The Importance of Forest-Nonforest Transition Zones for Avian Conservation in a Vegetation Disturbance Gradient in the Northern Neotropics

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Dallas R. Levey[1,2] ⓘ**, Alejandro Estrada[2], Paula L. Enríquez[3]** ⓘ**, and Adolfo G. Navarro-Sigüenza[4]**

Abstract

Tropical landscape connectivity and matrix quality near large stands of primary forest are important factors that dictate biodiversity trends in communities. Suitable matrix management surrounding primary forest may help conserve biodiversity, but areas with poor matrix management need attention to determine their long-term viability to support native levels of biodiversity. We examined variations in species and functional diversity and community composition using point-count surveys placed in preserved (PRES), transition (TRA), and disturbed (DIS) areas according to percent land cover of forest and cattle pasture along a human disturbance gradient in the northern Neotropics during an 8 month period from 2019–2020. We expected the gradient of human disturbance to drive species diversity loss of forest specialists from PRES to DIS, resulting in changes to functional diversity and community composition. We detected 228 species overall, with 163 in PRES (40 unique species), 159 in TRA (9 unique species), and 152 in DIS (20 unique species). TRA supported an avian community with shared aspects of PRES and DIS, leading to the highest functional, Shannon (85.8 estimated species), and Simpson (57.9 estimated species) diversity. Higher diversity of open-area specialists in TRA and DIS has led to shifts in functional traits and different species and functional community compositions relative to PRES. Land management in Neotropical human-modified landscapes must focus on increasing habitat quality in remnant forest fragments in the vicinity of large stands of primary forest to prevent species and ecosystem service loss from preserved areas and the distancing of local community compositions.

Keywords

avian community, ecosystem services, functional diversity, landscape conservation, Mexico, land-use change, community composition

Constant human encroachment of forest preserves leads to habitat degradation and reduced connectivity, both major drivers of biodiversity loss (Haddad et al., 2015; Laurance et al., 2012). Human impacts leading to deforestation in the tropics threatens ecosystems which harbor ca 70% of global plant and animal life (Gibson et al., 2011; Tucker et al., 2018). In spite of the threats to tropical rainforests, the global deforestation rate from 2001—2017 was 178.8 million ha per year, with most losses occurring in the Neotropics (83.5 million ha/year), Southeast Asia (54.3 million ha/year), Africa (38.5 million ha/year), and East Asia

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(1.9 million ha/year; Estrada et al., 2019). High rates of native habitat conversion to agricultural land heavily contributes to the deforestation rate in the tropics (Estrada et al., 2019).

In heavily-modified landscapes, changes to vegetation cover, structure, and composition drive species and functional diversity changes of bird species at various temporal and spatial scales (Bregman et al., 2016; Şekercioğlu, 2012; Sol et al., 2020). Since bird species will likely be found in areas that meet their resource and nesting requirements, species and functional diversity trends in avian communities provide insight into the conservation value of habitat and impacts of habitat disturbance (Şekercioğlu et al., 2019). At the habitat-level, disturbance to vegetation complexity (Mills et al., 1991), the introduction of exotic plants, and changes to abiotic conditions (e.g., soil moisture, light exposure) have indirect (e.g., bird prey abundance and landscape structure) and direct (e.g., higher body temperatures and greater predation risk) influences on avian communities (Boyce et al., 2019; Williams et al., 2020). At the landscape-level, human-induced habitat loss and fragmentation lead to the reduction of connectivity (Şekercioğlu et al., 2015) and composition (Ryberg & Fitzgerald, 2016). The resulting landscapes contain high contrast habitat matrices that disproportionately affect species with restricted distributions and strict habitat and resource requirements (Huang & Catterall, 2021; Şekercioğlu, 2012; Vázquez-Reyes et al., 2017). Whether bird species respond effectively to these pressures depends on their functional characteristics (e.g., dispersal ability and habitat breadth) and resource requirements (Boesing et al., 2021; Bueno et al., 2018). Bird species incapable of responding to rapid habitat- and landscape-level changes are at risk of local extinction (Feeley & Terborgh, 2008; Şekercioğlu et al., 2002).

Here, we report a study on the variation of species and functional diversity in an avian metacommunity along a human disturbance gradient in southeastern Mexico using data from standardized point-count sampling during an 8-month period (June 2019—April 2020). The study area includes remnant forest patches, some of which comprise protected areas (e.g., Palenque National Park) and Indigenous Peoples' lands. Such lowland tropical forests were part of a former extensive vegetation corridor that connected the northernmost reaches of the Selva Lacandona with rainforests of Central America (Patten et al., 2011). Currently, such forest remnants provide vital habitat for native wildlife, including resident and migrant Neotropical bird species (Patten et al., 2010). Our study contributes importantly to the understanding of how bird communities in the area are structured through the assessment of species and functional diversity in a landscape matrix with a gradient of vegetation cover.

We hypothesized that high levels of human disturbance in the form of land-use change (i.e., conversion of tropical rainforest to cattle pasture, plantations, and residential and tourism development) have resulted in a shift of bird species and functional traits in disturbed areas when compared to a preserved area, leading to changes in local community characteristics. We expected the vegetation disturbance gradient to drive species diversity loss of forest specialists and functional groups from a preserved area to more disturbed areas, leading to unique species and functional community compositions along the disturbance gradient.

Methods

Study Site

We conducted the study in a vegetation disturbance gradient in southeastern Mexico in the state of Chiapas, located between the natural protected area Palenque National Park (PNP; 17.4836° N, 92.0468° W) and the town of Palenque (17.5098° N, 91.9818° W), located about 8 km from PNP (Figure 1). The vegetation of the area occupied by the disturbance gradient was originally mature tropical rain forest. About 100 years ago the area was gradually converted to pasturelands and plantations, but some forest fragments were left by landowners to preserve the water supply and forest resources such as wood, medicinal plants, and shade for cattle (Patten et al., 2010, 2011). Since the 1970s, deforestation from urbanization, roads, hotels, and agricultural development has converted forested areas into an heterogenous landscape of different vegetation types (Estrada et al., 2002; Ibarra-Macias et al., 2011; OnlineSupplementary Figures A1-A2).

The landscape outside of PNP and towards the town of Palenque consists of patches of remnant tropical forest in various successional stages, rubber, oil palm and mango plantations, cattle pastures, and a few hotels and residential homes. Increasing levels of human disturbance are found as one approaches the town of Palenque and decreasing levels are evident towards PNP (Figures 1 and Online Supplementary Figure A2). Based on land cover we divided the gradient into 1) the preserved area (PRES; 100% total forest cover), which consists of undisturbed forest of PNP, 2) the transition area (TRA; 25–75% total forest cover), which consists mostly of secondary forest patches, and 3) the disturbed area (DIS; 0–50% total forest cover), consisting mainly of cattle pasture, small secondary forest patches, plantations, and paved and gravel roads (Figures 1 and Online Supplementary Figure A1).
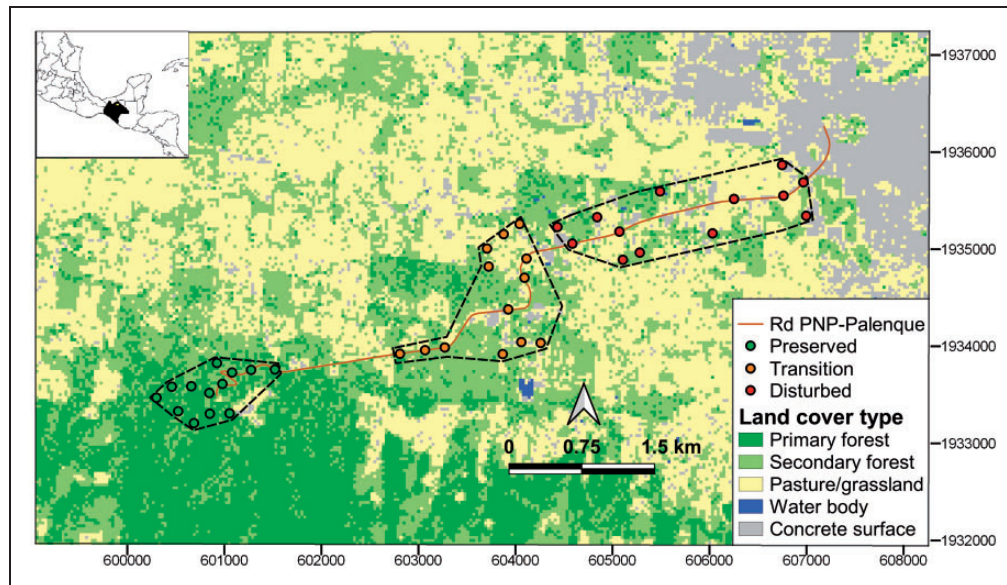
Figure 1. Map of land cover types in the study area. Land cover types were assigned to Landsat 8 remote sensing images from 2018—2019. Individual point-counts are represented by colored circles, and the three areas along the vegetation disturbance gradient are represented by polygons. Each polygon is separated by at least 450 m. The concrete surface category refers to buildings, roads, and parking lots.

Bird Community Sampling

We surveyed the study area over an 8 month span, accounting for 139 sampling days (6 days/week) from June—Nov (excluding Sep) 2019 and Feb—Apr 2020. We used point-counts (Bibby et al., 2000) with a fixed 50 m radius and an 8 min duration starting from sunrise—1130 hr on days without heavy rain or high wind to collect the number of bird species and individuals (Ralph et al., 1996). We used a fixed 50 m radius to consider birds that were actively using the habitat within each point-count and an 8 min duration to reduce double-counting of individual birds. We established 66 point-counts in total, separated by at least 200 m, including 33 in DIS, 20 in TRA, and 13 in PRES. For the data analysis, we randomly selected 13 point-count locations from TRA and DIS in order to have a balanced analysis between the three conditions (Figure 1). We alternated the order of visits to point-counts to control for differences in time-related detectability of birds. We performed 30 replicates of each point-count location, resulting in a total of 1170 replicates for data analysis. All survey work was carried out by a single observer (DRL) with over two years of experience with birds of Palenque prior to fieldwork.

Data Analysis

Land Cover Classification. To determine land cover types in the study area, we used remote sensing images (Landsat 8) to classify land cover types as primary forest,

secondary forest, cattle pasture/grassland, water bodies, and concrete surfaces. We calculated the percent cover of each land cover type in PRES, TRA, and DIS (Online Supplementary Figure A1). We assigned land cover types using the semi-classification plugin (Congedo, 2013) with the QGIS software platform version 3.8 Zanzibar (QGIS Development Team, 2019). The semi-classification plugin assigns classifications to areas of map images using Normalized Multi-band Drought Index (NMDI) values from spectral signatures from different land cover types. Water bodies and primary rainforest yield lower spectral signature values, while secondary forest, pasture, and concrete surfaces yield higher spectral signature values.

Species Diversity. For our calculations of species and functional diversity, we used observed abundances due to equal sample sizes for each condition (13 point-count locations) and point-count location (30 replicates). We included residents as well as migrant and wintering bird species in data analysis due to their lengthy stays (4—8 months) in the study area and sizeable ecological services in all habitat types (Şekercioğlu, 2012). Species names follow the American Ornithological Society checklist of North and Middle American birds (Chesser et al., 2020).

To assess differences in species diversity among local communities, we used the framework from Chao et al. (2020) using the R package iNEXT (Chao et al., 2014; Hsieh et al., 2016) to calculate overall species diversity

(Hill number 0), Shannon diversity (Hill number 1), and Simpson diversity (Hill number 2). Using absolute abundances of species in each data treatment, iNEXT provides interpolation and extrapolation of species accumulation curves for each diversity metric and calculates bootstrap (100 runs) 95% confidence intervals (CI) for comparison of data treatments (Chao et al., 2014). iNEXT also calculates the minimum estimated sample completeness for each sample, which is measure by sample coverage, or the proportion of the total number of individuals that pertain to the species detected in each sample (Hsieh et al., 2016). We checked for overlap of 95% confidence intervals, which represents significant differences among treatments. Due to differences in the observed abundances in each data treatment, iNEXT uses an extrapolation cutoff point of individuals equal to twice the number of individuals of the reference samples. We reported estimated species diversity for estimated overall species, Shannon, and Simpson diversity as mean $\pm$ 95% CIs.

Functional Trait Selection. To determine the functional diversity of local communities, we selected five response functional traits that provide information on avian species responses to habitat disturbance and ecological services: 1) average body mass (Dunning, 2008; Sibley, 2014), 2) diet—based on observed and documented main food item (i.e., insectivore, frugivore, nectarivore, carnivore, granivore, scavenger, and omnivore; González-Salazar et al., 2014), 3) feeding stratum (i.e., air-hawker, air-hawker above canopy, air-hawker under canopy, tree forager, bark excavator, bark gleaner, freshwater forager, ground-hawker, ground forager, ground gleaner, ground to lower canopy gleaner, ground to undergrowth gleaner, lower canopy foliage gleaner, and upper canopy gleaner; González-Salazar et al., 2014), 4) migratory status (i.e., neotropical migrant and sedentary; Patten et al., 2011), and 5) habitat breadth—the amount of habitat types (i.e., primary forest, secondary forest, forest edge, scrub, plantation, and cattle pasture) where each species was detected (range from 1—6; Online Supplementary Table A1). We log transformed average body mass values for each species to follow a normal distribution.

Functional Diversity. To determine differences in the foraging guild abundance among local communities, used paired-permutational tests with 9999 iterations (Farneda et al., 2020) and a false discovery rate (FDR) correction to significant ($\alpha < 0.05$) p—values to test for significant differences among abundances of foraging guilds. To determine community-level differences in functional diversity and uniqueness, we calculated three diversity indices. We calculated Simpson's index D, which considers all species maximally and equally

dissimilar (Ricotta et al., 2016). For functional diversity, we calculated Rao's quadratic diversity index Q to quantify differences in functional traits among species pairs for each point-count location (Ricotta et al., 2016). Rao's quadratic diversity index quantifies the average differences in functional diversity of a sampling location weighted by species abundances detected at that location. We calculated functional uniqueness U (Q/D) for each sampling location (Bello et al., 2007; Ricotta et al., 2016). Functional uniqueness U quantifies the decrease in diversity obtained when calculating functional diversity with interspecies dissimilarities (Ricotta et al., 2016). We calculated all values using the function "rao.diversity" with the R package SYNCSA (Debastiani & Pillar, 2012).

To determine differences in diversity indices and functional traits among local communities, we calculated community-weighted mean values for each point-count location (CWM; Lavorel et al., 2007). CWM values are calculated using a dissimilarity matrix (point-count locations in rows and bird species in columns) of community data and a list of species with assigned functional traits. CWM values represent the averages of functional traits assigned to species and are weighted by the abundances of species (Garnier et al., 2004; Lavorel et al., 2007). We calculated dissimilarity values of categorical functional traits using the Gower's distance with the function "daisy" with the R package cluster (Maechler et al., 2019). We calculated CWM values using the function "functcomp" with the R package FD (Laliberté & Legendre, 2010). We used paired-permutational tests with 9999 iterations (Farneda et al., 2020) and a false discovery rate (FDR) correction to significant ($\alpha < 0.05$) p—values to test for significant differences among CWM values of diversity indices and functional traits of local community pairs. We created Shared Control Estimation Plots using the R package dabestr (Ho et al., 2019) to show data as scatterplots with accompanying bootstrap (1000 runs) mean difference distributions with 95% confidence intervals for diversity indices and functional traits between PRES, TRA, and DIS. We used PRES as the shared control in the graphs, and we displayed paired mean differences between PRES and TRA and PRES and DIS.

Community Composition. To assess compositional differences in species and functional diversity among local communities, we performed a non-metric multidimensional scaling (NMDS) analysis with the abundance-based version of the Bray and Curtis (1957) dissimilarity index using the function "vegdist" (Oksanen et al., 2020). We assigned each species to a foraging guild based on González-Salazar et al. (2014). To test for significant differences in Bray-Curtis dissimilarity values among local communities, we performed a permutational
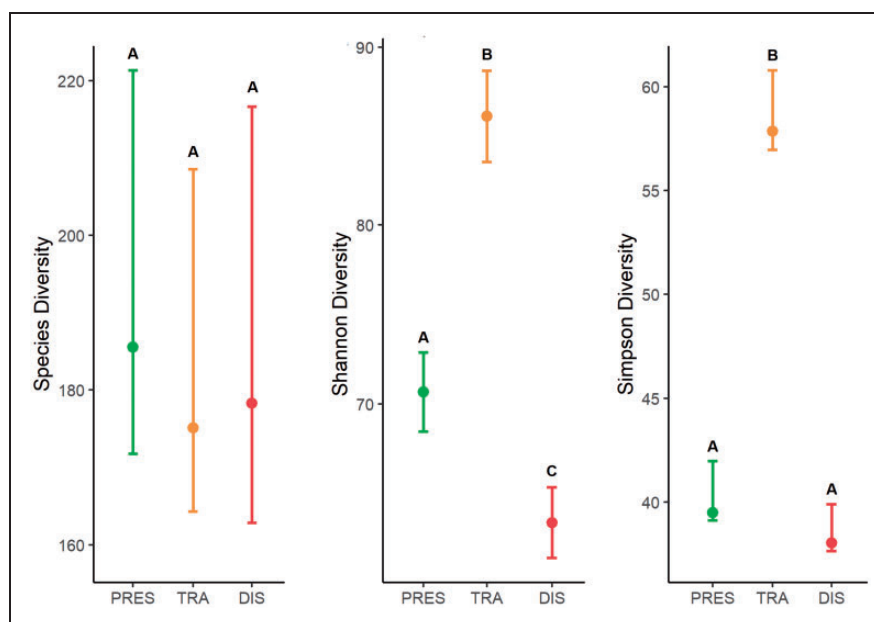
Figure 2. Patterns of estimated species diversity for overall species, Shannon, and Simpson diversity. Letters above confidence interval whiskers represent significant differences among avian communities. PRES = preserved, TRA = transition, DIS = disturbed.

multivariate analysis of variance using distance matrices (999 iterations) using the function "adonis" (Oksanen et al., 2020). To test for homogeneity in the variances of abundances, we performed an analysis of multivariate homogeneity of group variances using the function "betadisper" (Oksanen et al., 2020). We report stress values of the NMDS analyses and p—values from the permutational multivariate analysis of variance. We conducted all statistical analyses using R software (R Core Team, 2020) and all community composition analyses using the R package vegan (Oksanen et al., 2020).

Results

Species Richness and Diversity. We recorded 228 bird species (167 residents and 61 migrants) from 39 point-counts and 1170 point-count replicates. Overall species richness was highest in PRES (163 species), followed by TRA (159 species) and DIS (152 species). For overall estimated species diversity, there were no significant differences among PRES (185.5 species, CI: 171.7—221.3), TRA (175.2 species, CI: 164.3—208.5), and DIS (178.5 species, CI: 162.8—216.5; Figure 2 and Online Supplementary Figures A3-A4). For Shannon and Simpson diversity, estimated values were significantly higher in TRA (85.8, CI: 83.7—88.8 and 57.9, CI: 57.0—60.8 species, respectively) compared to PRES (70.4, CI: 68.6—73.0 and 39.5, CI: 39.1—42.0 species) and DIS (63.1, CI: 61.5—65.4 and 38.0, CI: 37.6—39.9

species, respectively; Figure 2 and Online Supplementary Figures A3-A4)

Functional Diversity. In PRES, we detected 40 species unique to the community (90% resident and representing 19% of total bird abundance in PRES), consisting mainly of lower canopy insectivores (54% of all unique species diversity in PRES) and upper canopy frugivores (19%), ground to lower canopy granivores (10%), and frugivores (10%). In TRA, we detected only 9 species unique to the community (33% resident, 4% total bird abundance in TRA), consisting mainly of freshwater herbivores (45% of all unique species diversity in TRA), air-hawking carnivores (41%), and nectarivores (7%). In DIS, we detected 20 species unique to the community (55% resident, 2% total bird abundance in DIS), consisting mainly of lower canopy foliage gleaning insectivores (33% of all unique species diversity in DIS), ground to undergrowth gleaning granivores (26%), and ground-foraging insectivores (14%).

Analysis of foraging guild abundance among local communities showed significant decreases from PRES to TRA and DIS in the lower canopy foliage gleaning insectivore ($p = 0.009$ and $p = 0.007$, respectively), nectivore ($p < 0.001$ and $p = 0.02$, respectively), and bark gleaning insectivore categories ($p = 0.001$ and $p < 0.001$, respectively; Figure 3). Foraging guild categories with significantly higher abundances in DIS relative to PRES and TRA include the bark excavating insectivore ($p = 0.002$ and $p = 0.002$, respectively), ground gleaning insectivore ($p < 0.001$ and $p < 0.001$, respectively), and
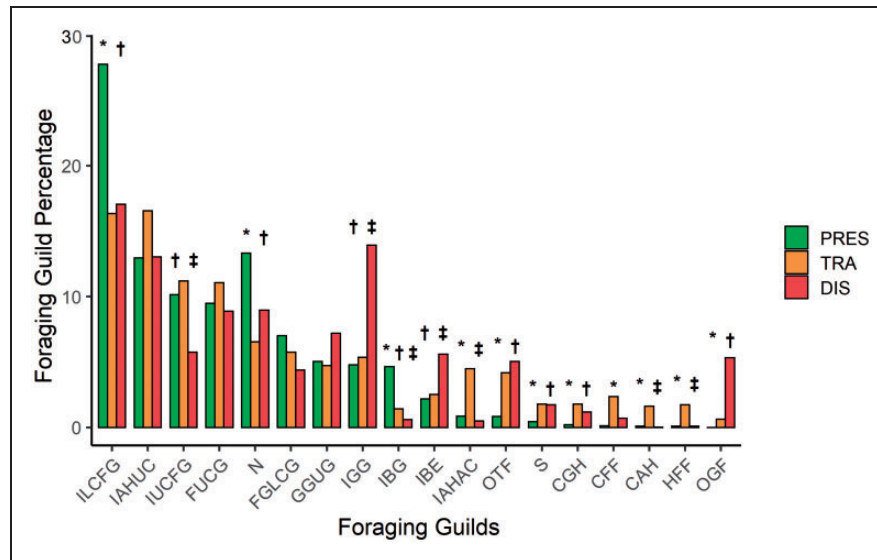
Figure 3. Percentages of foraging guild abundance in PRES (preserved), TRA (transition), and DIS (disturbed). Bird species were assigned to one of the following foraging guilds. ILCFG: insectivore—lower canopy foliage gleaner, IAHUC: insectivore—air-hawker under canopy, IUCFG: insectivore—under canopy foliage gleaner, FUCG: frugivore—upper canopy gleaner, N: nectivore, FGLCG: frugivore—ground to lower canopy gleaner, GGUG: granivore—ground to undergrowth gleaner, IGG: insectivore—ground gleaner, IBG: insectivore—bark gleaner, IBE: insectivore—bark excavator, IAHAC: insectivore—air-hawker above canopy, OTF: omnivore: tree forager, S: scavenger, CGH: carnivore—ground-hawker, CFF: carnivore—freshwater forager, CAH: carnivore—air-hawker, HFF: herbivore—freshwater forager, OGF: omnivore—ground forager. The markers above each triplet of bars represent significant differences ($\alpha < 0.05$) among pairs of local communities. * = significant difference ($p < 0.05$) between PRES and TRA, † = significant difference ($p < 0.05$) between PRES and DIS, ‡ = significant difference ($p < 0.05$) between TRA and DIS.

ground foraging omnivore categories (with PRES only: $p = 0.04$; Figure 3).

Rao and Uniqueness indices were highest in TRA, followed by DIS and PRES (Figure 4). The Simpson index was highest in TRA, followed by PRES and DIS (Figure 4). In PRES, the Rao index was significantly lower than TRA ($p = 0.004$) and DIS ($p = 0.004$; Figure 4). Using PRES as a control for the comparison of paired mean differences of CWM trait values, TRA and DIS had significantly less nectivore ($p < 0.001$ and $p = 0.006$, respectively) and omnivore diversity ($p = 0.003$ and $p = 0.004$, respectively; Figure 5). TRA had significantly more carnivore diversity than PRES ($p < 0.001$) and DIS ($p = 0.003$), and while DIS had significantly more scavenger diversity than PRES ($p = 0.04$; Figure 5). TRA had significantly larger body masses ($p < 0.001$), higher habitat breadths ($p = 0.01$), higher diversity of migratory species ($p = 0.004$), and a lower diversity of sedentary species ($p = 0.004$) than PRES and higher habitat breadths than DIS ($p = 0.008$; Figure 6). DIS had significantly larger body masses ($p < 0.001$) and higher habitat breadths ($p = 0.001$) than PRES (Figure 6).

Community Composition. Local community composition analysis highlights spacing of bird communities for species diversity (stress = 0.09) and foraging guilds

(stress = 0.11; Figure 7A and B). The community compositions of PRES, TRA, and DIS were significantly different from each other in permutational multivariate analyses of variances of species ($p = 0.001$; Figure 7A) and foraging guild diversity ($p = 0.001$; Figure 7B).

Discussion

Continual human encroachment through for-profit farming and urbanization of landscapes surrounding remaining large stands of Neotropical rainforest threatens biodiversity, vital ecosystem services, and human well-being (Estrada et al., 2019; Kremen & Merenlender, 2018; Scullion et al., 2019). In a landscape with a human disturbance gradient between a tropical rainforest preserve and a nearby encroaching human population, we detected important avian community-level differences. We also highlighted important community-level characteristics of the forest-nonforest transition (TRA) avian community in between extremes of the disturbance gradient. TRA contained the high species and functional diversity, indicating that the state of avian communities in forest-nonforest transition areas may dictate long-term biodiversity trends in Neotropical avian metacommunities.

Our estimated species diversity results support the notion that TRA has the potential to provide high
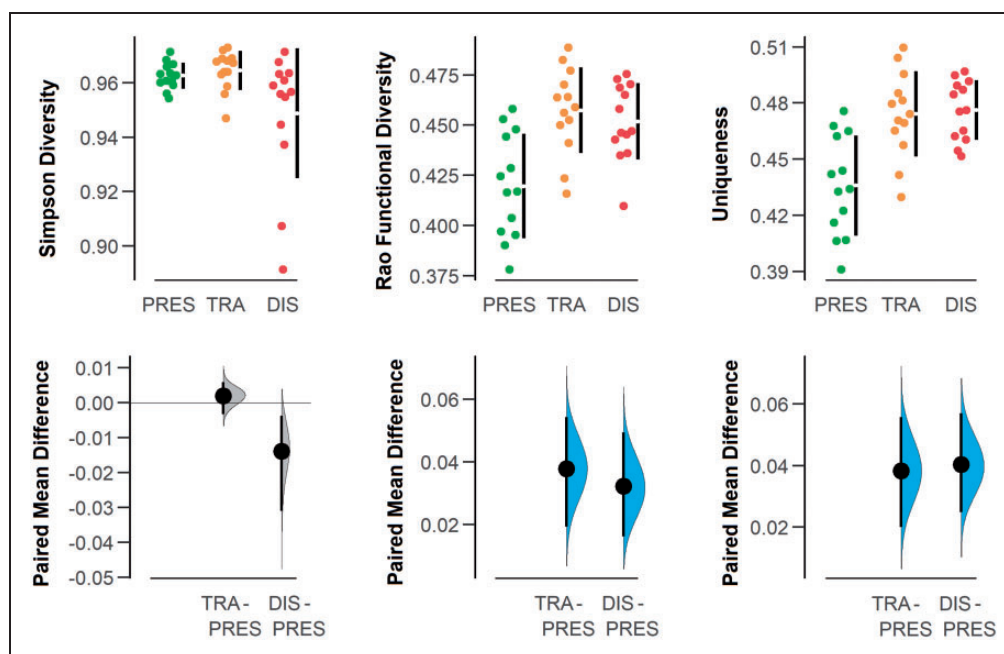
Figure 4. Patterns and paired mean differences of diversity indices Simpson, Rao, and Uniqueness in the preserved (PRES), transition (TRA), and disturbed (DIS) local communities. The colored dots represent the point-count locations for each local community, and the black vertical bar and break in the vertical bar represent the 95% confidence intervals and the group mean, respectively. Below each scatterplot of point-count locations, we present the paired mean differences for the corresponding diversity index. The paired mean differences use PRES as a control. For TRA and DIS, paired mean differences are plotted as a distribution calculated by bootstrapping (1000 runs). Blue colored distributions represent significant differences ($p < 0.05$) with the horizontal bar at 0, which represents the mean of PRES for each index.

conservation value for a wide range of species and functional traits and represents a tipping point for the entire metacommunity. We detected significantly higher species diversity in TRA for Shannon and Simpson diversity. This translates into a higher diversity of common and rare bird species from the entire landscape than PRES and DIS. TRA provided habitat for common species that favor open secondary forest (Rutt et al., 2019), forest edge with cattle pasture, and primary forest due to shared vegetation structure and composition qualities relative to PRES and DIS. The common species of PRES and DIS with high mobility find resources at sections of TRA that are adjacent to PRES and DIS (Atkins et al., 2019). However, TRA did not have higher overall species diversity relative to PRES and DIS. Bird species detected in TRA had low abundances that would otherwise be more abundant in PRES or DIS (e.g., *Amazilia tzacatl*, *Chlorestes candida*, and *Setophaga ruticilla*), likely due to the heterogenous landscape, diverse vegetation composition, and ecological interactions (i.e., competition; Boyce et al., 2019) with migrant species and resident bird species of PRES and DIS. The fluctuations in species diversity along the disturbance gradient represents important implications for functional diversity and ecosystem functioning in the local avian communities.

We detected higher functional diversity and uniqueness in TRA and DIS relative to PRES. In PRES, the documented decline and extirpation of understory insectivores and large game birds (Patten et al., 2010), paired with a potential lack of colonizing species, may be driving the decrease in functional diversity relative to TRA and DIS. Species with specialized resource and habitat requirements (e.g., *Tunchiornis ochraceiceps* and *Penelope purpurascens*) have been lost from primary forest in the study area over the last 80 years as a result of isolation from other areas of forest and hunting (Patten et al., 2011). Other primary forest species (e.g., *Basileuterus culicivorus*, *Habia fuscicauda*, and *Ceratopipra mentalis*) were drastically less abundant in TRA and DIS and may be the next species to become extirpated if disturbance in the study area continues. In DIS, intense disturbance of habitat has favored exotic species (e.g., *Streptopelia decaocto*), native, open-area specialists (e.g., *Troglodytes aedon* and *Zenaida asiatica*), and species with higher habitat breadths (e.g., *Myiozetetes similis*), all of which can thrive in landscapes with scattered trees and secondary forest fragments imbedded in cattle pasture (Espinosa-Méndez et al., 2020.)

Given the extensive rainforest conversion to agricultural areas in DIS, which has resulted in sharp
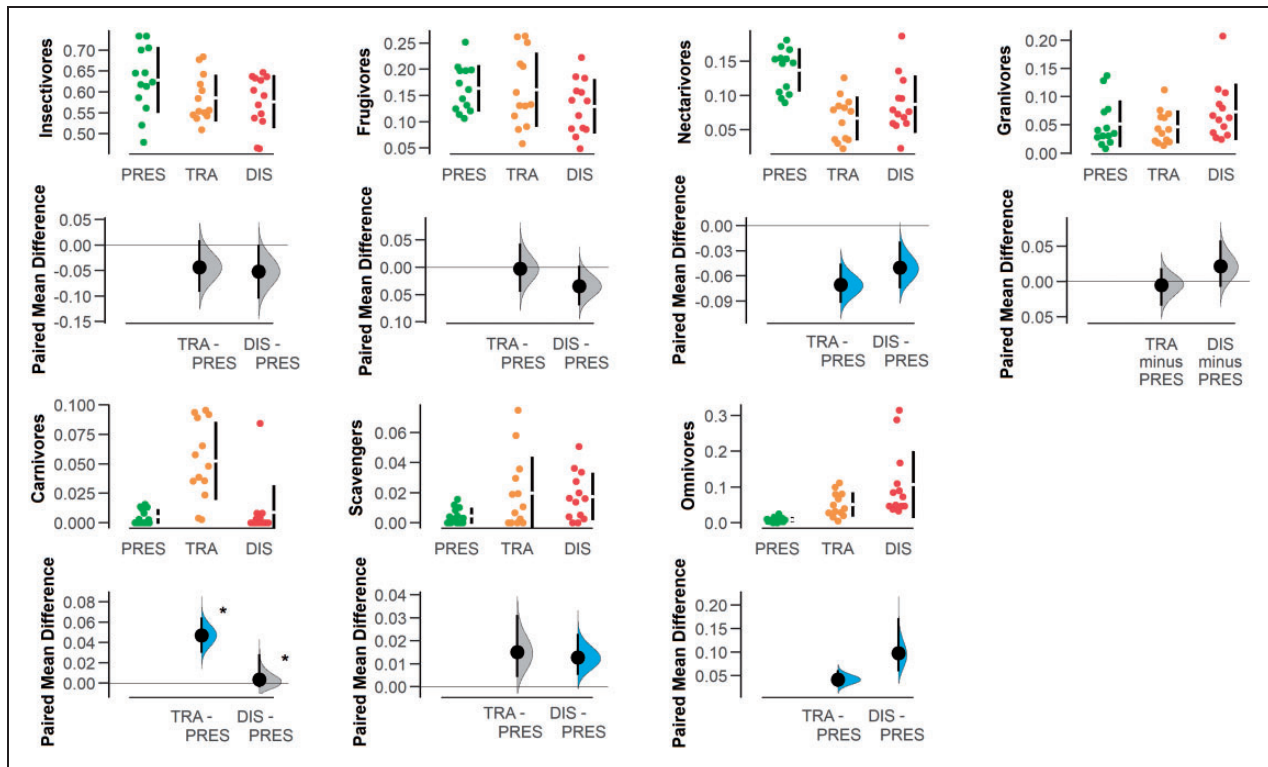
Figure 5. Patterns and paired mean differences of foraging items in the preserved (PRES), transition (TRA), and disturbed (DIS) local communities. The colored dots represent the point-count locations of each local community, and the black vertical bar and break in the vertical bar represent the 95% confidence intervals and the group mean, respectively. Below each scatterplot of point-count locations, we present the paired mean differences for the corresponding foraging item. The paired mean differences use PRES as a control. For TRA and DIS, paired mean differences are plotted as a distribution calculated by bootstrapping (1000 runs). Blue colored distributions represent significant differences ($p < 0.05$) with the horizontal bar at 0, which represents the mean of PRES for each foraging item. Asterisks indicate significant differences ($p < 0.05$) between TRA and DIS.

vegetation structure and composition contrast compared to PRES, the overall ecological health of the metacommunity will likely depend on the connectivity of secondary forest in TRA with primary forest in PRES (Mayhew et al., 2019). The secondary forest of TRA serves as a buffer between areas of intense human activity in DIS and primary forest in PRES, offering habitat for some bird species usually found in primary forest (e.g., *Trogon massena* and *Oncostoma cinereigulare*) and open-area specialists (e.g., *Dryobates scalaris* and *Crotophaga sulcirostris*). This has resulted in an avian community with a wide range of functional traits that mirrors PRES and DIS but contains several distinct characteristics, including a higher diversity of carnivores and long-distance migrants and a lower diversity of sedentary species. However, while secondary forest cover is relatively high in TRA, disturbance and clearing of forest understory has disproportionally affected small (Stirnemann et al., 2015), sedentary, and forest-dwelling species such as ground foraging insectivores (Şekercioğlu, 2012), nectarivores, and some understory insectivores (Şekercioğlu et al., 2002). Migrant species,

which provide similar ecological services to primary forest-dependent birds (Şekercioğlu et al., 2004), may provide a boost in functional diversity and ecosystem services that would otherwise be absent due to the loss of strict primary forest specialists and understory dependent species (Barros et al., 2019). The loss of vegetation and landscape structure outside of PRES also has indirect effects on the avian community of TRA and DIS through the loss of insect prey and ecological interactions such as avian attendance at army ant swarms (e.g., *Habia rubica*, *H. fuscicauda*, and *Dendrocolaptes sanctithomae*; Coates-Estrada & Estrada, 1989). The preservation of vegetation and landscape-level structure in TRA will play a crucial role in maintaining native biodiversity, especially in PRES.

TRA and DIS supported less insectivores, frugivores, and nectivores and more carnivores, scavengers, and omnivores than PRES. Greater human disturbance in TRA and DIS relative to PRES has favored the greater abundances of carnivores (e.g., *Rupornis magnirostris* and *Buteo plagiatus*) and frugivores that specialize in forest edge (e.g., *Trogon melanocephalus* and *Euphonia*
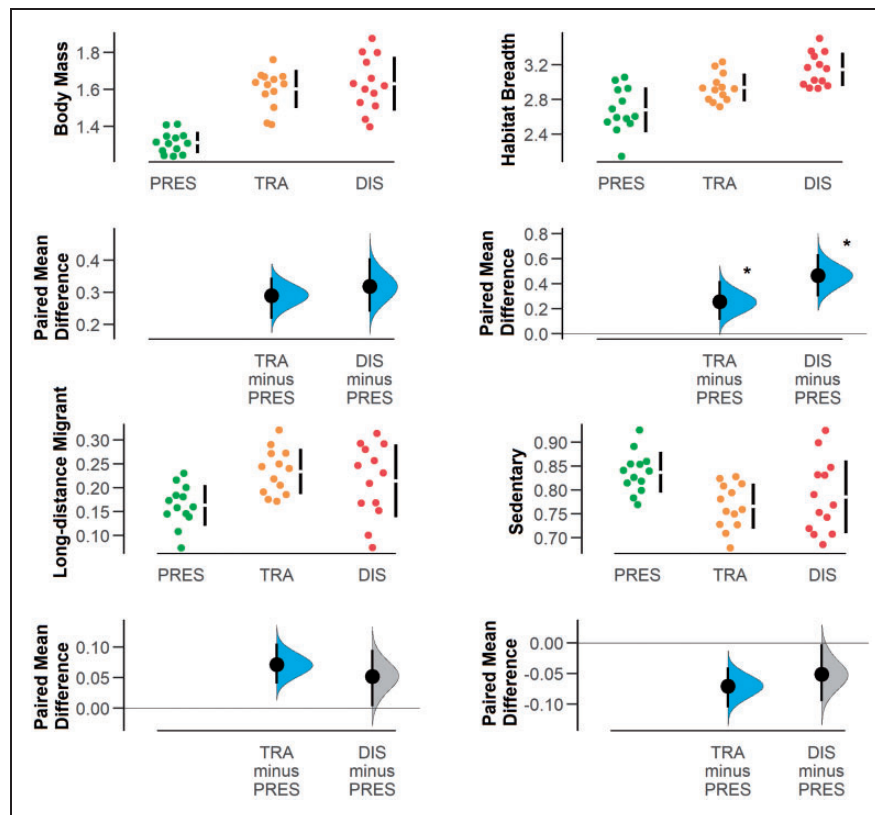
Figure 6. Patterns and paired mean differences of functional traits in the preserved (PRES), transition (TRA), and disturbed (DIS) local communities. The colored dots represent the point-count locations of each local community, and the black vertical bar and break in the vertical bar represent the 95% confidence intervals and the group mean, respectively. Below each scatterplot of point-count locations, we present the paired mean differences for the corresponding functional trait. The paired mean differences use PRES as a control. For TRA and DIS, paired mean differences are plotted as a distribution calculated by bootstrapping (1000 runs). Blue colored distributions represent significant differences ($p < 0.05$) with the horizontal bar at 0, which represents the mean of PRES for each functional trait. Asterisks indicate significant differences ($p < 0.05$) between TRA and DIS.

hirundinacea) and lower abundances of upper canopy foragers, especially frugivores (e.g., *Chlorophanes spiza* and *Patagioenas flavirostris*). Reduced and disturbed vegetation structure in secondary forests of TRA and DIS fail to provide adequate foraging and nesting resources for lower canopy insectivores (*Henicorhina leucosticta* and *Basileuterus culicivorus*) and nectarivores (e.g., *Phaethornis striigularis*, *P. longirostris*, and *Campylopterus hemileucurus*) that benefit from shaded and complex forest understory (Tchoumbou et al., 2020). Recent conservation measures such as the reintroduction of the large-bodied frugivore Scarlet Macaw (*Ara macao*) in TRA and DIS may bolster functional diversity, especially as Scarlet Macaws begin to acclimate and expand their foraging range (Amaya-Villarreal et al., 2015; Estrada, 2014).

Our species and functional diversity trends among PRES, TRA, and DIS highlight important variation along the disturbance gradient. The species turnover of forest specialists for open-area specialists has led to no net loss in overall species diversity, but key changes in functional groups have led to unique community compositions among local communities. Open-area specialists in DIS have boosted functional diversity after the loss primary forest-dependent understory insectivores, including higher abundances of upper-canopy frugivores (e.g., *Thraupis episcopus* and *T. abbas*) and omnivores (e.g., *Psilorhinus morio* and *Quiscalus mexicanus*) that adapt easily to or specialize in open areas. Resource-dependence of upper-canopy frugivores in DIS is largely tied to introduced tree species (e.g., *Ficus benjamina* and *Mangifera indica*), which dampens seed dispersal services. The loss of understory insectivores in DIS may have negative impacts on agricultural yields from declines in herbivorous insect predation (Şekercioğlu, 2012). Local farmers rely heavily on insecticides in DIS (DRL personal observation), what could be a result of decreased herbivorous insect predation by understory insectivores. This may increase negative impacts on insectivorous birds through the depletion of insect prey
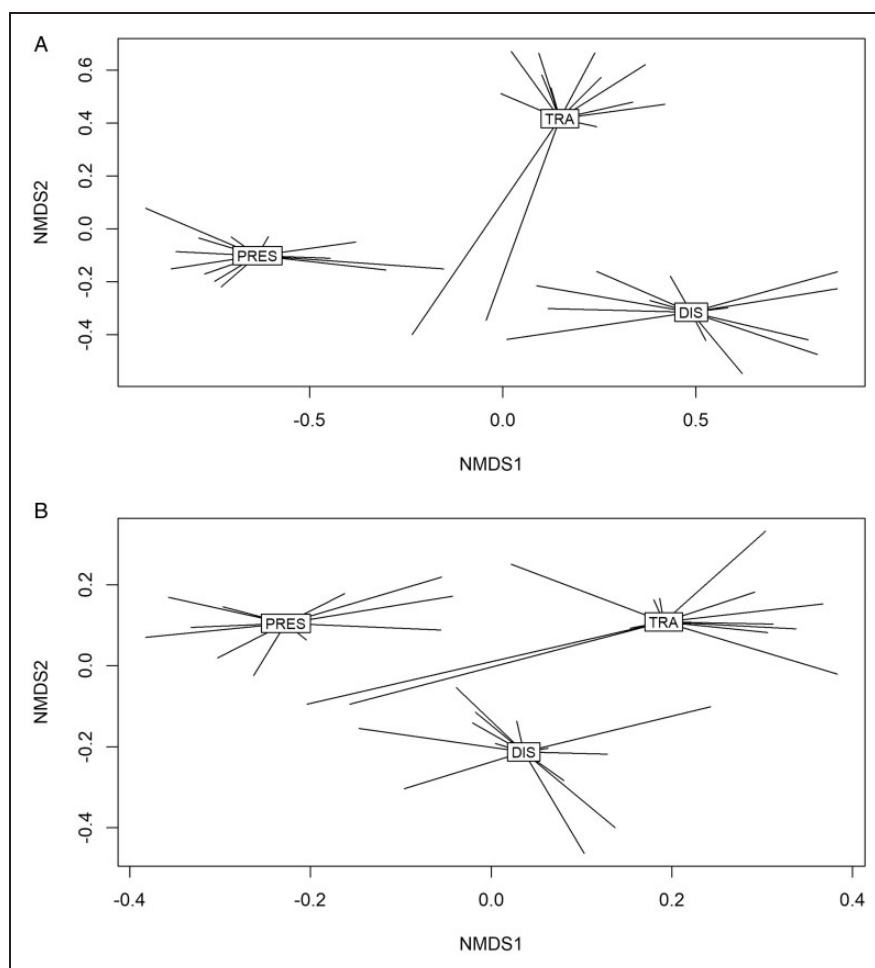
Figure 7. Non-Metric Dimensional Scaling (NMDS) plot of (A) species and (B) foraging guild diversity in each local community. Point-count locations are represented at the ends of lines extending from text boxes with community names. PRES = preserved, TRA = transition, DIS = disturbed.

populations (Şekercioğlu, 2012), leaving the future of PRES and the entire metacommunity in doubt.

Implications for Conservation

In most Neotropical landscapes, biodiversity and inherent ecosystem services are at risk due to for-profit agricultural activity, natural resource extraction, and economic activity at regional and global levels (Estrada et al., 2019). Human pressures that deforest and fragment Neotropical landscapes place vital importance on landscape-level land management that bolsters habitat quality in disturbed areas surrounding large forest tracts to avoid biodiversity loss (Driscoll et al., 2013). Our results suggest that a human-disturbance gradient in a Neotropical landscape has resulted in changes to avian community characteristics in three areas along the landscape, placing importance on the conservation of transition areas in between extremes of nonforest-forest gradients to preserve a natural range of avian biodiversity and ecosystem services and prevent rare and unique species declines in preserved areas. To contribute to the long-term conservation of avian biodiversity and ecosystem services, land management in the Neotropical areas should prioritize reducing the contrast between native habitat and surrounding matrices by strengthening the quality and connectivity of secondary forest patches (Barros et al., 2019) to mitigate the abiotic and biotic changes caused by agriculture and climate change on birds (Stouffer et al., 2021; Williams et al., 2020). The preservation and inclusion of native tree species through agroforestry practices in agricultural areas has been shown to reinforce species and functional bird diversity to levels close to native, primary habitat (Şekercioğlu et al., 2019) by increasing landscape connectivity (Mayhew et al., 2019), improving soil health (Kremen & Merenlender, 2018), and attracting resident and migratory (McDermott et al., 2015) nectivorous and

insectivorous birds that positively impact agricultural yields (Şekercioğlu, 2012).

We propose several measures that local government officials should emphasize to local landowners inside and outside of Palenque National Park. The tourism industry in Palenque and other tourism hotspots in the area stand to gain from the implementation of bird friendly land management practices, including the preservation of native vegetation and avoiding the replacement of native vegetation with ornamental plants that offer little resource value for emblematic native bird species in the study area (e.g., *Ara macao*, *Ramphastos sulfuratus*, and *Spizaetus ornatus*). Road use and construction should be approved only with proper evaluation of the environmental impacts, especially inside the grounds of PNP, considering the short- and long-term impacts of automobile disturbance on avian communities (Kang et al., 2015). In rapidly changing Neotropical landscapes, investigation of avian communities would benefit from joint efforts that combine survey work with a variety of other methods, including the evaluation of nest predation (Estrada, Rivera, & Coates-Estrada et al., 2002) and soundscapes along disturbance gradients to determine the impacts of anthropogenic noise on avian communities (Burivalova et al., 2018).

Data Accessibility Statement

Raw data used for data analysis are available online at Figshare.

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Supplemental Material

Supplemental material for this article is available online.

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