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Research Paper

## Neotropical bird communities in a human-modified landscape recently affected by two major hurricanes

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**ABSTRACT.** Agriculture affects biodiversity on a global scale and especially in the Neotropics, leading to land-management challenges in which native wildlife is forced to interact with high-contrast landscape matrices. Further, the direct and indirect effects of hurricanes impacting native habitat in human-modified landscapes increases reliance on agricultural areas and high-contrast matrices. To understand how avian communities in a human-modified landscape respond to hurricane disturbance, we evaluated post-hurricane trends in species richness, density, structure, and functional and taxonomic composition in avian communities at tropical dry forest and in three agricultural habitats using point-count surveys. We compared our results to a similar study that took place years before the hurricanes in the study area. Similar to pre-hurricane trends, tropical dry forest provided key habitat for endemic species relative to agricultural areas, and tree orchards continued to serve as key secondary habitat for a high species richness and community evenness. However, tree orchards, along with cattle pastures and crop fields, failed to serve as successful buffers of hurricane disturbance by supporting half the estimated bird density of tropical dry forest. Cattle pasture and crop fields were both relatively species poor and had low community evenness compared to tropical dry forest and tree orchards after the hurricanes. Tropical dry forest had distinct species and feeding guild compositions compared to the agricultural habitats. All habitat types after the hurricanes had higher numbers of granivores and a reduction of carnivores compared to pre-hurricane levels. Land management in the study landscape needs to incorporate strategies that raise the hurricane resilience of agricultural areas while providing resources to support higher species richness and density in agricultural systems. Such strategies include the preservation of native trees and shrubs and allowing for the natural succession of habitat in unused areas in tree orchards, cattle pasture, and crop fields.

## Des communautés d'oiseaux néotropicaux dans un paysage modifié par l'être humain récemment touché par deux ouragans majeurs

**RÉSUMÉ.** L'agriculture affecte la biodiversité à l'échelle mondiale et en particulier dans les régions néotropicales, ce qui aboutit à des difficultés en termes de gestion des terres sur lesquelles la faune native est obligée d'interagir avec des modèles de paysages hautement contrastés. En outre, les effets directs et indirects des ouragans sur l'habitat natif dans les paysages modifiés par l'homme augmentent la dépendance vis-à-vis des zones agricoles et des modèles fortement contrastés. Pour comprendre comment les populations aviaires dans un paysage modifié par l'homme réagissent aux perturbations engendrées par les ouragans, nous avons évalué les tendances post-ouragan en matière de richesse des espèces, de densité, de structure et de composition fonctionnelle et taxonomique des populations aviaires dans une forêt tropicale sèche et dans trois habitats agricoles en utilisant des enquêtes de dénombrement. Nous avons comparé nos résultats à ceux d'une étude similaire réalisée quelques années avant les ouragans dans la zone examinée. Tout comme les tendances pré-ouragan, la forêt tropicale sèche offrait un habitat essentiel aux espèces endémiques par rapport aux zones agricoles et trois vergers ont continué à servir d'habitat secondaire clé pour favoriser une grande richesse des espèces et l'égalité des communautés. Toutefois, les vergers, de même que les pâturages et les zones de récolte, ne constituaient pas des tampons efficaces contre les perturbations engendrées par les ouragans : ils n'ont préservé que la moitié de la densité aviaire estimée dans la forêt tropicale sèche. Suite aux ouragans, les pâturages et les champs cultivés étaient tous deux relativement pauvres en espèces et présentaient une faible égalité des communautés par rapport à la forêt tropicale sèche et aux vergers. La forêt tropicale sèche présentait des compositions d'espèces et de groupes trophiques distinctes par rapport aux habitats agricoles. Après les ouragans, tous les types d'habitat présentaient des nombres plus élevés de granivores et une réduction des carnivores par rapport aux niveaux antérieurs aux ouragans. La gestion des terres dans le paysage étudié doit intégrer des stratégies qui augmenteront la résilience des terres agricoles aux ouragans tout en fournissant des ressources aptes à soutenir une richesse et une densité accrues des espèces dans les systèmes agricoles. Ces stratégies comprennent la préservation des arbres et buissons natifs et une succession naturelle des habitats dans les zones inutilisées dans les vergers, les pâturages et les cultures.

**Key Words:** *agriculture; avian community; community ecology; natural disasters; Neotropics*

## INTRODUCTION

Hurricane intensity and impacts have increased over the past few decades (Emanuel 2005, Kossin et al. 2020), resulting in elevated disturbance to vegetation structure and composition that may impact animal communities (Emanuel 2005). The conversion of native habitat to agricultural land—a major driver of biodiversity decline (Haddad et al. 2015, Maxwell et al. 2016)—causes landscapes to lose resilience to hurricane disturbance and exacerbates the direct and indirect effects of hurricanes on community-level dynamics in a wide range of animals (Emanuel 2005). Considering human activities have actively modified 50-70% of the Earth's surface for agricultural and housing purposes (Seto et al. 2011, Haddad et al. 2015), urgent attention is needed to study how animal communities respond to hurricanes in human-modified landscapes. That attention is needed in hurricane-prone tropical regions, which contain species-rich terrestrial ecosystems (ca. 70% of plant and animal species worldwide; Myers et al. 2000, Şekercioğlu et al. 2019) and suffer the highest rates of habitat loss and conversion to agriculture in the world, especially in the Neotropics (Estrada et al. 2019).

In the Neotropics, agricultural activities have been shown to negatively affect avian communities by filtering out species dependent on complex native vegetation structure and composition (Daily et al. 2003, Şekercioğlu et al. 2019). When agricultural areas are incorporated into landscapes with native vegetation (i.e., corridors, live fences, and isolated trees, remnant forest patches), relatively high numbers of species can use those areas for foraging and nesting (Estrada and Coates-Estrada 2005, Vallejo et al. 2014, Şekercioğlu et al. 2015, Le Roux et al. 2018). Although previous studies have documented some of the impacts of agricultural activities on biodiversity in the Neotropics (MacGregor-Fors and Schondube 2011, Şekercioğlu et al. 2019, Levey et al. 2021), there is still a gap in knowledge regarding how avian communities adjust in the short- and long-term to vegetation structure and composition changes from hurricanes in heterogeneous agricultural landscapes (Johnson and Winker 2010, Martínez-Ruiz and Renton 2018).

Direct effects of hurricanes, including strong winds that break branches and uproot trees, change terrestrial vegetation structure (i.e., canopy cover and understory volume; Lynch 1991) and vegetation phenology (Renton et al. 2018). Further, indirect effects from changes in vegetation structure and phenology alter foraging stratum and food resources, disproportionately affecting avian functional groups dependent on foraging and nesting sites in the forest canopy and tree cavities, and food resources such as nectar, fruit, and seeds (Lynch 1991, Wunderle 2005, Renton et al. 2018). Changes in abiotic conditions (i.e., sunlight, wind, and landscape configuration) by direct hurricane effects disproportionately affect forest-dependent bird species, forcing local migrations to lesser impacted areas for nesting and foraging habitat (Wiley and Wunderle 1993). The success of local migration and the ability of birds to use lesser impacted habitat depends on landscape structure and composition and the habitat quality of less impacted areas. In landscapes with high matrix contrast between native habitats and agricultural areas, hurricane-prone bird species will likely decline, especially those with low dispersal capabilities (Şekercioğlu 2012). At the community level, direct and indirect effects of hurricanes can drive compositional shifts in avian species and functional diversity through local extinctions

when landscape structure and composition are inconducive to dispersal and when resource quality and availability are low in secondary habitats (e.g., agricultural areas; Lloyd et al. 2019).

We evaluated bird community species richness, density, structure, and species and functional composition in tropical dry forest and three agricultural systems recently affected by two major hurricanes, and we compared our results with a similar study that took place before the hurricanes. We did not make direct statistical comparisons of species richness and community structure from before and after the hurricanes because of: (1) confounding variables that we could not control, such as the use of different observers and different geographical locations of sampling point-counts and (2) the inherent intra- and inter-annual variation of tropical dry forest bird communities. We did, however, make direct statistical comparisons of the species and functional composition of the bird communities before and after the hurricanes using the presence and absence of bird species and feeding guilds to control for the annual variation in bird diversity in the study area. To make quantitative comparisons of the patterns found in the bird communities before and after the hurricanes, we followed the exact data collection methodology from MacGregor-Fors and Schondube (2011). We surveyed birds in agricultural systems, defined as human-modified areas with the purpose of crop and/or livestock production, with varying types of vegetation structure (planted fruiting trees, cattle pastures, and herbaceous plants). We compared these agricultural systems with tropical dry forest within a nearby biosphere reserve. Notably, MacGregor-Fors and Schondube (2011) found plantations of fruiting trees serve as key habitats for birds, supporting similar bird species richness and community structure as tropical dry forest before the hurricanes. We expected changes in the community characteristics of the tropical dry forest after hurricane disturbance, specifically lower total species richness and a shift in functional diversity as a result of an increase of granivores due to the opening of forested areas and a decrease in frugivores due to disturbance to vegetation structure and fruiting phenology.

## METHODS

### Study area

We conducted this study on the Pacific coast of Jalisco, Mexico, between the locality José María Morelos (19°40'40.8" N, 105°11'5.6394" W) and the Chamela-Cuixmala biosphere reserve (19°29'54.5994" N, 105°2'38.3994" W). Original vegetation in the region consisted of continuous tropical dry forest on hillsides and semi-deciduous forest along river drainages and alluvial flats (Maass et al. 2005). Tropical dry forest in the reserve is dominated by tree species *Caesalpinia eriostachys*, *Gliricidia sepium*, and *Plumeria rubra* (Durán et al. 2002) and has a canopy height of 8-12 m (Rzedowski 2006). Semi-deciduous forest retains leaves year-round, whereas tropical dry forest loses leaf cover for 6-8 months of the year (Rzedowski 2006). Each vegetation type supports a distinct composition of bird species (Renton 2002), and both face high rates of deforestation for agricultural development (Maass et al. 2005).

The area outside of the biosphere reserve is composed of remnant forest patches, small towns, and land devoted to agricultural activities, which include tree orchards, cattle pastures, and crop fields. Tree orchards include papaya, mango, citrus fruit trees, and

tamarind, and crop fields include herbaceous plants, such as maize, melon, chili pepper, banana, and sorghum (Martínez-Ruiz and Renton 2018). The conversion of tropical dry forest to cattle pastures generally involves the clearing of trees and understory with subsequent burning of the cleared vegetation (Maass et al. 2005). Large, isolated trees and shrubs occasionally remain, which serve as shade sources for cattle and are likely key resources for wildlife (Le Roux et al. 2018).

In the Chamela-Cuixmala biosphere reserve and surrounding areas, the impacts of hurricanes Jova (category 2) in 2012 and especially Patricia (category 5) in 2015 drastically altered vegetation phenology and structure, which has resulted in differential impacts on various vegetation types (Novais et al. 2018, Renton et al. 2018). Damage to tropical dry forest vegetation included broken limbs and branches, snapped trunks, and uprooted trees by the maximum hurricane winds of Patricia, resulting in a loss of canopy cover (Martínez-Ruiz and Renton 2018). Due to the trajectories of both hurricanes and the spatial structure of agricultural vegetation, damage dealt to agricultural areas was relatively low when compared to the reserve (Martínez-Ruiz and Renton 2018). A recent study in the reserve showed that the effects of Hurricane Patricia have affected fruit and flower abundance and reduced available nesting cavities, which have likely affected the reproductive output in the threatened Lilac-crowned Parrot (*Amazona finschi*; Renton et al. 2018).

## Bird surveys

To make quantitative comparisons of bird communities before and after the hurricanes in tropical dry forest and three habitats with different agricultural activities, we followed the exact bird survey methodology from MacGregor-Fors and Schondube (2011). We surveyed bird communities in May of 2019 using point-count surveys (Bibby et al. 2000) with a fixed 25 m radius for 5 min. from 0700-1000 hr., recording all birds seen and heard (Ralph et al. 1996). We used a 25 m point-count radius to follow methodology from MacGregor-Fors and Schondube (2011) and to compromise between the relatively high detection probabilities of birds at large distances in open habitats versus the relatively low detection probabilities at large distances in tropical dry forest habitat (Ralph et al. 1996, Bibby et al. 2000). Point-counts in human-modified habitat types were placed in three spatially independent groups separated by at least 750 m and by other habitat types to attain site independence (Ralph et al. 1996). For tropical dry forest, we surveyed 2 areas separated by 650 m inside the Chamela-Cuixmala biosphere reserve because of space restrictions.

To estimate distance-corrected densities, we used a rangefinder to measure distances from the observer to each bird. We used this methodology instead of using observed abundances to calculate abundance differences among avian communities as in MacGregor-Fors and Schondube (2011) because of the value and robustness of distance-corrected density estimations for detecting differences in abundances of birds per unit area.

## Data analysis

We compared bird species richness among treatments with a species richness statistical expectation using EstimateS (Colwell 2013, Colwell and Elsensohn 2014). The statistical expectation is calculated by the repeated resampling of pooled samples to create

statistically comparable values for different treatments. We calculated estimated species richness values using sample-based abundance data and 100 data randomizations to ensure smooth, comparable species accumulation curves (Colwell 2013). To compare the density of birds in each habitat type, we used Distance 7.0 (Thomas et al. 2010). Using the distance measurements to each bird seen in a sample, Distance calculates a probability function and effective distance radius to give a density estimate per unit area (Buckland et al. 2001). We chose the density analysis model for each treatment with the lowest Akaike's information criterion (AIC; Akaike 1998). This model selection criterion chooses the most parsimonious model in terms of model fit and parameter number (Burnham and Anderson 2002). To determine the statistical difference among treatments for species richness and densities, we calculated 84% confidence intervals (CI) following the protocol of MacGregor-Fors and Payton (2013) and checked for overlap. Non-overlapping CIs represented significant differences among treatments. We report estimated species richness as mean species  $\pm$  84% CIs and density values as mean birds/ha with 84% CIs.

We used rank/abundance plots (also known as Whittaker plots) to represent the abundance distribution and determine the structure (dominance/evenness) of the avian communities found at each habitat type (Magurran 2003). Steep curves represent the dominance of a small number of species and an uneven community structure, whereas flat curves represent the reduced dominance of a small number of species and an even community structure. We calculated the relative abundance for each species in each habitat type and log-transformed the data because they did not follow a normal distribution. To test for statistical differences in the dominance/evenness of the communities, we compared the slopes of the rank/abundance plots using ANCOVA and a Holm-Bonferroni correction to  $p$ -values to reduce the probability of Type 1 statistical errors (Holm 1979).

To determine compositional differences in species and functional diversity among habitat types, we assigned bird species to six feeding guilds (granivore, insectivore, frugivore, omnivore, nectarivore, and scavenger) based on primary diet item (Arizmendi et al. 1990). Using presence and absence data from before (MacGregor-Fors and Schondube 2011) and after the hurricanes for species and feeding guilds in each habitat type, we calculated the Bray and Curtis (1957) dissimilarity index for each habitat from before and after the hurricanes (Magurran 1988). We display dissimilarity results as similarity by subtracting the dissimilarity values from 1. We performed a Bray-Curtis multivariate cluster analysis (single-linkage) for the species and functional dissimilarity values for each habitat type from before and after the hurricanes with the "vegan" package (Oksanen et al. 2020). We conducted community structure and composition statistical analyses in R (R Core Team 2018).

## RESULTS

We recorded 64 bird species in total (with some species overlap among habitats), with 33 species in tropical dry forest, 33 species in tree orchards, 26 species in cattle pastures, and 20 species in crop fields. Endemic, quasi-endemic (species distributed in areas less than 35,000 km<sup>2</sup> outside of Mexico), and semi-endemic (endemic to one region during a large portion of the year; González-García and Gómez de Silva-Garza 2003) species to

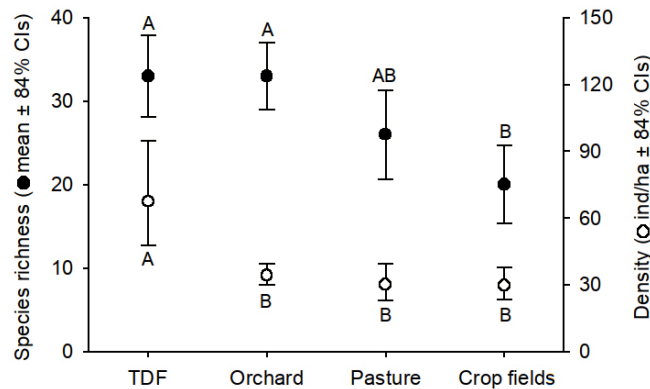
**Table 1.** Results from ANCOVA analysis of rank-abundance slopes. All paired comparisons were significantly different except the habitat pairs of tropical dry forest/tree orchards and cattle pasture/crop fields. Asterisks depict significant values with a Bonferroni-Holm correction to  $p < 0.008$ .

	Tropical dry forest	Tree orchards	Cattle pasture
Tree orchards	$F_{1,63} = 0.6, P = 0.40$	--	--
Cattle pasture	$F_{1,55} = 16.2, P = 0.001^*$	$F_{1,56} = 17.8, P = 0.001^*$	--
Crop fields	$F_{1,49} = 48.9, P < 0.001^*$	$F_{1,50} = 59.8, P < 0.001^*$	$F_{1,42} = 6.5, P = 0.04$

Mexico make up ~33% of the total species count (Appendix 1, Table A1.1). Feeding guild composition of all recorded species was 50% granivores, 29% insectivores, 12% omnivores, 6% frugivores, 3% nectarivores, and 1% scavengers.

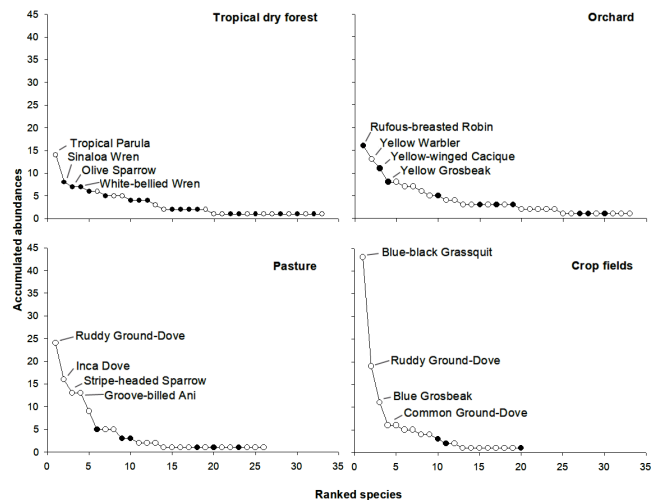
Estimated species richness did not differ significantly between avian communities at tropical dry forest ( $33.0 \pm 4.9$  calculated species), tree orchards ( $33.0 \pm 4.0$  calculated species), and cattle pastures ( $26.0 \pm 5.3$  calculated species; Fig. 1), but tropical dry forest and tree orchards differed significantly from crop fields ( $20.0 \pm 4.7$  calculated species; Fig. 1). Density estimations showed significantly higher bird density in tropical dry forest (mean 67.4 individuals/ha; 84% CIs: 47.9-94.8), compared to tree orchards (mean 34.4 individuals/ha; 84% CIs: 29.9-39.5), cattle pastures (mean 29.8 individuals/ha; 84% CIs: 23.5-37.9), and crop fields (mean 30.0 individuals/ha; 84% CIs: 22.9-39.4; Fig. 1).

**Fig. 1.** Pattern of estimated species richness (black dots) and density (white dots) in the surveyed habitats. Species richness was highest in tropical dry forest (TDF) but was not significantly higher than in tree orchards and cattle pasture. Crop fields had significantly lower species richness than the other habitats. The density estimation for tropical dry forest was significantly higher than the other habitats. Letters above and below confidence intervals represent statistical differences among habitats.



Comparisons of the rank/abundance slopes yielded significant differences in four of six paired habitat comparisons (non-significant habitat pairs: tropical dry forest/tree orchards and cattle pasture/crop fields; Table 1). Cattle pasture and crop fields yielded the steepest rank/abundance slopes, whereas the tropical dry forest and tree orchards yielded the shallowest slopes (Fig. 2).

**Fig. 2.** Rank-abundance plots for tropical dry forest, tree orchards, cattle pastures, and crop fields. Bolded dots reference endemic species found in each habitat type. We found significant differences between the slopes of the rank-abundance curves in all paired combinations of habitat types except the habitat pairs tropical dry forest/tree orchards and cattle pasture/crop fields. The species names represent the top four dominant species of the bird communities at each habitat type. See Appendix 1 for all species scientific names.

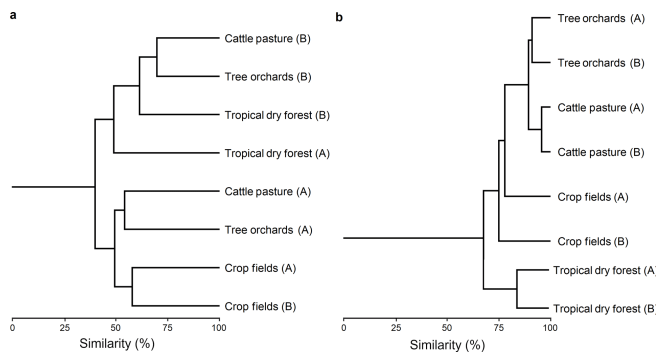


Results from the species composition analysis show that crop fields were the least similar to tropical dry forest before (28% similarity) and after the hurricanes (19% similarity). Tree orchards and cattle pastures were more similar to tropical dry forest before the hurricanes (64% and 59% similarity, respectively) than after (42% and 27% similarity, respectively). The Bray-Curtis cluster analysis grouped pre- and post-hurricane habitats into two major groups at 40% similarity, including one group with pre- and post-hurricane tropical dry forest and pre-hurricane tree orchards and cattle pastures and a second group with post-hurricane cattle pastures and tree orchards and pre- and post-hurricane crop fields (Fig. 3a). Functionally, the pre- and post-hurricane tropical dry forest were grouped at 85% similarity and were least similar to all human-modified habitats, both from before and after the hurricanes. Crop fields were the most dissimilar in composition relative to tropical dry forest from before (62% similarity) and after the hurricanes (50% similarity). Tree orchards and cattle pastures were intermediate in functional similarity to tropical dry forest before (82% and 75% similarity, respectively) and after the



hurricanes (70% and 68%, respectively). The Bray-Curtis cluster analysis grouped tropical dry forest, tree orchards, and cattle pasture to their pre- and post-hurricane equivalent, with the highest similarity in cattle pastures (91% similarity), followed by tree orchards (88% similarity) and tropical dry forest (83% similarity; Fig. 3b). Pre- and post-hurricane crop fields were not grouped, while post-hurricane crop fields were more similar to pre- and post-hurricane tree orchards and cattle pasture (86% similarity; Fig. 3b) than pre-hurricane crop fields.

**Fig. 3.** Bird community compositions for (a) species level and (b) functional diversity at the habitats tropical dry forest, tree orchards, cattle pasture, and crop fields for before (B) and after (A) the hurricanes. At the species level, the Bray-Curtis cluster analysis grouped the habitats into two clusters at 40% similarity, each including three of four habitats solely from before and after the hurricanes. Functionally, cattle pasture and crop fields retained the highest similarity in functional composition among the habitats, while crop fields were the only habitat that shifted after the hurricanes.



## DISCUSSION

Human activities that modify the vegetation structure and composition of Neotropical landscapes threaten the ability of avian communities to respond effectively to hurricane disturbance. Species and functional diversity of avian communities change when the availability of food and nesting resources is altered by hurricane disturbance, forcing bird species to locally migrate to alternative habitats (Renton et al. 2018). Our results show that tropical dry forest served as species-rich habitat after the hurricanes, especially for endemic species. Species composition in tropical dry forest became less similar to agricultural areas with tree cover (i.e., tree orchards and cattle pasture), whereas functional composition was largely similar from before the hurricanes (39% insectivores, 30% granivores, 10% omnivores, 9% nectarivores, 5% frugivores, 5% carnivores, and 2% scavengers) to after, outside of a slight decrease in insectivores and a notable increase in granivore representation. Avian communities at tropical dry forest and tree orchards had similar community structure to pre-hurricane communities, which bolsters previous knowledge that tree orchards offer habitat to tropical dry forest birds (Renton 2001) and provides evidence that tree orchards may have sufficient resources for tropical dry forest-dependent birds and endemic species after hurricane disturbance. However, hurricane disturbance has resulted in the distancing of the similarity of species and functional composition between

avian communities at tropical dry forest and tree orchards. Given that bird density and species and functional composition of bird communities in agricultural areas differ from the avian communities at tropical dry forest before and after the hurricanes, more land management work is needed to raise hurricane resilience in the study landscape outside the tropical dry forest reserve.

In Neotropical landscapes with intense agricultural activity, tree orchards provide food resources and more complex vegetation structure not found in cattle pastures and crop fields, which may result in similar community characteristics to native habitat (MacGregor-Fors and Schondube 2011, Şekercioğlu et al. 2019). Before the hurricane disturbance, the tropical dry forest community structure was more even than the avian community at tree orchards (MacGregor-Fors and Schondube 2011). In our assessment, we found that the structure of the avian community at tree orchards is more similar to tropical dry forest after hurricanes. Vegetation structure simplification in tropical dry forest after hurricane disturbance and more complex vegetation structure in tree orchards relative to cattle pasture and crop fields likely explains the similarity in community structure because species that rely on complex vegetation structure were likely forced to lesser impacted areas of the landscape (e.g., *Dryocopus lineatus* and *Attila spadiceus*), such as tropical dry forest and semi-deciduous forest further away from the coast. Tree orchards supported hurricane-sensitive avian functional groups (i.e., frugivores and granivores) from tropical dry forest (i.e., *Ortalis poliocephala* and *Geotrygon montana*). Also, bird species that were detected in both tree orchards and tropical dry forest before the hurricanes (e.g., *Cyanocorax sanblasianus*) were found only in tree orchards after the hurricanes. In terms of functional diversity, we found increases in omnivores and frugivores and decreases in nectarivores and carnivores in tree orchards compared to before the hurricanes. Hurricane disturbance to tropical dry forest resulting in changes to fruit and seed abundance (Renton et al. 2018) may be driving frugivorous and granivorous bird species to tree orchards. Carnivorous species may have also been driven out of tropical dry forest to less affected habitat in the study landscape after the hurricane disturbance for foraging and nesting resources (e.g., mangroves; Martínez-Ruiz and Renton 2018).

Unlike tree orchards, cattle pastures and crop fields failed to support similar community characteristics to tropical dry forest before and after the hurricanes. Cattle pastures and crop fields have abiotic conditions (e.g., temperature, light intensity, landscape configuration, etc.) and biotic conditions that alter community characteristics relative to native habitat by driving out forest specialists with limited dispersal capabilities and specialized resource requirements, such as understory insectivores (Şekercioğlu et al. 2002, Williams et al. 2020). Hurricane disturbance did not drastically alter patterns for the majority of community characteristics in cattle pastures and crop fields compared to pre-hurricane trends. Cattle pastures and crop fields had similar species richness (before: 28 and 18 species, respectively; after: 26 and 20 species, respectively) and density, and functional composition in cattle pastures was similar to before the hurricanes (MacGregor-Fors and Schondube 2011). However, post-hurricane structure did not differ significantly for cattle pastures and crop fields because of greater relative dominance of two ground-foraging granivores (*Columbina*

*talpacoti* and *Columbina inca*). Before the hurricanes, community structure at cattle pastures was dominated by a different ground-foraging granivore (*Volatinia jacarina*). Hurricane disturbance to remnant vegetation (e.g., bushes and small trees for breeding displays; Fandiño-Mariño and Vielliard 2004) in cattle pastures after the hurricanes may have negatively affected the species. Functional composition in post-hurricane crop fields was more similar to tree orchards and cattle pastures than pre-hurricane crop fields, likely due to the local migration of some granivorous (e.g., *Columbina talpacoti*) and frugivorous species (e.g., *Turdus rufopalliatu*s) that typically use tropical dry forest and tree orchards rather than crop fields. New species detected in crop fields after the hurricanes (e.g., *Streptopelia decaocto* and *Saltator coerulescens*) may also highlight how hurricane disturbance has favored the establishment of invasive and native species that have expanded their range (Stanturf et al. 2007).

The proximity of cattle pastures to tropical dry forest may be another factor influencing avian species richness in cattle pastures. Cattle pastures are often created adjacent to tropical dry forest on hillsides, which facilitates the movement of tropical dry forest species into cattle pastures (Maass et al. 2005). The proximity may explain why certain tropical dry forest-dependent species (i.e., *Thryophilus sinaloa* and *Amazilia rutila*) were found using cattle pastures and not crop fields after the hurricanes. However, of the total number of endemic and quasi-endemic bird species, cattle pastures (29%) and crop fields (14%) supported far less than tropical dry forest (86%) and tree orchards (48%). MacGregor-Fors and Schondube (2011) found similar endemic and quasi-endemic species richness trends, including fewer in cattle pastures (45%) and crop fields (0%) compared to tropical dry forest (91%) and tree orchards (55%) in the study area in 2007. This demonstrates that after hurricane disturbance, some endemic species not detected in cattle pastures (e.g., *Arremonops rufivirgatus* and *Thryophilus sinaloa*) and crop fields (e.g., *Turdus rufopalliatu*s and *Passerina leclancherii*) before the hurricanes may have been forced to secondary habitats in response to vegetation damage in the landscape. However, because of the low levels of endemic species detected in cattle pastures and crop fields, these areas continue to provide low conservation value relative to tropical dry forest and tree orchards. Bird density may help to further highlight the impacts of agricultural activities and hurricanes on human-modified habitat.

Post-hurricane bird density at tropical dry forest was significantly higher than at tree orchards, cattle pastures, and crop fields, representing a distinct trend relative to before the hurricanes. However, different methods in MacGregor-Fors and Schondube (2011) were performed to determine bird density before the hurricanes. High bird density in tropical dry forest relative to agricultural areas is likely linked to more complex structures and a higher volume of vegetation (Mills et al. 1991). The destruction of vegetation in tropical dry forest after the hurricanes likely had a minimal effect on bird density because the losses of some species from hurricane-prone functional groups (e.g., frugivores) were replaced by functional groups (e.g., omnivores and insectivores) that could use the increase in open areas, such as forest edge and open canopy patches within the forest. Also, insect communities in tropical dry forest were positively affected by the hurricane disturbance (Novais et al. 2018), which likely influenced the higher observed number of insectivores. Tree orchards, cattle pastures,

and crop fields had equally low-density estimations, meaning that although tree orchards were able to support species found in tropical dry forest, they do not contain adequate habitat to support the same abundances of birds relative to native areas. The lack of a diverse range of vegetation structure and resources likely influenced the density trends in agricultural areas (Posa and Sodhi 2006, Giacomo and Casenave 2010), signaling the low-value agricultural areas represent to the local bird communities and the low habitat quality they contain as secondary habitats for locally migrating birds searching for resources after hurricane disturbance. Also, the abundance of insect prey in tropical dry forest after the hurricanes may be attracting insectivorous birds that used agricultural areas before the hurricanes, highlighting the importance of tropical dry forest for the local bird communities after hurricane disturbance.

Agricultural activities (MacGregor-Fors and Schondube 2011, Şekercioğlu et al. 2019) and hurricane disturbance (Martínez-Ruiz and Renton 2018, Lloyd et al. 2019) drive differential composition changes of avian communities in human-modified habitats compared to native habitats. After hurricane disturbance, communities showed similar functional composition trends with pre-hurricane communities, with similar functional compositions between the habitat pairs tropical dry forest/tree orchards and cattle pastures/crop fields. Tropical dry forest-dependent birds tended not to use cattle pastures and crop fields because of a lack of vegetative complexity (Philpott and Bichier 2012), a reduction of food sources such as fruit and insects (Şekercioğlu 2012), and lower dispersal capabilities, especially among understory insectivores (Şekercioğlu 2002). Hurricane damage to tropical dry forest vegetation structure and changes to vegetation phenology may explain why some forest-dependent species are using agricultural areas, such as the granivore, *Geotrygon montana*, and the insectivore, *Polioptila nigriceps*. Frugivorous species, which usually depend on tropical dry forest, were found feeding on fruit in tree orchards, including *Trogon citreolus* and *Cyanocorax sanblasianus*, providing further evidence that native frugivores can use resources in tree orchards. In crop fields, hurricane disturbance did not lead to shifts in species composition. Functional composition did not change in tree orchards, cattle pastures, and tropical dry forest. The presence of native and complex vegetation may have conferred resilience to hurricane disturbance in these areas, which may have led to conserved functional composition. To sustain future hurricane disturbance, native vegetation should be allowed to become incorporated into agricultural areas, which will also support more native (Vallejo et al. 2014) and forest-dependent bird species (Şekercioğlu et al. 2019) and species that locally migrate from areas that have sustained greater relative damage from hurricane disturbance (Martínez-Ruiz and Renton 2018).

## CONCLUSION

The impacts of hurricanes on wildlife communities in heterogeneous, human-modified Neotropical landscapes deserve attention because hurricane intensity and frequency is expected to increase in the near future (Kossin et al. 2020). Our findings suggest that a tropical dry forest reserve, which received heavy structural damage after hurricane disturbance, served as a buffer for avian species richness and functional groups after such disturbance and supported a bird density twice as high as nearby

agricultural areas. Homogeneous agricultural systems near the tropical dry forest reserve make up an overall low-quality matrix, highlighting the importance of conserving native vegetation for bird species that are forced to rely on secondary habitats after hurricane disturbance. Allowing the natural succession of vegetation in human-modified landscapes is another tool that can lower the habitat contrast between agricultural areas and tropical dry forest (Douglas et al. 2014) while facilitating the local migration of birds to alternative habitats after hurricane disturbance. The inability of tropical dry forest-dependent and endemic bird species to use the human-modified landscape after hurricane disturbance is concerning considering the rate of tropical dry forest conversion to agricultural land in the study area and the projected increase of hurricane frequency and intensity (Kossin et al. 2020). However, because our study highlights aspects of the local bird community in a small timeframe, we could not capture the temporal fluctuations in the bird community as deforestation of tropical dry forest continues and as vegetation recovers from hurricane damage in the study area. Thus, long-term studies focused on the impacts of different agricultural activities in the Neotropics are essential to understand how birds cope with human-caused vegetation disturbance and how bird communities in human-modified landscapes respond to hurricane disturbance.

*Responses to this article can be read online at:*  
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**Appendix 1.** Table A1.1. List of bird species and relative abundances found at tropical dry forest (TDF), tree orchards (TO), cattle pasture (CP), and crop fields (CF). Main foraging guild categories and endemism are provided for each species. †Endemism: ‡Endemic to Mexico, ††Quasi-endemic to Mexico, †††Semi-endemic to Mexico (sensu González-García and Gómez de Silva 2003).

Scientific name†	English Common Name	Feeding Guild	TDF	TO	CP	CF
<i>Ortalis poliocephala</i> ‡	West Mexican Chachalaca	Frugivore	0.019	0.022		
<i>Streptopelia decaocto</i>	Eurasian Collared-Dove	Granivore		0.015		
<i>Columbina inca</i>	Inca Dove	Granivore		0.052	0.139	0.034
<i>Columbina passerina</i>	Common Ground Dove	Granivore		0.03		0.051
<i>Columbina talpacoti</i>	Ruddy Ground Dove	Granivore	0.01	0.045	0.209	0.161
<i>Geotrygon montana</i>	Ruddy Quail-Dove	Granivore		0.007		
<i>Leptotila verreauxi</i>	White-tipped Dove	Granivore	0.019	0.015		
<i>Zenaida asiatica</i>	White-winged Dove	Granivore		0.007		0.034
<i>Crotophaga sulcirostris</i>	Groove-billed Ani	Insectivore		0.022	0.113	
<i>Chordeiles acutipennis</i>	Lesser Nighthawk	Insectivore				0.008
<i>Chlorostilbon auriceps</i> ‡	Golden-crowned Emerald	Nectarivore	0.038			
<i>Amazilia rutila</i>	Cinnamon Hummingbird	Nectarivore	0.058	0.007	0.009	
<i>Amazilia violiceps</i> †††	Violet-crowned Hummingbird	Nectarivore			0.009	
<i>Nyctanassa violacea</i>	Yellow-crowned Night-Heron	Insectivore		0.007		
<i>Coragyps atratus</i>	Black Vulture	Scavenger		0.007		
<i>Cathartes aura</i>	Turkey Vulture	Scavenger			0.009	0.008
<i>Trogon citreolus</i> ‡	Citreoline Trogon	Frugivore	0.01			
<i>Melanerpes chrysogenys</i> ‡	Golden-cheeked Woodpecker	Insectivore	0.01	0.022	0.009	
<i>Eupsittula canicularis</i>	Orange-fronted Parakeet	Granivore	0.01			
<i>Xiphorhynchus flavigaster</i>	Ivory-billed Woodcreeper	Insectivore	0.01			
<i>Camptostoma imberbe</i>	Northern Beardless-Tyrannulet	Insectivore	0.01			
<i>Myiopagis viridicata</i>	Greenish Elaenia	Insectivore	0.019			
<i>Myiarchus tuberculifer</i>	Dusky-capped Flycatcher	Insectivore	0.01			
<i>Myiarchus tyrannulus</i>	Brown-crested Flycatcher	Insectivore	0.029			
<i>Deltarhynchus flammulatus</i> ‡	Flammulated Flycatcher	Insectivore	0.019			
<i>Pitangus sulphuratus</i>	Great Kiskadee	Insectivore		0.007		
<i>Myiozetetes similis</i>	Social Flycatcher	Insectivore			0.009	
<i>Tyrannus melancholicus</i>	Tropical Kingbird	Insectivore		0.015	0.009	0.042

<i>Empidonax minimus</i>	Least Flycatcher	Insectivore				0.017
<i>Empidonax occidentalis</i> ‡‡‡	Cordilleran Flycatcher	Insectivore	0.01			
<i>Empidonax difficilis/occidentalis</i>	Western Flycatcher	Insectivore	0.01			
<i>Vireo hypochryseus</i> ‡	Golden Vireo	Insectivore	0.019			
<i>Vireo bellii</i>	Bell's Vireo	Insectivore				0.009
<i>Vireo flavoviridis</i>	Yellow-green Vireo	Insectivore	0.048			
<i>Calocitta formosa</i>	White-throated Magpie-Jay	Omnivore				0.009
<i>Cyanocorax sanblasianus</i> ‡	San Blas Jay	Omnivore		0.022		
<i>Stelgidopteryx serripennis</i>	Northern Rough-winged Swallow	Insectivore				0.008
<i>Hirundo rustica</i>	Barn Swallow	Insectivore		0.03	0.043	0.042
<i>Pheugopedius felix</i> ‡	Happy Wren	Insectivore	0.019	0.007		
<i>Thryophilus sinaloa</i> ‡	Sinaloa Wren	Insectivore	0.077	0.037	0.009	
<i>Uropsila leucogastra</i> ‡‡	White-bellied Wren	Insectivore	0.067			
<i>Polioptila nigriceps</i> ‡	Black-capped Gnatcatcher	Insectivore	0.01	0.007		
<i>Turdus rufopalliatu</i> ‡‡	Rufous-backed Robin	Frugivore	0.01	0.119		0.017
<i>Melanotis caerulescens</i> ‡	Blue Mockingbird	Insectivore	0.01			
<i>Peucaea ruficauda</i>	Stripe-headed Sparrow	Granivore		0.052	0.113	0.051
<i>Arremonops rufivirgatus</i> ‡‡	Olive Sparrow	Granivore	0.067		0.026	
<i>Chondestes grammacus</i>	Lark Sparrow	Granivore			0.017	
<i>Cassiculus melanicterus</i> ‡‡	Yellow-winged Cacique	Omnivore	0.058	0.082		
<i>Icterus spurius</i>	Orchard Oriole	Omnivore		0.015		
<i>Icterus pustulatus</i>	Streak-backed Oriole	Omnivore	0.048	0.06	0.009	0.017
<i>Molothrus aeneus</i>	Bronzed Cowbird	Granivore	0.01	0.022	0.009	0.008
<i>Quiscalus mexicanus</i>	Great-tailed Grackle	Omnivore		0.022	0.043	0.008
<i>Setophaga pitaiayumi</i>	Tropical Parula	Insectivore	0.135			
<i>Setophaga petechia</i>	Yellow Warbler	Insectivore		0.097	0.017	
<i>Pheucticus chrysopheplus</i> ‡‡	Yellow Grosbeak	Omnivore	0.038	0.06		
<i>Granatellus venustus</i> ‡	Red-breasted Chat	Insectivore	0.038			
<i>Cyanocompsa parellina</i>	Blue Bunting	Granivore	0.048			
<i>Passerina caerulea</i>	Blue Grosbeak	Granivore		0.022		0.093
<i>Passerina cyanea</i>	Indigo Bunting	Granivore				0.008
<i>Passerina leclancherii</i> ‡	Orange-breasted Bunting	Granivore		0.007	0.043	0.025
<i>Volatinia jacarina</i>	Blue-black Grassquit	Granivore		0.037	0.078	0.364

<i>Sporophila torqueola</i> ‡	Cinnamon-rumped Seedeater	Granivore			0.026	0.008
<i>Sporophila minuta</i>	Ruddy-breasted Seedeater	Granivore			0.009	
<i>Saltator coerulescens</i>	Grayish Saltator	Frugivore	0.01	0.015	0.009	0.008

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