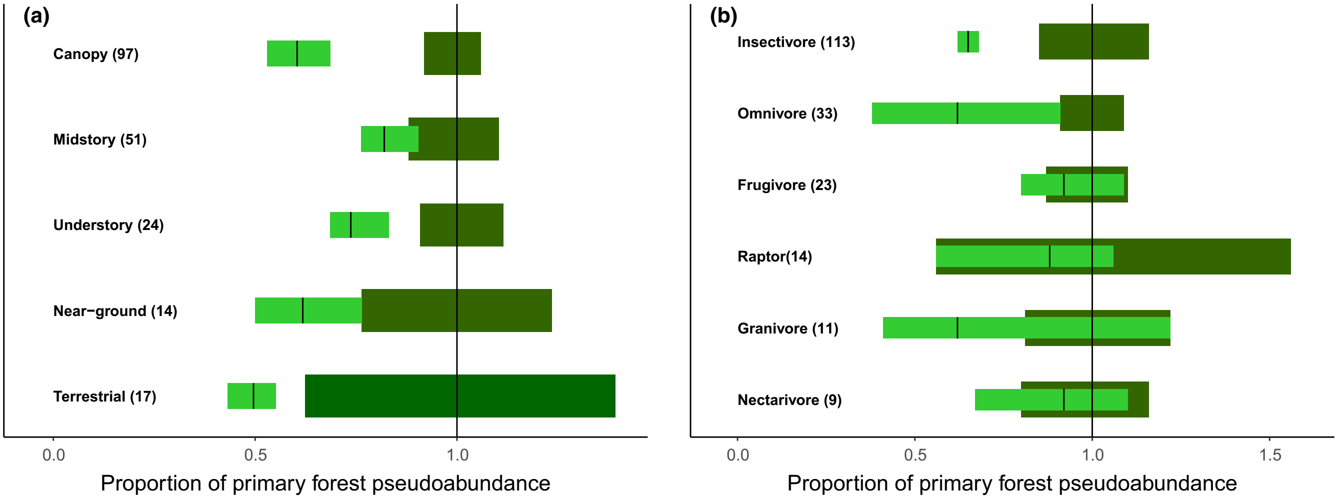


FIGURE 5 Pseudoabundance summed for all species in each stratum (a) or foraging guild (b), scaled as the proportion of mean pseudoabundance in PF sites (vertical line at 1.0). Solid bars indicate the range of values for the three PF sites (dark green) and the three SF sites (light green, with a vertical bar for the SF mean). Numbers in parentheses indicate the number of species in each stratum or foraging guild. *Lurocalis semitorquatus*, which forages above the canopy, is excluded from this comparison.

We also examined differences among strata by first summing the pseudoabundance values for all species within a given stratum to obtain a stratum-level value at each site. We represented the range and mean for the three PF sites, scaled to 1 (Figure 5a). Finally, we showed the range and mean of the SF sites as a proportion of the PF mean. Canopy and terrestrial species reached only about 50% of PF abundance at most SF sites, although midstory (82% of the PF mean) and understory (74% of the PF mean) species were closer to their PF counterparts; midstory species in SF even overlapped the range of PF. These results suggest that although some species had comparable abundance in PF and SF, or even greater abundance in SF (points above the solid line in Figure 4), many more species were

TABLE 1 Functional diversity metrics (functional richness [FRic], functional evenness [FEve], and functional divergence [FDiv]) and community-weighted means of principle component scores at each site. Grayscale ramps represent the range of values for each column, indicating that only PC3 showed a consistent difference between PF and SF.

Site	Species	FRic	FEve	FDiv	PC1	PC2	PC3
P1	138	0.741	0.732	0.896	−0.370	0.096	−0.155
P2	148	0.951	0.705	0.878	−0.295	0.190	−0.084
P3	142	0.866	0.744	0.894	−0.276	0.127	−0.122
S1	108	0.783	0.695	0.868	−0.406	0.251	−0.222
S2	109	0.759	0.698	0.906	−0.193	0.108	−0.244
S3	106	0.689	0.719	0.917	−0.177	0.150	−0.287

poorly represented in SF, particularly canopy, near-ground, and terrestrial birds. Midstory and understory pseudoabundance in SF was closer to PF levels.

In contrast to results by stratum, some trophic guilds were well represented in SF, with at least one SF site falling within the range of PF for all guilds but insectivores (Figure 5b). Paired *t*-tests showed significant differences only for insectivores ($t_{112}=5.04$, $p<.001$) and omnivores ($t_{32}=2.18$, $p=.036$, all other guilds $t<0.700$, $p>.5$). Frugivores, raptors, and nectarivores showed little difference in abundance between PF and SF, while insectivores were consistently about 2/3 as abundant in SF. Some SF sites were particularly depauperate in omnivores and granivores.

In general, PF and SF communities did not show consistent differences in functional diversity metrics (Table 1, see also Supporting Information). Sites in PF had the highest FRic and FEve, but for both metrics, an SF site had higher values than one of the three PF sites. Two SF sites showed the highest FDiv, but the third SF site had the lowest value of all six sites. Similarly, for morphology, community-weighted means of PC1 and PC2 did not differ consistently between PF and SF. The only exception was PC3, for which the PF mean was about twice as high in all three PF sites. A higher score on this axis reflects short-billed, long-winged birds with high hand-wing index. This pattern might be best explained by the higher abundance of toucans in SF, as toucans had the lowest scores for PC3. Several species with higher-than-average scores for PC3 were absent from SF, also lowering means in SF (e.g., *Pachyramphus* spp., *Sirystes subcanescens*, *Lamprospiza melanoleuca*; Tables S2, S4).

4 | DISCUSSION

Our results provide a calibration for bird community recovery in Amazonian second growth forest under maximally favorable conditions. Because of the juxtaposition of our SF sites immediately adjacent to vast PF (Figure S1), our system is not limited by colonization across an inhospitable landscape for either birds or the plants that provide resources and structure (Mayhew et al., 2019). Similarly, our SF sites are minimally confounded by landscape heterogeneity, such as age and configuration of PF patches (Arroyo-Rodriguez et al., 2023). Finally, our analysis is standardized by patch size, as all sample sites are embedded within a large area of the same habitat (Fahrig, 2013). Under these conditions, the SF bird communities we sampled reflect habitat suitability in SF combined with export of colonists from PF. After 31–36 years, SF supported a bird community composed almost entirely of PF species, but with 22% fewer detections and 20% fewer recorded species than PF (Figure 2). Compared to the overall community, cavity nesters were slightly less abundant in SF. Midstory and understory species approached PF abundance in SF, as did frugivores, nectarivores, and raptors (Figure 5). Conversely, canopy species, terrestrial species, and insectivores were less abundant in SF.

As documented previously at the BDFFP, bird communities in SF include few habitat generalists or SF specialists, but instead accumulate PF species as forest develops (Rutt et al., 2021; Rutt, Jirinec, et al., 2019; Stouffer, 2020). Our SF sites included just three species that were common in SF but absent from PF (Table S2). These three species — *Crypturellus soui*, *Lophotriccus galeatus*, and *Pheugopedius coraya* — could be characterized as SF specialists. We also recorded a few species that are more common earlier in succession, which we predict will soon be absent from SF as it continues to develop (*Cercomacroides tyrannina*, *Empidonomus varius*, *Cyclarhis gujanensis*). Some of the species we detected only in SF occur regularly in PF and SF at the BDFFP (e.g., *Campylopterus largipennis*, *Hylocharis sapphirina*). Significantly, four species that we recorded only in SF are uncommon species that we had previously considered to be restricted to PF at the BDFFP (*Harpagus bidentatus*, *Leucopternis melanops*, *Celeus elegans*, *Cotinga cayana*; Rutt et al., 2017). These results correspond to other studies showing that SF provides habitat for PF birds, and that the value of this habitat will increase with time (Bradfer-Lawrence et al., 2018; Latta et al., 2017; Loiselle & Blake, 1994).

In 2013, five years before our bird surveys, extensive surveys of cavity availability at the BDFFP revealed about half as many suitable nest cavities in SF as in PF (Dantas Oliveira et al., 2024). Similarly, in 2011, Figueira et al. (2015) found reduced abundance of cavity-nesting parrots perching in SF. We anticipated that cavity limitation would reduce the abundance and species richness of cavity-nesting species in SF (Cockle et al., 2010, Katayama et al., 2017, reviewed in Newton, 1998). Our results indicate that cavity-nesting species are reduced by about 20%–30% in SF, both in number of detections and number of species, but these differences translate to only slight underrepresentation in the overall SF community (Figure 2). The general trend masks considerable variation among sites; the Chao2 estimate for S2 was only 31 of the 62 species we detected at all sites combined, perhaps due to a paucity of woodpeckers, the primary excavators responsible for cavities (Table S2). Interestingly, S1 did not lag in detections of cavity nesters, largely because it was regularly used by the parakeet *Brotogeris chrysoptera*. Based on cavity measurements, Dantas Oliveira et al. (2024) predicted few cavities in SF would be large enough for birds >200 g. Our SF observations of parrots and other large-bodied, frugivorous cavity nesters, such as toucans, suggest that even if cavities are not available, birds may be taking advantage of resources within SF. Alternatively, based on some of the cavity nesters we detected, relatively large cavities may be becoming available. For example, we repeatedly detected presumably territorial *Micrastur* forest-falcons calling in SF sites. Even so, the large, tall trees necessary for the largest cavity nesters, such as *Ara* and *Amazona* parrots, are likely unavailable in SF at the BDFFP (e.g., De La Parra-Martínez et al., 2015; De Labra-Hernández & Renton, 2016).

The dearth of canopy birds in SF likely relates to incomplete development of structural complexity, as expected from the trajectory of tree species composition and woody biomass accumulation in SF (Elsy et al., 2023; Martin et al., 2013; Rozendaal et al., 2019). SF reached an average height of 21 m, with few trees >25 m, compared to an average of 29 m in PF, with a heterogeneous canopy formed by many trees stretching above 35 m (Figure 1). Thus PF provided ~10 m more vertical space within the canopy, including many more epiphytes (Martin et al., 2013). This space likely includes microhabitats for common canopy species absent from SF, such as *Myiopagis gaimardii*, *Zimmerius acer*, *Vireolanius leucotis*, and *Lamprospiza melanoleuca*. Among common canopy insectivores, only *Pachysylvia muscicapina* reached comparable abundance in both forest types.

In contrast to canopy birds, midstory and understory species were better represented in SF. For example, understory flocks led by *Thamnomanes caesius* have reassembled in SF, although they lack several core species and show reduced network complexity (Rutt et al., 2020; Rutt & Stouffer, 2021), as revealed by the absence of *Philydor erythrocercum* and *Tunchiornis ochraceiceps* in our SF sites. Our vegetation results suggest that understory habitat remains structurally distinct from PF below 10 m, but is similar from 10–20 m (Figure 1d). Many understory flock species regularly forage above 10 m (Coddington et al., 2023), so increasing similarity between PF and SF in that stratum may provide appropriate structure for these species and other midstory to subcanopy species. Other studies have reported weaker recovery of understory species compared to canopy species (Barlow et al., 2007; Bradfer-Lawrence et al., 2018), but these studies examined forests that were more isolated from sources of colonists. Canopy species are better colonizers than understory species (Burney & Brumfield, 2009), so studies showing better representation of canopy species in SF likely reflect quicker colonization by these species, not quicker recovery of canopy habitat. This colonization advantage likely becomes increasingly apparent as patches of PF and SF become more separated.

Terrestrial and near-ground species showed mixed recovery. Some terrestrial insectivores were absent or nearly absent from SF sites (e.g., *Myrmornis torquata*, *Formicarius analis*, *Sclerurus rufigularis*, *Corythopis torquatus*, *Cyphorhinus arada*), highlighting their vulnerability at the BDFFP and elsewhere in the tropics (Canaday & Rivadeneyra, 2001; Kupsch et al., 2019; Lees & Peres, 2008; Powell et al., 2013; Powell, Cordeiro, & Stratford, 2015; Rutt, Midway, et al., 2019; Stouffer et al., 2021). In contrast, tinamous, trumpeters, and curassows were well represented in SF, a situation that would be unlikely if the BDFFP faced the hunting pressure typical of disturbed Amazonian landscapes (Peres, 2001).

As expected, given the large difference in species richness, community structure differed consistently between the two forest types (Figure 3). Even so, functional diversity measurements generally overlapped between PF and SF sites (Table 1). This suggests that the roles of birds in the community are broadly similar based on their morphology, stratum, foraging, and sociality. In an analysis of mist-netted birds, Luther et al. (2022) found functional differences in understory bird communities between PF and disturbed forest (defined as including 1- and 10-ha PF fragments in addition to SF). We suspect several factors contribute to these seemingly disparate results. First, functional indices in the larger sample used by Luther et al. (2022) broadly overlapped between forest types, as did our results. Second, our analysis includes the entire community rather than just a subset of understory species that can be reliably sampled with nets. Perhaps the reduced abundance of some understory species in SF is partially compensated by functionally similar midstory species. These species, which are poorly represented in net samples, show relatively high similarity between PF and SF (Figure 5a). Third, the best colonists in Amazonia are medium to large species (Lees & Peres, 2009), especially frugivores and granivores. These species are absent from net samples but well represented in our spot-map surveys, where they may homogenize PF and SF functional diversity.

Some common and conspicuous PF birds were absent from SF. In addition to the canopy species, terrestrial insectivores, and core flock species discussed above, examples include the woodcreepers *Sittasomus griseicapillus* and *Deconychura longicauda*, and the understory frugivore *Schiffornis olivacea*. Why were so many species absent? Typical explanations include general lack of vagility that reduces dispersal (Moore et al., 2008), reluctance to move through open habitat or matrix (Ewers & Didham, 2006; Ibarra-Macias et al., 2011), or unsuitability of SF for any other species-specific reason. In our system, low vagility and poor gap crossing seem unlikely limitations, as SF sites were connected to PF through ~1 km of comparable SF without large gaps or other obvious barriers (Figure S1). Assuming birds could move into SF, properties of SF that could limit PF birds might include microclimatic conditions or habitat structure related to foraging, nesting, or predation, most of which are poorly understood, as are birds' ability to perceive and evaluate these factors (e.g., Patten & Kelly, 2010). For terrestrial insectivores, which show narrow light and thermal niches associated with specific microhabitats, physical structure creating those microhabitats may be important limitations (Jirinec, Elizondo, et al., 2022; Jirinec, Rodrigues, et al., 2022; Patten & Smith-Patten, 2012). Understanding drivers of abundance patterns and the ultimate suitability of SF will require additional information on not just foraging, but also territory establishment, persistence, and breeding success.

In addition to these standard explanations, we propose that density and demographic processes in PF are underappreciated contributors to SF use. Put simply, PF species do not occur in SF based on just vagility and habitat suitability, but also because colonists are available to leave PF (i.e., density dependent dispersal in a source–sink context; Amarasekare, 2004). For example, understory mixed-species flocks saturate available habitat in PF (Develey & Stouffer, 2001; Johnson et al., 2011), with the consequence that many young birds are forced to disperse into adjacent habitat (see also Luther et al., 2024). If that habitat includes SF, some flock species will use it. In contrast, the many species that are patchy in PF (Johnson et al., 2011) will not only produce fewer potential dispersers, but those dispersers may find vacancies within PF. From this perspective, species present in SF represent a process that occurs downstream from production of potential colonists that are unable to find open territories in PF. To the extent that the trajectory of climate change in Amazon rainforests will reduce survival (Wolfe et al. 2024), SF bird communities may be increasingly limited by lack of colonists, even from adjacent undisturbed PF. Results for *T. ochraceiceps*, *P. erythrocercum*, and *S. olivacea*, all absent in SF, may hint at this effect. Based on known foraging strategies, foraging opportunities seem an unlikely explanation for the absence of the core flock species *T. ochraceiceps* and *P. erythrocercum* given that insectivore flocks have reestablished foraging and breeding in SF (Rutt et al., 2021), or for *S. olivacea*, given the high abundance of frugivorous understory manakins in SF (Table S2). On the other hand, all three species show significant effects of warmer dry seasons on survival, which may in turn limit production of colonists to SF (Wolfe et al. 2024).

Tallying species in SF provides useful information, but assessing recovery requires a baseline for comparison (Martin et al., 2013). Typically, this comes from a nearby area of undisturbed forest (e.g., Prieto et al., 2022). While that might be the most appropriate baseline, it is important to remember that abundance and community structure in "undisturbed" forest may not reflect earlier conditions (Blake & Loiselle, 2024; Pollock et al., 2022; Sigel et al., 2006; Stouffer et al., 2021). For example, abundance of terrestrial insectivores has declined in undisturbed PF at the BDFFP, making these species less available to colonize SF and masking the difference between the modern disturbed landscape and its historical antecedent (Stouffer et al., 2021). Similarly, in addition to fewer terrestrial and near-ground insectivores, had our study been conducted closer to the city of Manaus, we would also have expected depauperate understory communities due to much reduced abundance of many understory species in PF there (Rutt et al., 2023). Thus, in heavily degraded areas, this downstream effect of a lack of colonists would extend to even more species (e.g., Moura et al., 2014). Temporally shifting baselines appear to be pervasive for both biological processes and how humans perceive them (Soga & Gaston, 2018). In the absence of long-term data from undisturbed forest, all we can do is recognize that SF recovery, although significant, may never return to prior baselines.

AUTHOR CONTRIBUTIONS

Conceptualization- PCS, CLR; Data curation- PCS; Formal analysis- PCS, CLR; Funding acquisition- PCS; Investigation- PCS, CLR; Methodology- PCS, CLR; Project administration- PCS; Supervision- PCS; Validation- PCS, CLR; Visualization- PCS, CLR; Writing- original draft- PCS; Writing- review and editing- PCS, CLR.

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DATA AVAILABILITY STATEMENT

Data available at dryad.kh18932ht

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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