






# Low species turnover of upland Amazonian birds in the absence of physical barriers

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## Abstract

**Aim:** One of the oldest and most powerful ways for ecologists to explain distinct biological communities is to invoke underlying environmental differences. But in hyper-diverse systems, which often display high species richness and low species abundance, these sorts of community comparisons are especially challenging. The classic view for Amazonian birds posits that riverine barriers and habitat specialization determine local and regional community composition. We test the tacit, complementary assumption that similar bird communities should therefore permeate uniform habitat between major rivers, regardless of distance.

**Location:** Upland (*terra firme*) rainforests of central Amazonia.

**Methods:** We conducted intensive whole-community surveys of birds in three pairs of 100-ha plots, separated by 40–60 km. We then used dissimilarity indices, cluster analysis, and ordination to characterize differences among the six avian communities.

**Results:** In all, we detected 244 forest-dependent birds, with an average of 190 species (78%) per plot. Species turnover was negligible, no unique indicator species were found among plot pairs, and all documented species were already known from a complete inventory at one of the three sites.

**Main Conclusions:** Our study corroborates the classic biogeographical pattern and suggests that turnover contributes little to regional avian diversity within upland forests. Using a grain size of 100 ha, this implies that upland birds perceive the environment as uniform, at least over distances of ~60 km. Therefore, to maximize both local species richness and population persistence, our findings support the conservation of very large tracts of upland rainforest. Our analyses also revealed that the avifauna at Reserva Ducke, encroached by urban sprawl from the city of Manaus, shows the hallmarks of a disturbed community, with fewer vulnerable insectivores. This defaunation signals that even an enormous preserve (10 × 10 km) in lowland Amazonia is not insulated from anthropogenic degradation within the surrounding landscape.

David A. Luther and Mario Cohn-Haft are considered joint senior authors.

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## KEYWORDS

Amazonia, beta diversity, bird communities, defaunation, distance decay, environmental gradient, similarity, species composition, *terra firme*

## 1 | INTRODUCTION

Using environmental differences to compare biological communities is perhaps the oldest, simplest and most powerful tool to recognize patterns of species distribution and identify the factors that cause them (Hort, 1916; Whittaker, 1960, 1972). In general, species diversity and composition differ among sites due to both differences in site habitability and the presence of dispersal obstacles (Nekola & White, 1999). In other words, species present at one site may not occur at another because something about that second site is unsuitable or because those species simply cannot get there. Identifying exactly which factors are at play is a major challenge in ecology and includes evaluation of abiotic characteristics, environmental integrity, interactions among species and the dispersal propensity of organisms. Recognizing distributional patterns and attributing underlying causes is useful because it allows us to predict not only the effects of future environmental change but also which species should occur in areas that have never been inventoried (Ferrier & Guisan, 2006; Guisan & Rahbek, 2011; Pinto-Ledezma & Cavender-Bares, 2021). Thus, biodiversity inventories are the building blocks of a great deal of ecological and conservation science.

Community comparisons are especially challenging in tropical forests. In these hyper-diverse systems, it is difficult to determine the contribution of local (alpha) species diversity versus species turnover across the landscape (beta diversity), let alone what may drive turnover across seemingly uniform tracts of forest. A natural correlate of high species richness is low species abundance, and the phenomenon of many rare species is well-documented across the tropics (Black et al., 1950; Karr, 1971). Where abundances are low, seemingly random subsets of species might co-occur at particular localities, raising the question of sampling scale (Hill & Hamer, 2004; Phillips et al., 2003; Terborgh et al., 1990). These basic questions, coupled with a still debilitating lack of taxonomic stability for tropical biota (Kim & Byrne, 2006), continue to impede tropical ecologists and obscure how such high species diversity is maintained. Perhaps more importantly, these questions make it difficult to understand what constitutes 'normal' or baseline communities, frustrating efforts to identify anthropogenic changes, be they local habitat modification and fragmentation or the results of ecosystem-scale contamination and global climate change (Bernhardt et al., 2017; Phillips, 1996; Stouffer et al., 2021).

The Amazon contains the world's richest and most extensive tropical forests (Zapata-Ríos et al., 2021), where biological inventories routinely lead to discoveries of new species, major taxonomic revisions and the steady accumulation of natural history information (<https://mol.org/patterns/discovery>). However, balancing the need to compare sites with this dynamic influx of data is a daunting problem, tackled in some cases with massive collaborative

databases (e.g., the Amazon Tree Diversity Network; <https://atdn.myspecies.info/>). In the absence of clear factors that lead to species turnover, distance is often taken as a surrogate for the multitude of unknown or unmeasured characteristics likely to vary and affect species composition. The 'distance decay' model of species turnover (Nekola & White, 1999) often serves as a default or null hypothesis, even if that distance is strongly correlated with environmental variables (Harrison et al., 1992) and not reflective of distance *per se* (i.e., isolation by distance; Fluck et al., 2020). For birds, which are good dispersers and tend to show strong habitat specialization, it is conceivable that vegetation type and major dispersal barriers are the most important determinants of community species composition. As in other parts of the world, many Amazonian birds show strong habitat specificity (Alonso et al., 2013; Kratter, 1997; Remsen & Parker, 1983; Stotz et al., 1996; Terborgh, 1985). Yet the Amazon also covers an enormous geographic extent, and many upland species only occur in relatively small subregions, often replaced by closely related species on the opposite banks of major rivers (Cracraft, 1985; Haffer, 1978; Naka et al., 2012; Sick, 1967). Thus, the area between rivers (interfluves) also matters. If these two factors (habitat and interfluve) are the most important determinants of avian occurrence and distribution in the Amazon, then sampling within the same habitat and interfluve should yield similar bird communities, independent of distance.

Another important source of community variability is anthropogenic factors. These human-caused changes are typically recognized as habitat types and then either controlled or tested directly. Specific anthropogenic habitats like secondary forests or urban environments are of course treated as distinct from natural vegetation classes. However, in seemingly undisturbed forests, recent long-term studies of birds have detected the kinds of community change normally associated with anthropogenic disturbance and have largely attributed these changes to indirect human influences (Blake & Loiselle, 2015; Pollock et al., 2022; Stouffer et al., 2021). For example, at two Amazonian sites, terrestrial and near-ground insectivores displayed the most pronounced declines (Blake & Loiselle, 2015; Stouffer et al., 2021), whereas losses were much more widespread among Panamanian birds (Pollock et al., 2022). Thus, for temporal snapshots, incorporating anthropogenic effects at a landscape scale could help to explain local community differences. For Amazonian birds, then, a test of distance decay versus the classic 'habitat-interfluve' model (as we call it) should also include some measure of indirect human influence across the landscape.

As part of a larger, long-term study of Amazonian biota (Section 2), we sampled birds repeatedly over 5 years across six plots within the same interfluve, all containing the same basic habitat and embedded within a vast expanse of continuous upland rainforest. Nevertheless, despite controlling habitat and interfluve, sites differ

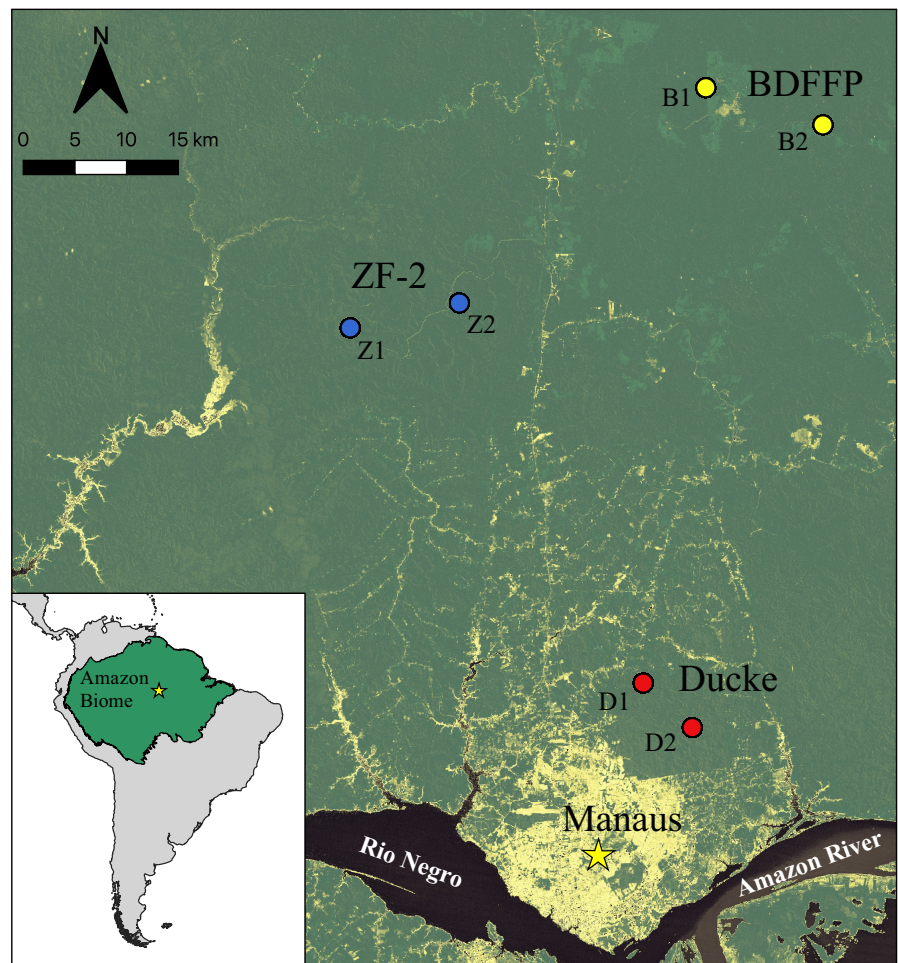
in their proximity to roads, scattered farms and the urban sprawl from a nearby city. We ask, then: (1) Do our study samples accurately represent the known fauna? (2) If so, do these bird communities differ in species richness and composition? And, finally, (3) Do distance or anthropogenic effects better explain these differences? Our expectation is that sites should differ very little if at all with distance, because habitat and interfluvium were held constant. However, we anticipate that the proportion of forest cover in the broader landscape might subtly influence local bird communities, even within large expanses of unbroken forest.

## 2 | METHODS

Intensive whole-community surveys were conducted in six plots of continuous primary forest north of Manaus, Brazil (3°06'S, 60°01'W), as part of the Tropical Ecology Assessment and Monitoring (TEAM) network (Rovero & Ahumada, 2017). This region of the Amazon is characterized by a consistently warm, moist climate, with a modest dry season from June to November (Candido et al., *in prep*). Throughout the year, average monthly temperatures only vary by 1–2°C and average annual precipitation ranges from 1800 to 3500mm (Candido et al., *in prep*; Laurance, 2001). Local topography undulates relatively little (40–50m on average) between

plateaus and stream valleys (Gascon & Bierregaard, 2001). And despite nutrient-poor soils in this region, the dense upland (*terra firme*) forests attain canopy heights of 25–30m, with emergent trees ascending considerably higher (CLR pers. obs., Almeida et al., 2019; Chauvel et al., 1987). Further, this region just north of Manaus contains what is arguably the best-documented avifauna anywhere in the Amazon (Cintra, 2011; Cohn-Haft et al., 1997; Naka, 2004; Rutt et al., 2017; Stotz & Bierregaard, 1989; Willis, 1977).

We surveyed pairs of 100-ha plots (1×1 km) at three distinct sites ( $n = 6$  plots), distributed over an area ~60km in diameter, amounting to a total of 600ha of Amazonian rainforest (Figure 1, Table 1). Sample plots of 100ha (1 km<sup>2</sup>) are regularly used to inventory birds in the Amazon, because they tend to contain the full composition of local species, including most rare or low-density ones (Robinson et al., 2021). The most conspicuous difference among our three sites is their distance from Manaus, the largest city in the Amazon (Figure 1). All sites are managed by the Instituto Nacional de Pesquisas da Amazônia (INPA): Reserva Ducke (hereafter Ducke), the Reserva do Cuieiras (hereafter ZF-2), and the Biological Dynamics of Forest Fragments Project (BDFFP). An advantage of our experimental design is that it allows us to distinguish between sister plots (two nearby plots at the same site, separated by 6–12 km) and distant plots (all other plot combinations). Each 100-ha plot contained an evenly spaced grid of 36 points (six parallel 1-km lines of six points



**FIGURE 1** Location of the three pairs of 100-ha plots, north of Manaus, Brazil, in the central Amazon. The textured, dark green background represents upland primary rainforest, light green polygons refer to regenerating second-growth, and tan indicates human disturbance and natural bare ground. Sister plots are colour-coded by site, with the same colour scheme used throughout all figures.

TABLE 1 Effort and avian species richness at each of the 100-ha plots sampled in this study.

Site	Plot	Location	Points	Surveys	Observed species	Estimated species <sup>a</sup>	% of core avifauna <sup>b</sup>
Ducke	D1	2.93°S, 59.95°W	36	14	183	196 (7.2)	68
	D2	2.96°S, 59.91°W	36	13	189	222 (15.6)	69
ZF-2	Z1	2.61°S, 60.21°W	36	14	192	215 (11.1)	70
	Z2	2.59°S, 60.11°W	36	14	185	220 (17.8)	68
BDFFP	B1	2.40°S, 59.90°W	36	14	194	219 (13.1)	72
	B2	2.44°S, 59.79°W	36	14	198	233 (17.8)	72

Note: Paired plots were located at three distinct sites in the central Amazon of Brazil: Reserva Ducke, along the ZF-2 road, and the Biological Dynamics of Forest Fragments Project (BDFFP).

<sup>a</sup>Chao2 species richness estimator (with standard error).

<sup>b</sup>The core avifauna is catalogued in Rutt et al. (2019) and lists the 268 species regularly found in upland primary rainforest.

each, separated by 200m; Appendix S2: Figure S1). To complete a single avian survey, 10-min point counts (visual and auditory) were executed at all 36 points within a plot. Only birds detected within 50m of the census point were included in this analysis. All bird surveys were conducted by a team of experienced tropical ornithologists (CBA, TVVC and CFV), after local training by MCH. A single observer censused 12 points per morning (05:00–10:00), and each plot was fully surveyed in a period that ranged from one day (three observers working simultaneously in parallel pairs of lines) to three consecutive days (one person for the entire plot). Each plot was sampled 1–4 times annually over 5 years: 2005 (2 surveys), 2006 (4), 2007 (4), 2008 (2–3), and 2009 (1). We considered a single plot survey to be the sample unit, as points were sampled at characteristic times (forward or reversed order) and vocal output is not directly comparable between different temporal windows. With the exception of plot D2 (13 surveys), each plot was sampled 14 times altogether. Point counts were conducted February–December, but were concentrated in the dry season (74%).

To determine species composition at the plot level, we first began by focusing on the forest-dependent community. We therefore eliminated all species whose preferred habitat is not upland primary forest (as classified in Appendix I of Rutt et al., 2017, as well as *Crotophaga major*). This removed detections of species associated with open water or aquatic habitats (i.e., *Tachybaptus dominicus*), white-sand forest (e.g., *Thamnophilus punctatus*, *Neopelma chrysocephalum*, *Hemitriccus inornatus*) and anthropogenic disturbances (e.g., *Ortalis motmot*, *Cercomacroides tyrannina*, *Myiozetetes cayanensis*), as not all plots had habitat heterogeneity to support these birds. Because our sampling stratification allowed equal opportunity to detect all remaining forest birds, we retained flyovers, nocturnal species (detected near dawn), intra-Amazonian migrants and the trivial addition of long-distance migrants (i.e., eight total detections of *Elanoides forficatus*, *Coccyzus euleri*, *Contopus virens* and *Tersina viridis*). For each plot, we calculated observed and estimated species richness (the Chao2 estimator) using the 'vegan' package (Oksanen et al., 2020) and R Statistical Software (R Core Team, 2020), which predicts expected richness by estimating undetected species. We then created detection/non-detection (1/0) matrices for species

in each plot as well as for each plot survey. For each species, we treated the number of surveys in which it was detected in a given plot (summed presence-absence data, ranging from 0 to a maximum of 13–14) as a conservative index of its abundance in that plot (Appendix S1). Species-specific differences in detectability will lead to unwanted variation in 'abundance' scores (e.g., overestimating the prevalence of vocal species), therefore our objective was not to compare interspecific differences, only within-species differences across sites. We computed beta diversity using pairwise Jaccard (presence-absence) and Bray-Curtis (pseudo-abundance) dissimilarity indices for all plot-plot combinations (3 combinations of sister plots + 12 combinations of distant plots = 15 in total) using the package 'betapart' (Baselga et al., 2021). For the Jaccard index (presence-absence), we further partitioned pairwise dissimilarity values into their two additive components: nestedness (species loss) and turnover (species replacement; Baselga, 2010). Because the turnover component accounted for 88% of Jaccard dissimilarity (Appendix S2: Table S1), on average, we hereafter refer exclusively to both metrics of beta diversity as species turnover. Finally, we employed Mantel tests in 'vegan' to determine whether pairwise species turnover correlated with geographic distance and linear regressions to identify the intercept of that relationship.

Next, we used cluster analysis and ordination to further explore differences among these six avian communities. To visually and statistically illustrate relationships among communities, we performed hierarchical cluster analysis using the 'pvclust' package (Suzuki et al., 2019). We clustered plots using Bray-Curtis dissimilarity (pseudo-abundance data) and the average linkage method, which produced a cluster dendrogram based on similar species composition. To evaluate the statistical support for each cluster, we calculated Approximately Unbiased (AU) probability values using multiscale bootstrap resampling ( $n = 10,000$  bootstraps; Suzuki & Shimodaira, 2006). If a cluster is strongly supported, the AU  $p$ -values will be  $\geq .95$  (significant at the .05 level). To gain insight about which species drive community differences, we used non-metric multidimensional scaling (NMDS) to visualize how plots separated in species space. We collapsed the pseudo-abundance data for all species down to just two axes using Bray-Curtis dissimilarity in the package



'vegan'. With only six plots, we have scant data to populate an NMDS ordination and the stress was nearly zero; however, repeat runs produced convergent solutions that were all qualitatively similar.

Because our analyses revealed the strongest differences between one site (Ducke) and the other two sites (Section 3), we investigated whether anthropogenic disturbance may be affecting avian communities. First, we extracted the species-specific scores from Axis 1 of the NMDS ordination, which largely separated sites. Second, for a subset of shared species ( $n = 75$ ), we compared those scores to abundance trends in nearby communities that are known to be disturbed (secondary forest and small forest fragments at the BDFFP). Abundance trends were derived from Figure 2b of Stouffer et al. (2021; change from historical primary forest to the modern disturbed landscape). We then ran a simple linear regression to determine whether vulnerable species—those with reduced abundance in disturbed forest—were absent or less common at Ducke. To simplify, we also grouped species into 10 guilds (Appendix S1), which we generated by combining position/microhabitat from Cohn-Haft et al. (1997) and dietary preference in Johnson et al. (2011), inserting dietary information when needed. Using the pseudo-abundance data for each site, we aggregated detections by guild to determine which groups of birds might be over- or underrepresented at Ducke. Lastly, we performed a buffer analysis in GIS to classify the landscape at increasing distances (1–20 km) from the centroid of each plot. We first conducted a supervised landscape classification using the Image Classification Wizard tool in ArcGIS Pro (v2.8.3; ESRI) with a Normalized Difference Vegetation Index (NDVI) composite across the study area, derived from Landsat 5 Thematic Mapper imagery (2008), courtesy of the U.S. Geological Survey. A classification schema was created based on six classes: (1) barren, (2) developed, (3) water, (4) planted/cultivated, (5) secondary forest and (6) primary forest. We chose to split closed-canopy forests into primary and secondary forests to quantify both the amount of current disturbance and the percentage of remaining primary forest surrounding each plot. We then used Training Samples Manager in ArcGIS Pro to collect training samples based on the delineation of known areas for each classification. Approximately 15–30 segments were chosen in the Image Classification Wizard as training data for each class. These training samples were saved as a feature dataset to be used during supervised classification. In the training step, we used a support vector machine classification with a maximum of 500 samples per class. We then used the zonal statistics tool to summarize the percent cover of these classifications within each buffered area.

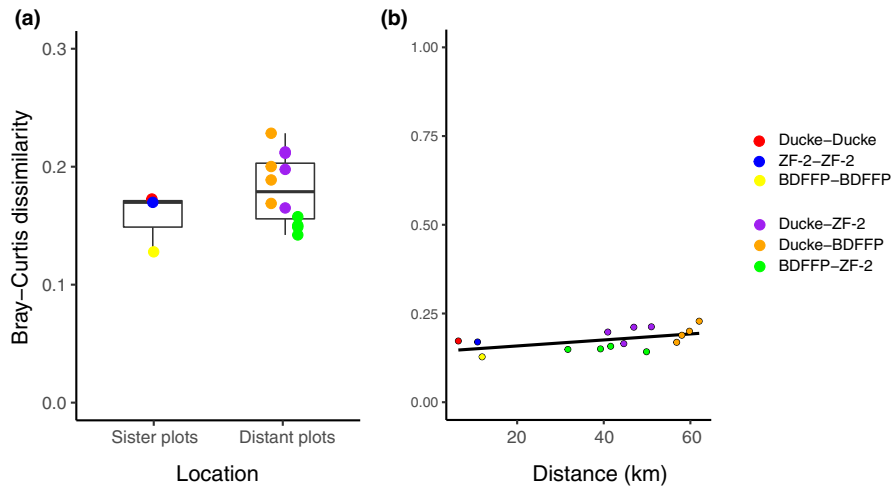
### 3 | RESULTS

Overall, this 5-year effort revealed a consistent, well-sampled avifauna across all six plots (Appendix S2: Figure S2). After removing non-forest birds, we detected a cumulative total of 244 species (Appendix S1), all of which are known to occur at the BDFFP (Cohn-Haft et al., 1997; Rutt et al., 2017). The number of observed species ranged from 183 to 198 per plot (Appendix S2: Figure S2),

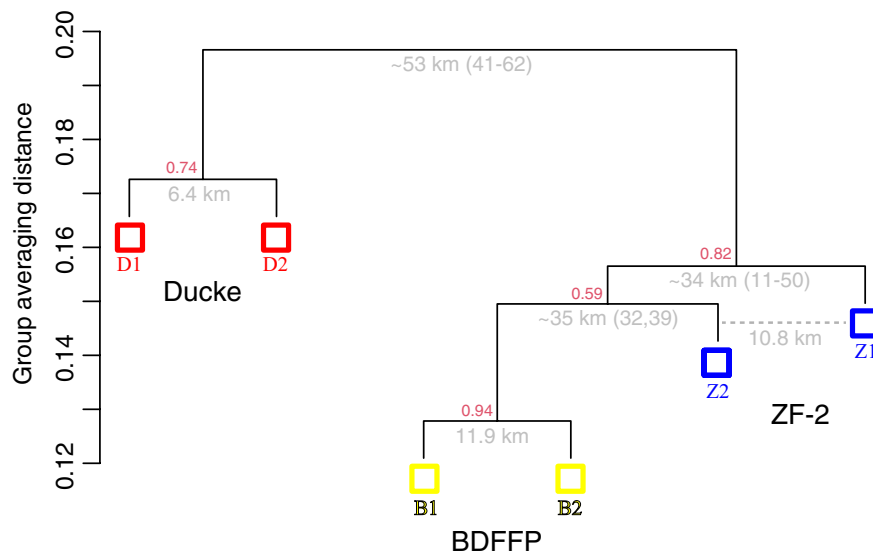
while estimated species richness expanded to 197–234 per plot (Table 1). Most species (139; 57%) were found on every plot, and only 23 were detected from just a single plot (1–2 species at the BDFFP, 4–5 at ZF-2, and 5–6 at Ducke), but these were mostly rare or difficult-to-detect species, such as diurnal raptors, nocturnal species and canopy birds (detected on 1–3 surveys;  $\bar{x} = 1.2$ ). For the remaining 221 species, only four were restricted to just a single site (pair of sister plots), totalling 2–3 survey detections apiece. The average cumulative pseudo-abundance was 33.2 survey detections (8110 total detections/244 species), which equals roughly 5.5 detections per species at each plot. The two BDFFP plots averaged the most species per survey (104 each), whereas D2 at Ducke had the fewest (90). Compared with the core forest avifauna (Rutt et al., 2019)—species regularly found in upland primary forest—we detected the vast majority of available species (88%; 236 of 268 species). However, at the plot level, observed species richness ranged from 68 to 72% of the core avifauna. This means that, even at the most well-sampled plots (BDFFP), 28% of the expected avifauna was missed, which drops to 22% when the two BDFFP plots are considered jointly.

Species turnover metrics were similar across all plot-plot comparisons (Figure 2, Appendix S2: Figures S3 and S4). Using the Jaccard index (presence-absence), all pairwise comparisons clustered around .23 ( $\bar{x}$ ), regardless of whether comparisons were between sister or distant plots (Appendix S2: Figure S3). Thus, the relationship between geographic distance and pairwise Jaccard dissimilarity was not significant (Mantel correlation coefficient [ $r$ ] = .32,  $p = .054$ ; linear regression intercept = .21). Using the pseudo-abundance data (Bray-Curtis index), pairwise differences diminished further ( $\bar{x} = .18$ ; Figure 2a). However, unlike the presence-absence data, there was a significant, moderate correlation between distance and dissimilarity ( $r = .52$ ,  $p = .026$ ; linear regression intercept = .14; Figure 2b). Following Qian and Ricklefs (2012), we interpret the two intercepts to represent (local) dissimilarity that is unrelated to distance, with the null expectation of complete similarity at 0 km (i.e., dissimilarity = 0; Buckley & Jetz, 2008). Together, these two dissimilarity metrics provide weak support for species turnover with distance (i.e., distance decay). Overall, the most similar sister plots were at the BDFFP, whereas the two Ducke plots were most dissimilar. Among distant plots, comparisons between the ZF-2 and the BDFFP were the most similar, suggesting that Ducke was driving the slight distance trend. Our cluster analysis revealed similar patterns among plots (Figure 3). Although none of the clusters were strongly supported (AU  $p$ -values  $\geq .95$ ), the two Ducke plots separated from all others. Sister plots also tended to cluster with each other; however, instead of clustering with its sister plot (11 km away), the more easterly plot along the ZF-2 (Z2) joined the two BDFFP plots (32–39 km distant).

The NMDS ordination confirmed the distinctness of Ducke, illustrating that shifts in bird abundance separated Ducke from all other plots (Figure 4). The ZF-2 and the BDFFP were differentiated from Ducke along the first axis, whereas the second axis mostly



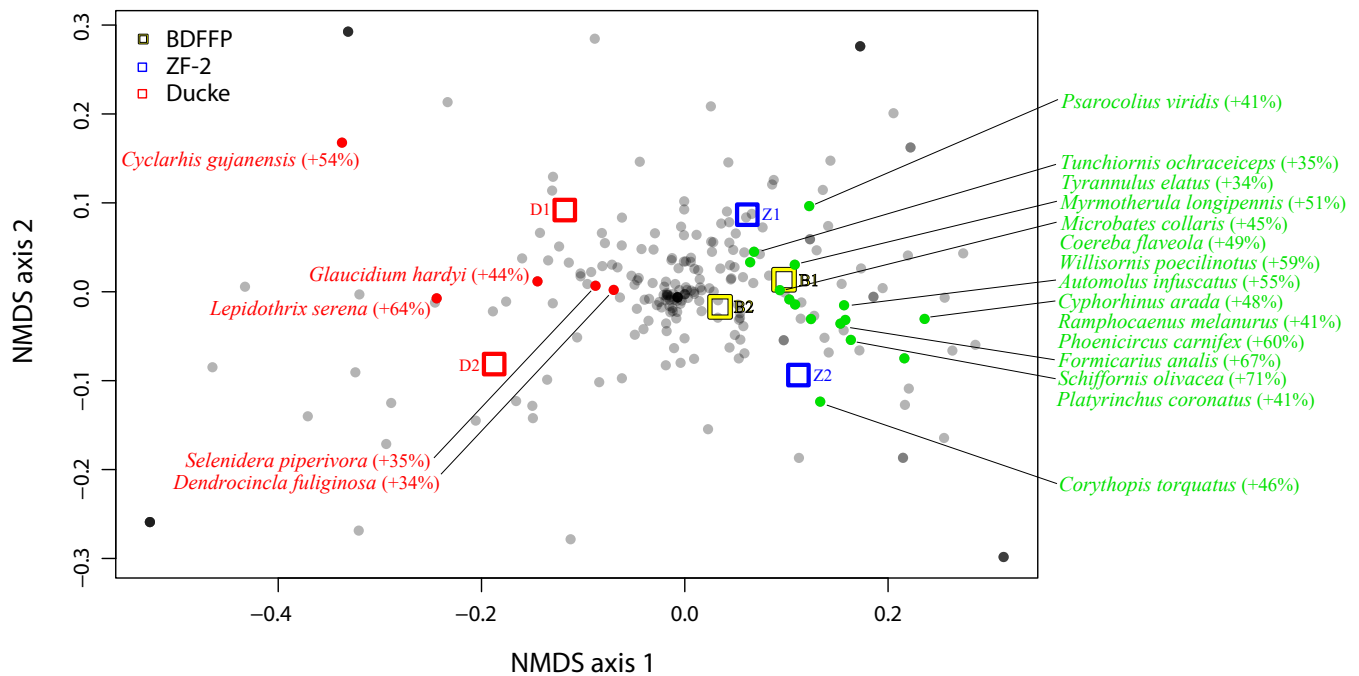
**FIGURE 2** Using the Bray-Curtis dissimilarity index, avian species turnover in the central Amazon increased moderately with geographic distance. Across all pairwise comparisons, sister plots (separated by 6–12 km) were on average more similar to each other than distant plots (separated by 32–62 km [a]), providing weak support for distance decay (b). Here, we treated the number of survey detections in a plot as an index of species abundance (i.e., pseudo-abundance within that plot). Note the relative distinctiveness of Ducke (orange and purple dots), in contrast to comparisons between the other two sites (green dots).



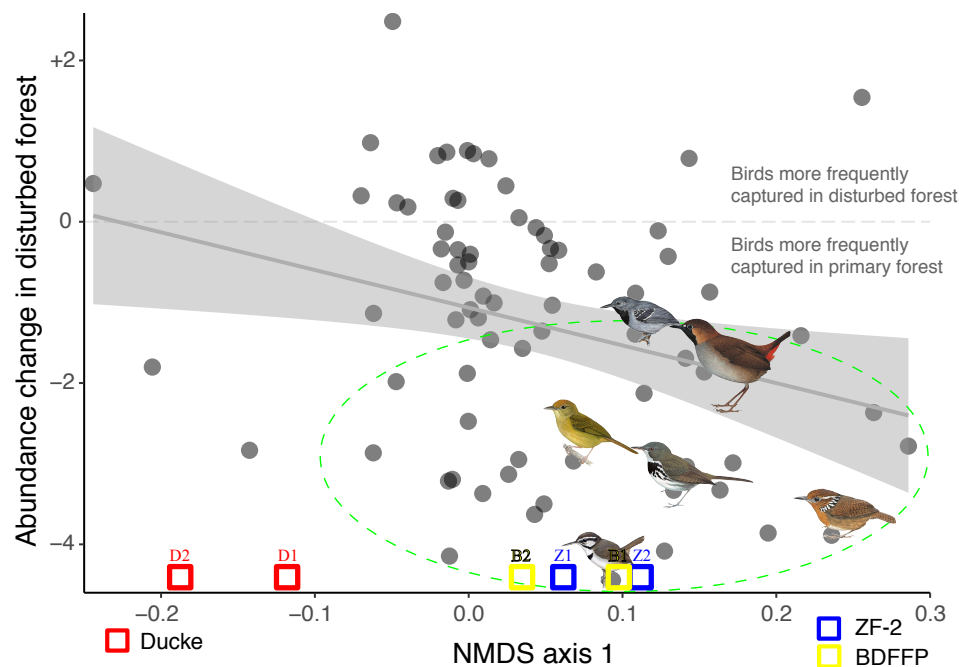
**FIGURE 3** A cluster dendrogram reveals that the largest difference in avian species composition is between Reserva Ducke and the other two Amazonian sites. We clustered plots using Bray-Curtis dissimilarity distance on the pseudo-abundance data. Although none of the clusters were strongly supported after multiscale bootstrap resampling (Approximately Unbiased  $p$ -values  $\geq .95$ ), values in red denote the relative support for each cluster. At each node, we also indicate the distance between plots or the range and average distance among three or more plots. With one exception (Z2), sister plots clustered with each other.

distinguished plots within sites. To determine the most influential species separating Ducke and the ZF-2/BDFFP, we highlighted those with the most divergent pseudo-abundance data (a difference in survey detections of  $>33\%$ ;  $n = 20$  species). This criterion focuses on species that were regularly detected at one or both ends of Axis 1, thus avoiding genuinely rare or difficult-to-detect species. For instance, *Cyclarhis gujanensis* was highlighted because it was detected on 56% of surveys at Ducke (15/27) but only 2% of surveys at the ZF-2 and BDFFP combined (1/56), for a difference of 54%. At the other extreme, *Cyphorhinus arada* was never detected during 27 surveys at Ducke (0%) but was found on nearly

half of all surveys from the ZF-2/BDFFP (27/56; 48%). Among the 20 most divergent species, these two were most strongly associated with either Ducke or the ZF-2/BDFFP. In total, five of these species were more often detected at Ducke, whereas 15 were more frequently found at the ZF-2/BDFFP (Figure 4). For  $\sim 31\%$  of species in the ordination ( $n = 75$  understory birds), we found a negative correlation between their Axis 1 scores and abundance trends in a nearby disturbed landscape (Figure 5;  $F = 6.5$ ,  $df = 1,73$ ,  $p = .01$ , Adjusted  $R^2 = .07$ ). The significant relationship indicates that species known to decline most strongly in disturbed habitat at the BDFFP (i.e., species vulnerable to landscape change)



**FIGURE 4** Shifts in bird abundance (pseudo-abundance) distinguished the two Reserva Ducke plots from all other upland Amazonian communities. To visualize plots in species space (transparent dots), we used non-metric multidimensional scaling (NMDS). This ordination revealed that Ducke was primarily differentiated from the ZF-2/BDFFP along the first axis, whereas the second axis largely separated plots within sites. We also labelled the 20 species that showed the most divergent pseudo-abundance data (>33% difference) between Ducke and the ZF-2/BDFFP. Species in red ( $n = 5$ ) were detected more often at Ducke, while those in green ( $n = 15$ ) more often at the ZF-2/BDFFP. The black dots in each corner depict 20 cumulative species that were unique to the two Ducke plots (top-left and bottom-left) and the two ZF-2 plots (top-right and bottom-right). However, these rare and difficult-to-detect species are all found at the BDFFP (Rutt et al., 2017).



**FIGURE 5** Avian communities at Reserva Ducke were not associated with vulnerable birds. For a subset of shared species ( $n = 75$ ; ~31%), abundance trends in nearby disturbed habitat (derived from Figure 2b in Stouffer et al., 2021) were correlated with species-specific scores from Axis 1 of the NMDS ordination (Figure 4). For illustrative purposes, each plot square is reproduced at its respective location along Axis 1 of the ordination (Figure 4). Those species encircled in green declined most strongly in local secondary forest and small forest fragments and were not associated with Ducke, implying that Ducke's avifauna now shows characteristics of human-modified habitat. In fact, very few understory insectivores were associated with Ducke at all, regardless of disturbance sensitivity. Bird illustrations reproduced by permission of Lynx Edicions.

were associated with the ZF-2/BDFFP and not with Ducke. In fact, very few understory birds were associated with the two Ducke plots at all, regardless of disturbance sensitivity (Figure 5). Grouping all 244 species into 10 broad guilds, understory insectivores showed the largest reduction at Ducke (−27%; Appendix S2: Figure S5). Subdivided even further, Ducke had fewer detections of near-ground (−51%), understory (−35%) and terrestrial insectivores (−29%) than the ZF-2 and BDFFP combined.

Finally, our landscape classification revealed that all plots contained a large amount of nearby closed-canopy forest, but percentages declined sharply with increasing distance for the two Ducke plots (Appendix S2: Figure S6). Within 5 km, all six plots displayed 91%–100% closed-canopy forest, but only the ZF-2/BDFFP plots retained those high percentages at 20-km radii (96%–99%). In contrast, 20-km buffers around the two Ducke plots consisted of only 66%–72% closed-canopy forest. However, distinguishing primary from secondary forest further complicates the picture around the BDFFP. Because of close proximity to historical cattle ranches, the two BDFFP plots show pronounced dips in the amount of primary forest at short to intermediate distances (<5–10 km), although much of this area was >20-year-old second-growth forest at the time of the bird sampling. At 20-km radii, ZF-2 and BDFFP plots all converged on high percentages of primary forest (90%–96%). In contrast, buffers around the two Ducke plots only circumscribed 58%–62% primary forest at that distance. Note that, for all plots, surrounding forest cover appears to approach stable percentages by ~20 km (Appendix S2: Figure S6).

## 4 | DISCUSSION

Across tens of kilometres of upland Amazonian rainforest, we find very little evidence for directional species turnover within a single interfluvium, corroborating the classic biogeographical pattern for birds. Without major dispersal barriers or biogeographic boundaries, the uniform environment of upland rainforest supports similar avian communities at fine scales. In particular, the avifauna of the ZF-2 and the BDFFP were remarkably similar, despite being separated by ~40 km. At the site level, unique indicator species were absent, and no species was detected at Ducke or the ZF-2 that had not already been recorded at the more well-sampled BDFFP (Cohn-Haft et al., 1997; Rutt et al., 2017). Thus, across our spatial extent, compositional differences were negligible and all six assemblages represented the same pool of upland birds. However, in place of species turnover, our results illustrated more subtle shifts in abundance between Ducke and the two farthest sites. Based on the reduction of a distinct subset of disturbance-sensitive species, we argue that the avifauna currently found at Ducke is impoverished, associated with Ducke's increased isolation from surrounding continuous forest.

At the scale of this study, our results suggest that species turnover contributes little to regional avian diversity within the same habitat type. In regions of uniformly high species richness, similar communities with low turnover would be expected, simply because

most of the available species pool has already been detected (Lennon et al., 2001). In our study, similarity averaged .77–.82 across all pairwise comparisons (the complement, respectively, of the Jaccard and Bray-Curtis dissimilarity indices presented in Section 3). Using the two intercepts to estimate local heterogeneity (i.e., the average dissimilarity at zero distance), we find that local heterogeneity accounts for most of the remaining dissimilarity (93% and 80%, respectively). On average, our sampling units contained 22% fewer observed species (~190) and 10% fewer estimated species (~219) than the overall species list (244). Therefore, the number of compositional units in our dataset (i.e., 'true' beta diversity; *sensu* Tuomisto, 2010) ranges from 1.12 to 1.28 (i.e.,  $190.17 \times 1.283 = 244$ ). This modest excess of species is likely attributable to incomplete sampling (observed species richness) and patchiness at large scales (>100 ha; estimated species richness). Together, this suggests a trivial underlying environmental gradient across relatively small spatial scales of upland rainforest. Our inference, however, is limited by the study's scale, which can be decomposed into grain (size of the sampling unit) and extent (area of the study region; Nekola & White, 1999; Wiens, 1989). To truly characterize a community, grain size needs to be sufficiently large (Tuomisto, 2010). For bird studies in the lowland Neotropics, 100 ha has been the gold standard (97–104 ha; Blake, 2007; Johnson et al., 2011; Robinson et al., 2000; Terborgh et al., 1990; Thiollay, 1994). Still, sampling on our six 100-ha plots was incomplete (Appendix S2: Figure S2), as the estimate for species richness was 15% larger than observed richness (see also the 228 species detected within a 100-ha BDFFP plot in Johnson et al., 2011). However, another study at the BDFFP, across a comparable extent (40 km), found a similar pattern of very slight species turnover with distance (Figure S3 in Stouffer et al., 2021). That study used mist nets to sample the understory community, but because sampling was sparse ( $\bar{x} = 5\text{--}6$  days/site), the average dissimilarity was twice as large (.47). Yet these studies cannot address how species turnover changes at smaller grain sizes or across even larger extents of upland rainforest (>40–60 km).

The slight signature of species turnover was only evident because of Ducke, which showed early hallmarks of a disturbed avian community. In each of our analyses, Ducke repeatedly emerged as the most distinct site (Figures 2–4, Appendix S2: Figure S3). Comparing our two species turnover metrics (Figure 2, Appendix S2: Figure S3), the distinctiveness of Ducke was especially apparent using the pseudo-abundance data (note the five relatively large dissimilarity values among the seven farthest comparisons in Figure 2b). This may be due to the fact that abundance-based dissimilarity metrics are more sensitive to disturbance and environmental differences than presence-absence metrics (Nekola & White, 1999). Irrespective of distance, however, disturbance can cause species turnover to increase or decrease, depending upon whether it triggers a gain or loss of species and individuals (e.g., the arrival of generalists or the loss of rare or specialist species; Socolar et al., 2016). Our study suggests that, in part, Ducke is differentiated because it contains fewer individuals of vulnerable species (Figures 4 and 5, Appendix S2: Figure S5). Of the 20 species that differed most in pseudo-abundance data (highlighted



in Figure 4), three times as many (15) were rarer at Ducke than vice versa, with *C. arada* missed at Ducke altogether. Like *Cyphorhinus*, many of these species are known to be highly vulnerable to habitat disturbance. This includes two of the most vulnerable obligate mixed-species flock-followers (*Myrmotherula longipennis* and *Tunchiornis ochraceiceps*), which are absent from flocks in 30-year-old secondary forest (Rutt et al., 2020), as well as a number of terrestrial and near-ground insectivores, the two most sensitive guilds to fragmentation and deforestation (Powell et al., 2013; Stouffer et al., 2021). For example, *Formicarius analis* (a terrestrial insectivore) averaged just 2–3 survey detections at Ducke compared with 12 in each of the other plots, and *Microbates collaris* (a near-ground insectivore) averaged five detections at Ducke compared with 11–12 elsewhere. The latter species was estimated to be the most vulnerable understory bird in disturbed landscapes (Figure 2b in Stouffer et al., 2021). Overall, very few understory species were associated with Ducke, particularly those that suffered most in disturbed forests (Figure 5). In fact, the understory insectivores with the largest reductions at Ducke (Appendix S2: Figure S5) represent four of the five guilds most vulnerable to disturbed habitat (Figure 3b in Stouffer et al., 2021). Species turnover can increase with these subtractive processes, such as when species become rarer (subtractive heterogenization; *sensu* Socolar et al., 2016)—an undesirable outcome from a conservation perspective.

The depauperate avifauna of Reserva Ducke signals that even a very large preserve (10 × 10 km) is not insulated from degradation over time. With fewer terrestrial, near-ground, and understory insectivores, the two Ducke plots do not compare favourably to the other, more homogeneous sites, which are surrounded by larger tracts of undisturbed forest (Appendix S2: Figure S6). At a radius of 20 km, however, the Ducke landscape still encompasses vast swaths of primary (~60%) and closed-canopy forest (~69%; Appendix S2: Figure S6). But this deforestation is not evenly distributed (Figure 1). Although initially surrounded by continuous forest (1963), sprawling settlements along the outskirts of Manaus abutted against the reserve's southern and western borders by the year 2000 (Oliveira et al., 2008; Ribeiro et al., 1999). At that time, only the eastern boundary remained linked to continuous rainforest (Cintra & Naka, 2012; Ribeiro et al., 1999), but roads and deforestation now sinuously encircle both the northern and eastern sides, transforming Ducke into a large urban forest fragment, as previously predicted (Ribeiro et al., 1999). Although we only sampled 2% of Ducke's 10,000 ha, our 2005–2009 bird community data already supported this disturbed characterization. Therefore, treating Ducke as representative primary rainforest has two intrinsic problems. When degraded habitat is used as a surrogate for pristine forest (Cintra & Naka, 2012), it limits our inference about natural patterns and processes. Second, it underscores an inherent problem of space-for-time substitutions (Stouffer et al., 2021), as diminished baselines ('control' sites) will underestimate the severity of effects at more disturbed sites (Borges & Guilherme, 2000). Unfortunately, because Ducke itself lacks baseline abundance data, we cannot assert whether its avian communities have always been diminished compared with nearby tracts of forest. Nonetheless, our documentation of disturbance has

far-reaching implications for other research on 'baseline' conditions at Reserva Ducke, which is considered to be one of the most well-studied patches of Amazonian rainforest (Ribeiro et al., 1999).

Beyond regional disturbance, additional factors may influence the avian communities at Ducke. For instance, the climate at Ducke is apparently somewhat drier (~11%) than at the BDFFP (mean annual rainfall from 1988 to 1998; Candido et al., *in prep*; Laurance, 2001), which could affect habitat and food resources. The urban heat island effect (Oke, 1982), which is especially pronounced in humid climates (Zhao et al., 2014), could also be a direct or indirect driver of microclimate changes. However, prevailing wind direction (east), Ducke's geographic position (northeast of the city) and several kilometres separating our plots from the urban perimeter (Figure 1) would all serve to negate or weaken its local impacts. Close proximity to Manaus could also increase the penetration and accumulation of other human impacts such as pollutants or contaminants. But reduced connectivity is likely a major contributor for many birds with presumably limited dispersal ability (Moore et al., 2008; Robinson & Sherry, 2012). Regardless of the mechanism(s), if defaunation continues, the further loss of disturbance-sensitive birds may have important consequences for ecosystem processes at Ducke, such as seed dispersal and insect predation (Bregman et al., 2016).

With low species turnover across tens of kilometres (i.e., little habitat heterogeneity), our findings suggest that conserving very large tracts of remote, undisturbed Amazonian rainforest is preferable for upland birds. Because disparate areas within the same interfluvium have a high degree of community overlap—and most of our dissimilarity is due to local heterogeneity (patchiness at scales >100 ha)—maximizing grain size would be more advantageous than maximizing spatial extent (grain size > spatial extent for preserve design). This would serve to increase both species richness and population persistence (Nekola & White, 1999), while reducing the emphasis on the location of the protected area (Socolar et al., 2016). Within such a high-diversity, homogeneous habitat, genuine species turnover among forest taxa would likely be unwanted, as it might indicate symptoms of anthropogenic disturbance. Even for vagile taxa such as birds, remote disturbances may be capable of generating species turnover in upland rainforest. Further, the impoverished avian community at Ducke implies that simply preserving a large tract of land may be inadequate (Newmark, 1987) depending on the broader landscape context. For example, the single, wide corridor (~9 km) along the reserve's eastern boundary may not have been sufficient to maintain connectivity with nearby continuous forest. To sustain upland biodiversity through time, it will also be necessary to preserve ample, pristine buffers around Amazonian forest reserves and restrict development within those buffers.

This study also accentuates the importance of replication for community inventories, especially replication within the same biogeographical region. With just one exception—two adjacent 100-ha plots, ~1.5 km apart (Blake, 2007; Blake & Loiselle, 2009)—all prior surveys of Neotropical avian communities were from lone ~100-ha plots without nearby replication. Although we cumulatively sampled 600 ha of forest patches, much larger networks of

well-sampled plots will be necessary to characterize how community composition varies across both space and time (Robinson et al., 2021), strengthening our ability to resolve differences among plots using ordination. In the absence of riverine barriers, these extensive networks could uncover subtle patterns of species turnover across larger geographic and environmental gradients within upland rainforest. To facilitate cross-study comparisons, maintaining common sampling methods and turnover metrics (e.g., 'true' beta diversity) will be necessary to ensure future ecologists and conservationists get the most out of these great efforts. Lastly, we emphasize the importance of knowing the total (gamma) diversity at a regional scale (Cohn-Haft et al., 1997; Rutt et al., 2017), which is particularly difficult in remote tropical regions (Socolar et al., 2016). A study like this was only possible because the regional avian diversity had already been well-catalogued (Cohn-Haft et al., 1997; Naka et al., 2008), providing us with complete knowledge of the regional species pool.

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## CONFLICT OF INTEREST

The authors have no conflict of interest to declare.

## DATA AVAILABILITY STATEMENT

The data underlying the findings of this study are summarized in the Supporting Information of this article (Appendix S1) and permanently archived at the Dryad Digital Repository (<https://doi.org/10.5061/dryad.dr7sqvb2k>).

## PEER REVIEW

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## BIOSKETCH

**Cameron Rutt** is a conservation ecologist who is passionate about avian natural history. His foremost academic interest has been trying to describe and understand the decline and disappearance of tropical birds. To do so, he relies upon intensive fieldwork, which often takes many months and hundreds of hours to collect, and an intimate, first-hand knowledge of the birds. He is also interested in the cryptic processes that may operate in seemingly pristine rainforest and the loss of globally rare and obscure species.

Author contributions: MCH conceived and designed the study. CBA, TVVC, and CFV conducted all avian point count surveys. PCS and DAL later revived the investigation, which CLR then led. WJC compiled and curated the data, which WJC and CLR analysed and used to create all data visualizations. CLR wrote the original draft, alongside contributions from all co-authors. DAL and MCH both administered the final iteration of this collaborative project.

## SUPPORTING INFORMATION

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

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