UNIVERSIDAD NACIONAL AUTÓNOMA DE MÉXICO
POSGRADO EN CIENCIAS BIOLÓGICAS
INSTITUTO DE BIOLOGÍA
ECOLOGÍA

DIVERSIDAD DE AVES EN UN PAISAJE ANTROPOGÉNICO EN LA VECINDAD DEL PARQUE NACIONAL PALENQUE, CHIAPAS, MÉXICO

TESIS

(**POR ARTÍCULO CIENTÍFICO**)
THE IMPORTANCE OF FOREST-NONFOREST TRANSITION ZONES FOR AVIAN CONSERVATION IN A VEGETATION DISTURBANCE GRADIENT IN THE NORTHERN NEOTROPICS

QUE PARA OPTAR POR EL GRADO DE:
MAESTRO EN CIENCIAS BIOLÓGICAS

PRESENTA:
DALLAS ROBERT LEVEY

TUTOR PRINCIPAL DE TESIS: **Dr. Jesús Alejandro Estrada Medina**
Instituto de Biología, UNAM
COMITÉ TUTOR: **Dra. Paula Lidia Enríquez**
Departamento Conservación de la Biodiversidad, ECOSUR
Dr. Adolfo Gerardo Navarro-Sigüenza
Facultad de Ciencias, UNAM

Ciudad Universitaria, CD. MX.,Abril, 2021

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ASUNTO: Oficio de Jurado

M. en C Ivonne Ramírez Wence
Directora General de Administración Escolar, UNAM

Presente

Me permito informar a usted que en la reunión ordinaria del Comité Académico del Posgrado en Ciencias Biológicas, celebrada el 1° de marzo del 2021, se aprobó el siguiente jurado para el examen de grado de **MAESTRO EN CIENCIAS BIOLÓGICAS** en el campo de conocimiento de **ECOLOGÍA** del alumno **LEVEY DALLAS ROBERT** con número de cuenta **519493933** por la modalidad de graduación de **tesis por artículo científico** titulado: **"The value of forest-nonforest transition zones for avian conservation in a vegetation disturbance gradient in the northern Neotropics"**, que es producto del proyecto realizado en la maestría que lleva por título: **"Diversidad de aves en un paisaje antropogénico en la vecindad del Parque Nacional Palenque, Chiapas, México"**, ambos realizados bajo la dirección del **DR. JESÚS ALEJANDRO ESTRADA MEDINA,** quedando integrado de la siguiente manera:

Presidente:	**DRA. KATHERINE RENTON**
Vocal:	**DR. LUIS DANIEL ÁVILA CABADILLA**
Vocal:	**DRA. EK DEL VAL DE GORTARI**
Vocal:	**DR. HERNÁN VÁZQUEZ MIRANDA**
Secretario:	**DR. ADOLFO GERARDO NAVARRO SIGÜENZA**

Sin otro particular, me es grato enviarle un cordial saludo.

ATENTAMENTE
"POR MI RAZA HABLARÁ EL ESPÍRITU"
Cd. Universitaria, Cd. Mx., a 15 de abril de 2021

COORDINADOR DEL PROGRAMA

DR. ADOLFO GERARDO NAVARRO SIGÜENZA

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RESUMEN

La pérdida de selva tropical como resultado de las actividades humanas representa una amenaza para las reservas de hábitat nativo o áreas naturales protegidas que restan en el mundo, lo cual presenta desafíos para las comunidades de vida silvestre. La mayoría de las comunidades de aves dependen de la estructura y composición de la vegetación nativa que les permite reproducirse y alimentarse exitosamente. Cuando las actividades humanas, tales como las actividades agrícolas y la expansión de las áreas urbanas, interrumpen la estructura y composición de la vegetación, las comunidades de aves silvestres se ven obligadas a ajustarse a los nuevos factores bióticos y abióticos de su entorno o a dispersarse hacia áreas menos afectadas. Esto destaca la importancia de la conectividad en los paisajes tropicales y la calidad de la matriz transformada, especialmente cuando se encuentra cerca de reservas grandes de selva primaria, ya que estos factores influyen en las tendencias de biodiversidad de las metacomunidades. El manejo adecuado de la matriz transformada que rodea selvas primarias puede favorecer a la conservación de la biodiversidad; sin embargo, las áreas con un manejo deficiente necesitan atención para determinar su viabilidad para sustentar a la biodiversidad nativa a largo plazo. Examiné las variaciones en la diversidad de especies, diversidad funcional y la composición comunitaria de aves utilizando puntos de conteo colocados a lo largo de un gradiente de perturbación humana en Palenque, Chiapas, México. Dividí el paisaje a lo largo del gradiente en tres áreas: preservada (PRES), de transición (TRA) y perturbada (DIS) según el porcentaje de cobertura de selva primaria y secundaria y pastizales para ganado. Predije que el gradiente de perturbación humana influiría en el intercambio de aves especialistas de selva por aves especialistas de áreas abiertas de PRES a DIS, lo que resultaría en: (1) la ausencia de cambios netos en la diversidad de especies, (2) un decremento en la diversidad funcional y (3) en composiciones comunitarias únicas para cada área. Detecté un total de 228 especies de aves durante un período de ocho meses. TRA presentó una composición de comunidad con aspectos compartidos de las comunidades PRES y DIS, conduciendo a la mayor diversidad funcional de Shannon (85,8 especies estimadas) y de Simpson (57,9 especies estimadas). El reemplazo de aves especialistas de selva por aves especialistas de áreas abiertas en TRA y DIS dio lugar a cambios en los rasgos funcionales y diferentes composiciones comunitarias en relación con PRES. Las estrategias de conservación que disminuyan el contraste entre

las matrices agrícolas con los parches de selva remanente en TRA y DIS son necesarias para evitar más pérdidas de especies y servicios ambientales en PRES y un mayor distanciamiento entre las composiciones de las comunidades locales. Estas acciones deben incluir la preservación e implementación de corredores de vegetación nativa que conecten parches remanentes y aumenten la complejidad de los contextos agrícolas.

ABSTRACT

Native tropical forest loss as a result of human activities threatens the world's remaining stands of tropical conserved land, presenting challenges for wildlife communities and the conservation of native biodiversity. Most terrestrial animal communities are dependent upon native vegetation structure and composition for resources that allow successful reproduction and foraging; when human activities, such as agricultural activities and urban expansion, disrupt vegetation structure and composition, wildlife communities are forced either to acclimate to novel biotic and abiotic factors in their environment or disperse to less impacted areas. This places importance on tropical landscape connectivity and matrix quality near large stands of primary forest, which are important factors that dictate biodiversity trends in metacommunities. 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 biodiversity. I examined the variations in species and functional diversity and community composition using point-count surveys placed along a human disturbance gradient in the northern Neotropics. I divided the study landscape into preserved (PRES), transition (TRA), and disturbed (DIS) areas along the gradient according to percent land cover of forest and cattle pasture. I expected the gradient of human disturbance to drive the exchange of forest specialists for open-area specialists from PRES to DIS, resulting in: (1) no net changes in species diversity, (2) decreasing functional diversity, and (3) unique community compositions for each local community. I detected 228 species overall during an 8-month period. TRA supported an avian community with shared compositional aspects of communities PRES and DIS, leading to the highest functional and Shannon (85.8 estimated species) and Simpson (57.9 estimated species) diversity. The replacement of forest specialists by open area specialists in TRA and DIS has led to shifts in functional traits and different community compositions relative to PRES. Conservation strategies that work to decrease the contrast of agricultural matrices with remnant forest patches in TRA and DIS are necessary to prevent further species and ecosystem service loss from PRES and further distancing of local community compositions. These actions should include the preservation and implementation of native vegetation corridors that connect remnant patches and increase the complexity of agricultural contexts.

INTRODUCCIÓN GENERAL

La deforestación de los paisajes tropicales para la expansión de la agricultura, pastizales y plantaciones arbóreas y no arbóreas ha resultado en la pérdida de hábitat para muchas especies (Haddad et al., 2015; Kremen y Merenlender, 2018). Una de las mayores amenazas para la biodiversidad es la pérdida de hábitat, ya que resulta en la reducción del tamaño de las poblaciones, incrementa el riesgo de extirpación y extinción de diversas especies (Feeley y Terborgh, 2008) y permite el recambio de especies nativas con especies que se especializan en áreas perturbadas (Dornelas et al., 2014). Estos procesos se desarrollan a partir de cambios drásticos en los paisajes naturales, incluyendo el desarrollo de un matriz de vegetación distinta al hábitat original (Wethered y Lawes, 2003; Herrera, 2011) y la formación de fragmentos de selva aislados (Buelow et al., 2017; Fahrig, 2002; Mayhew et al., 2019). Este cambio en el uso de suelo y sus consecuencias son clave en países tropicales, los cuales destinan hasta el 80% de su área terrestre para actividades agrícolas y contienen ~70% de las especies en el mundo (Şekercioğlu et al., 2019). Por lo tanto, es importante entender los efectos de la pérdida de hábitat y cambio de uso de suelo en la biodiversidad de los países tropicales.

Existen varios factores que necesitan ser investigados para entender cómo la flora y fauna silvestre responderán a los cambios en el paisaje. En áreas perturbadas, el paisaje se compone típicamente de un mosaico de hábitat, con diferentes escalas de daño y sucesión con respecto a la vegetación original (Herrera, 2011). La matriz en áreas perturbadas realiza una función crucial en el mantenimiento (Herrera, 2011) y cambio en la estructura comunitaria (Dornelas et al., 2014), incluyendo servir como paso para el movimiento animal entre parches restantes de hábitat (Estrada y Coates-Estrada, 2005), hábitat nuevo para especies nativas (Herrera, 2011) e invasoras (MacGregor-Fors et al., 2009) y la preservación de funciones ecológicas como la dispersión de semillas y depredación (Şekercioğlu et al., 2007).

Las comunidades de aves Neotropicales enfrentan fuertes presiones debido al cambio de uso de suelo y la expansión de entornos urbanos homogéneos. Las especies de aves que dependen de áreas grandes de selva conservada están en mayor riesgo debido al aislamiento y degradación de las reservas de selva restantes. La deforestación destinada para la expansión de la agricultura y desarrollo urbano (p. ej. carreteras, casas, vías de tren y aeropuertos) presenta un riego significante de mortalidad para los animales terrestres, además de introducir ruido antropogénico (Jack et al., 2015). Las especies de aves con requisitos altamente especializados de hábitat y recursos (p. ej. insectívoros del sotobosque de selva primaria) son las más afectadas por los cambios en las condiciones abióticas, generalmente resultando en la disminución de sus poblaciones y extirpación (Şekercioğlu et al., 2002). Además, la expansión de las actividades humanas resulta en un mayor contacto entre la vida silvestre y los humanos, lo que genera impactos directos como un aumento de la caza e impactos indirectos como la exposición a animales domésticos o ferales (p. ej. perros y gatos domésticos; Patterson et al., 2016).

Los fragmentos de selva remanente también juegan un papel importante en la persistencia de la flora y fauna de las áreas perturbadas. El valor de conservación de los fragmentos de selva se debe a diversas características funcionales como su tamaño (Bovo et al., 2018), su conectividad con otros fragmentos (Mayhew et al., 2019) y la cantidad de borde expuesto a la matriz del paisaje antropogénico (Ferraz et al., 2007; Haddad et al., 2015). También es importante considerar la alteración del hábitat, es decir, la alteración en la estructura y composición de la vegetación que las especies usan para la dispersión, forrajeo, anidación y protección (Alexandrino et al., 2017; Doherty y Driscoll, 2018). Los efectos de borde, como el tamaño del borde, aumento de luz y calor, daño provocado por el viento y la introducción de depredadores pueden cambiar la composición de flora y fauna en los fragmentos de selva (Haddad et al., 2015). Finalmente, la protección local y federal pueden influir en la biodiversidad, ya que las actividades humanas tales como la cacería y el comercio ilegal de aves pueden alterar el tamaño y estructura de sus poblaciones en cada hábitat selvático (Sodhi et al., 2004; Tucker et al., 2018), incluyendo los fragmentos de selva de varios tamaños (Peres, 2001).

Los países neotropicales preocupados por la vulnerabilidad de la flora y fauna silvestre han tomado medidas de protección, incluyendo el establecimiento de áreas naturales protegidas (ANP). En 2020, 14% del territorio en México estaba bajo protección legal (UNEP-WCMC, 2020). Desafortunadamente, hay espacios vacíos en el conocimiento acerca de la salud de las ANP (Gaston et al., 2008) y aspectos asociados con la eficacia de estas (Laurance et al., 2012). Además, muchas ANPs no cuentan con fondos, personal, ni planes de manejo adecuados para combatir problemas de aislamiento y degradación, haciendo que la planificación para su conservación se vuelva más difícil (Chape et al., 2005). Para medir y mantener la biodiversidad en las ANP, las matrices que se encuentran a su alrededor necesitan ser consideradas ya que afectan la conectividad estructural y funcional de las zonas protegidas (Fahrig et al. 2011; Herrera 2011). Esto destaca la necesidad de estudiar los paisajes alrededor de las ANP para aumentar el éxito de los esfuerzos de conservación (Buelow et al., 2017; Mayhew et al. 2019; Tobias et al., 2013).

A menudo, las comunidades de aves son utilizadas por ecólogos que evalúan la condición de las áreas naturales debido a que estos animales responden al proceso de perturbación de acuerdo con los requisitos de su hábitat, dieta y su capacidad de dispersión (Alexandrino et al., 2017; Wielstra et al., 2011). Sus respuestas a la perturbación humana nos permiten monitorear las dinámicas ecológicas de los fragmentos de selva y el paisaje en áreas perturbadas (Alexandrino et al., 2017; Bregman et al., 2016; Tobias et al., 2013). Con el fin de evaluar los impactos de la expansión de las actividades humanas en las comunidades de aves neotropicales, generalmente se estudia su estructura, composición, diversidad de especies y funcional, riqueza estimada y abundancia de especies para comparar áreas con altos niveles de perturbación humana con áreas con menor perturbación.

La estructura comunitaria proporciona información acerca del estado de las especies que la integran a través de la comparación de sus abundancias. Usando las especies dominantes y raras, así como sus historias naturales, se pueden hacer inferencias sobre cómo las condiciones ambientales y el nivel de perturbación humana afectan la abundancia de cada especie. Comparar la composición comunitaria permite evaluar el recambio de especies como resultado del cambio de uso de suelo. Asimismo, la abundancia de cada especie de ave y gremio de forrajeo permite hacer inferencias sobre la distancia que existe entre las comunidades y si el distanciamiento de la composición de especies se refleja en la composición funcional de la comunidad. La comparación de la riqueza estimada de especies y la abundancia relativa permite evaluar la calidad del hábitat y la heterogeneidad de la estructura de la vegetación en escala de hábitat y de paisaje. Las áreas con menor riqueza de especies probablemente contienen menor estructura y composición de la vegetación, así como niveles de perturbación más altos (p. ej., el ruido y la presencia humana; Mills et al., 1991).

La evaluación de las tendencias de diversidad funcional de las comunidades de aves proporciona información valiosa sobre cómo los gremios de forrajeo y las aves de ciertas masas corporales, capacidades de dispersión y amplitud de hábitat responden a la pérdida de selva como resultado de la perturbación humana. Las aves realizan funciones ecológicas importantes, incluyendo dispersión de semillas, polinización de plantas y control de plagas y/o especies invasoras (Şekercioğlu et al., 2015; Wielstra et al., 2011). El uso de los gremios de forrajeo proporciona un modelo útil para inferir procesos biológicos en áreas perturbadas debido a que la dieta de las aves está relacionada con su nicho ecológico (Kissling et al., 2012). Finalmente, la importancia cultural de las aves representada en a través de historias de aves emblemáticas (p. ej., *Ara macao* y *Pharomachrus mocinno* en Chiapas, México) ayudan a definir la cultura y sentido de pertenencia. Aparte de su valor ecológico y cultural intrínseco, la protección de las aves y la conservación de su hábitat se ha convertido en una economía viable (Şekercioğlu, 2002) y gratificante para la gente local de algunas áreas tropicales (p. ej., Costa Rica; Şekercioğlu, 2004).

Usar grupos funcionales permite determinar los efectos de la perturbación humana a través de la evaluación de la susceptibilidad de las comunidades de aves ante cambios en su ambiente. Por ejemplo, los frugívoros, granívoros e insectívoros son más vulnerables a los cambios del paisaje que los carnívoros y omnívoros, y las aves con mayor capacidad de dispersión pueden persistir en fragmentos de selva pequeños, contrario a las aves sedentarias (Castaño-Villa y Patiño-Zabala, 2008; Tobias et al., 2013). Los frugívoros grandes requieren áreas selváticas grandes y con alta conectividad (Bovo et al., 2018), mientras que los insectívoros pequeños del sotobosque son sensibles al proceso de fragmentación y aislamiento debido al su inhabilidad de colonizar o desplazarse a través de hábitats deforestados (Şekercioğlu et al., 2002). La presencia o ausencia de ciertos grupos de aves puede indicar el estado de alteración del ecosistema y proveer información vital para los esfuerzos de conservación (Alexandrino et al., 2017).

La porción noreste del estado de Chiapas contiene el segmento más norteño de la selva Lacandona (25% de la biodiversidad de México; Medellín, 1994), donde se encuentra el Parque Nacional Palenque (PNP). Desde la década de 1970, la selva Lacandona se ha ido perdiendo a un ritmo de 3.5-12.4% cada año y el paisaje ha sufrido transformaciones continuas por los humanos (Patten et al., 2009). Actualmente, el PNP es una isla de selva desconectada de la selva Lacandona debido a la conversión de la selva original a pastizales y plantaciones de aceite de palma, hule y otros cultivos. En el paisaje en donde se ubica el PNP también se presentan fragmentos de selva y corredores de la vegetación original (Estrada et al., 2002; Patten et al., 2011; Fig. 1). Debido al desarrollo del turismo arqueológico en el PNP desde hace varias décadas, algunos fragmentos de selva ubicados en la parte oriental del PNP han sido conservados al ser propiedad de hoteles o campamentos turísticos privados. Otros fragmentos de selva no tienen este tipo de protección al encontrarse en áreas dedicadas a la cría de ganado, plantaciones o agricultura de subsistencia. La carretera que conecta a la ciudad de Palenque con el PNP representa otra forma importante de perturbación humana, ya que continúa hasta la entrada del sitio arqueológico, generando una fuente de ruido constante, tráfico y peligro para la fauna silvestre que intenta cruzar (Jack et al., 2015).

Los inventarios de aves más recientes (10 años atrás) para el PNP reportan 353 especies, de las cuales 57.2% son residentes y 24.6% son migratorias neotropicales (Patten et al., 2011). Este inventario puede considerarse incompleto ya que los datos están mayormente basados en conteos históricos y en un estudio corto (~50 días). Todavía no existe información acerca de las aves que se encuentran en el paisaje antropogénico en la vecindad del PNP, por lo que su implementación es importante para favorecer la conservación de las poblaciones de las aves que residen en el paisaje (Laurance et al., 2012). Como ejemplo de esto, entre junio y diciembre de 2017 realicé sondeos preliminares en el PNP y en 7 fragmentos de selva en su vecindad, resultando en la detección de 254 especies (73% residentes, 27% migratorias neotropicales), de las cuales 22% fueron únicas del PNP, 27% únicas a los fragmentos de selva y 51% fueron encontradas en ambos. Esto sugiere la probabilidad de que la presencia de los fragmentos y corredores de selva en combinación con el PNP favorezcan la conservación de una alta diversidad de especies de aves residentes y migratorias en el paisaje donde se ubica el PNP.

El objetivo general de este estudio fue evaluar durante un periodo de 8 meses, las especies de aves presentes en el PNP y en un paisaje antropogénico ubicado al este del PNP y en dirección al poblado de Palenque. Para lograr esto, usamos 39 puntos de conteo abarcando un área de aproximadamente 318 ha. Desde el punto de vista de la conservación, intentamos evaluar el valor de la vegetación selvática remanente y de otros tipos de vegetación en el paisaje que sustenta a las poblaciones de aves existentes. Hasta la fecha no existen estudios sistemáticos sobre la estructura y composición de la comunidad de aves en el PNP ni en el paisaje antropogénico indicado. Por lo tanto, nuestro estudio proveerá información novedosa y crítica sobre el valor del PNP, de los fragmentos de selva y corredores cercanos para la conservación a largo plazo de las especies de aves en el paisaje de Palenque. Adicionalmente, la información puede ser de interés social y motivar a los pobladores y al gobierno local para preservar los fragmentos de selva y corredores de vegetación original remanentes en el paisaje. Asimismo, con esta investigación y con el uso de datos de ciencia ciudadana, el gobierno local y CONANP contarán con una lista actualizada de especies de aves que podrán usar para arrancar programas de aviturismo en el área, lo que traerá beneficios financieros y un papel inherente para la conservación de las áreas naturales (Şekercioğlu, 2002). Esto aumentará el valor social de la conservación de la diversidad de aves en el área y al mismo tiempo contribuirá al sustento de la gente local a través del turismo ecológico.

CAPÍTULO 1

The importance of forest-nonforest transition zones for avian conservation in a vegetation disturbance gradient in the northern Neotropics

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

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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).

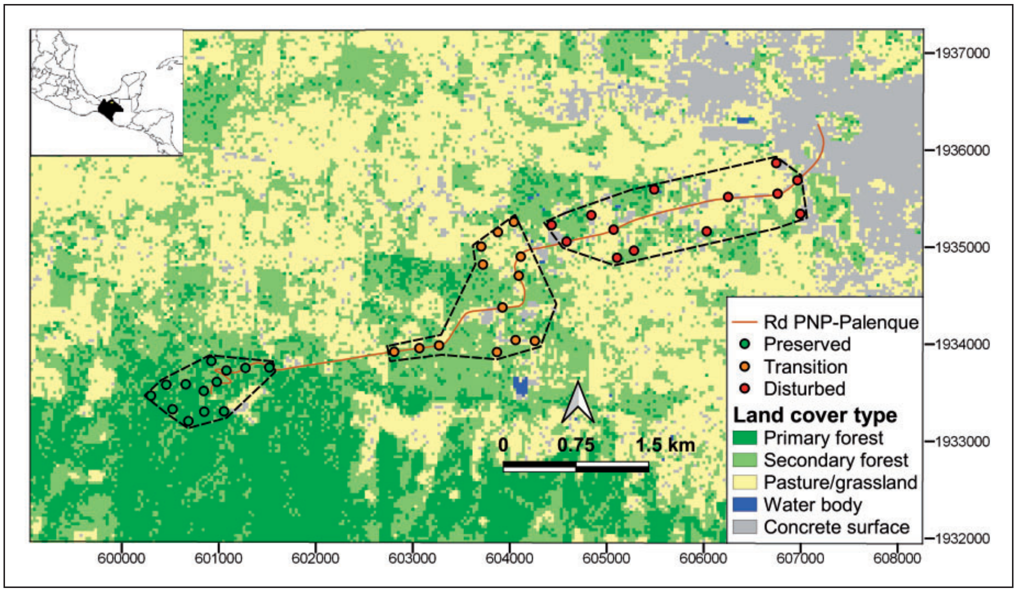

Figure 1. Map of land cover types in the study area. Land cover types were assigned to Landsat 8 remote sensing images from 2018—2019. Individual point-counts are represented by colored circles, and the three areas along the vegetation disturbance gradient are represented by polygons. Each polygon is 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 ± 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

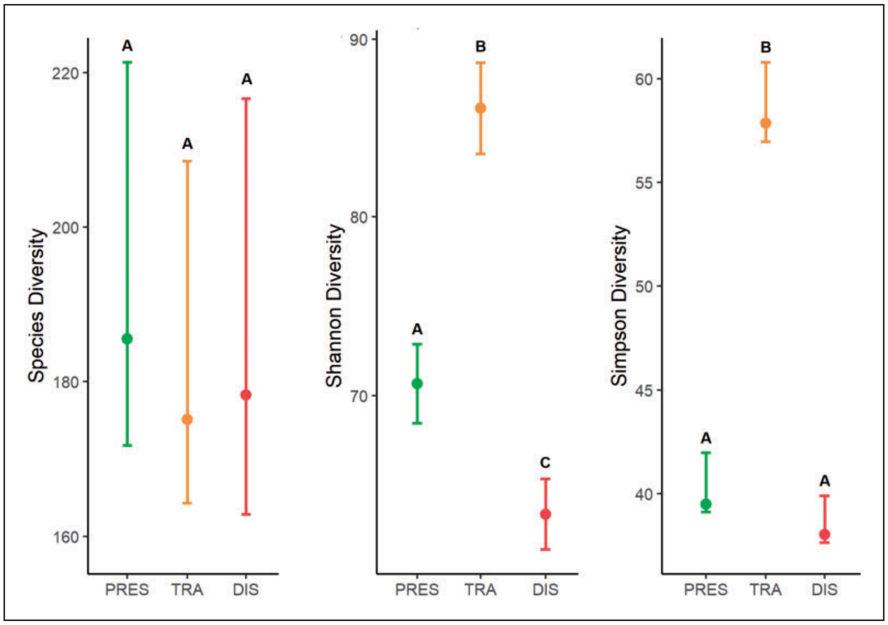

Figure 2. Patterns of estimated species diversity for overall species, Shannon, and Simpson diversity. Letters above confidence interval whiskers represent significant differences among avian communities. PRES = preserved, TRA = transition, DIS = disturbed.

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

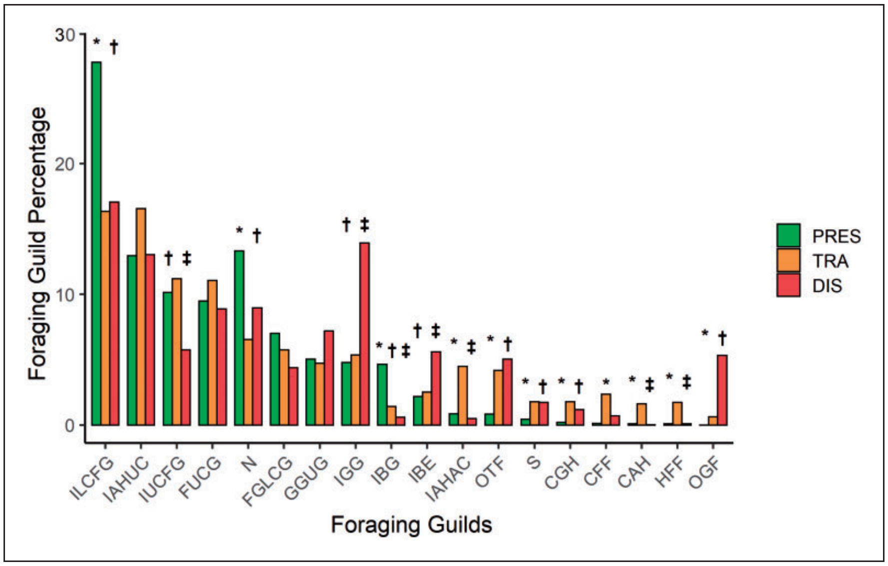

Figure 3. Percentages of foraging guild abundance in PRES (preserved), TRA (transition), and DIS (disturbed). Bird species were assigned to one of the following foraging guilds. ILCFG: insectivore—lower canopy foliage gleaner, IAHUC: insectivore—air-hawker under canopy, IUCFG: insectivore—under canopy 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

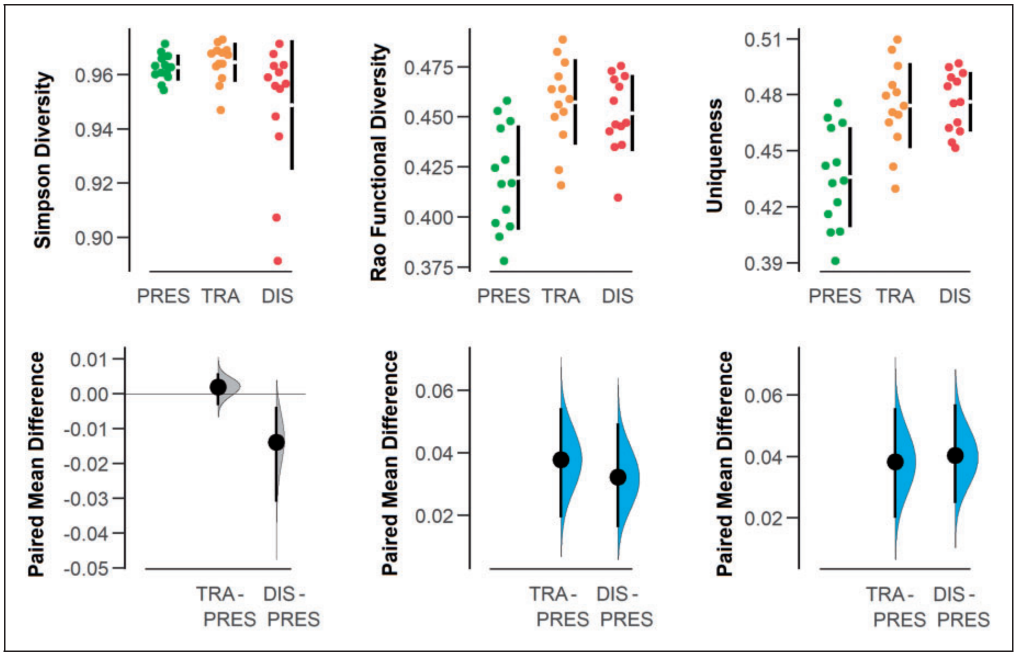

Figure 4. Patterns and paired mean differences of diversity indices Simpson, Rao, and Uniqueness in the preserved (PRES), transition (TRA), and disturbed (DIS) local communities. The colored dots represent the point-count locations for each local community, and the black vertical bar and break in the 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

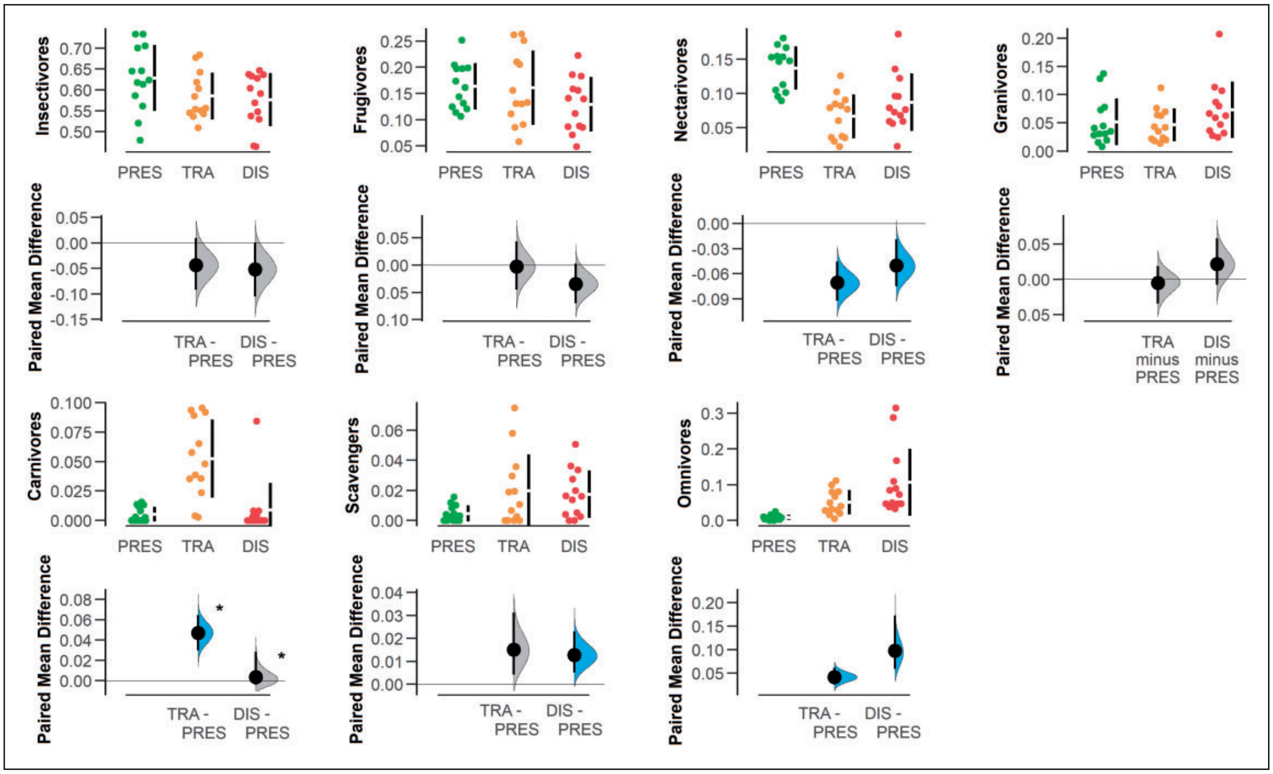

Figure 5. Patterns and paired mean differences of foraging items in the preserved (PRES), transition (TRA), and disturbed (DIS) local communities. The colored dots represent the point-count locations of each local community, and the black vertical bar and break in the vertical bar represent the 95% confidence 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*

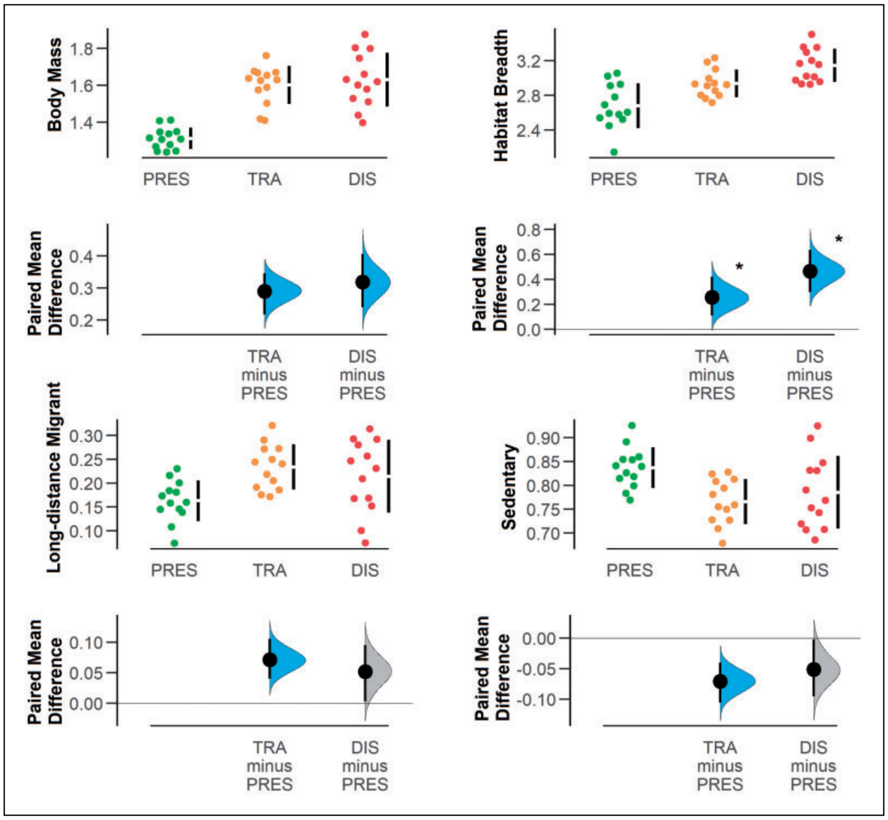

Figure 6. Patterns and paired mean differences of functional traits in the preserved (PRES), transition (TRA), and disturbed (DIS) local communities. The colored dots represent the point-count locations of each local community, and the black vertical bar and break in the vertical bar represent the 95% 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

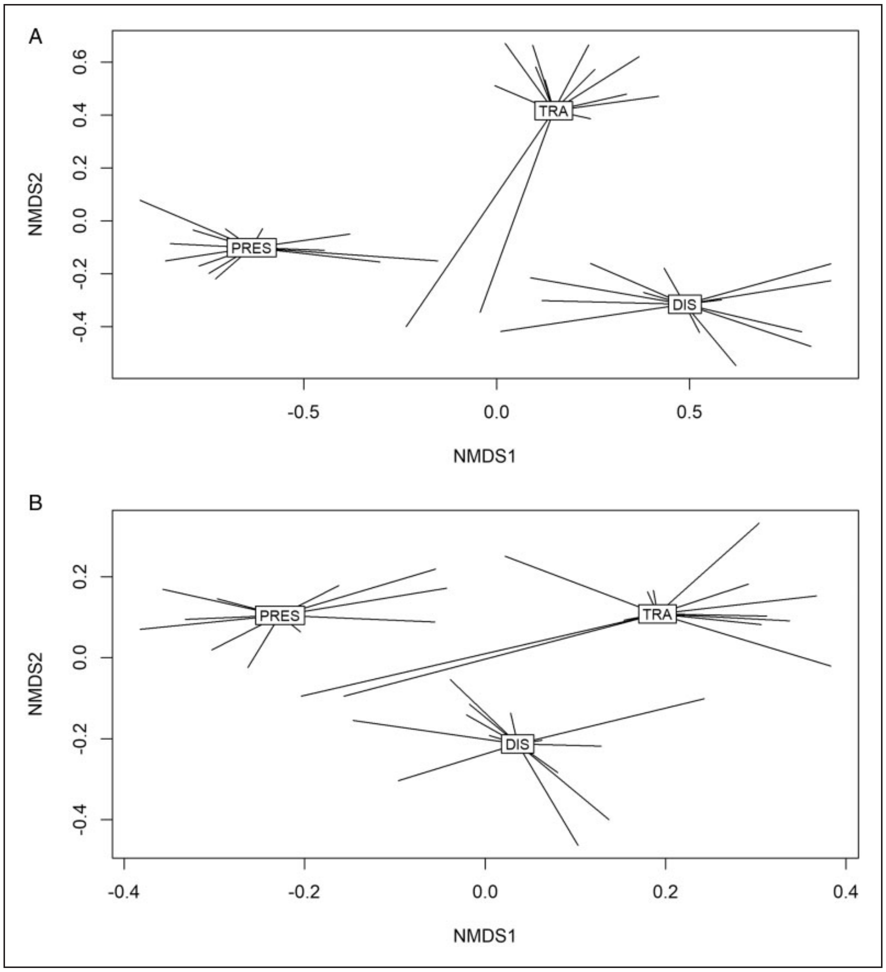

Figure 7. Non-Metric Dimensional Scaling (NMDS) plot of (A) species and (B) foraging guild diversity in each local community. Point-count locations are represented at the ends of lines extending from text boxes with community names. PRES = preserved, TRA = transition, DIS = disturbed.

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).

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Data Accessibility Statement

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

Declaration of Conflicting Interests

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Supplemental Material

Supplemental material for this article is available online.

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DISCUSIÓN GENERAL

La conversión de selva a zonas agrícolas y urbanas representa un desafío clave para las comunidades de vida silvestre. Las áreas con alta biodiversidad, como el Neotrópico, actualmente están en riesgo debido a la creciente demanda humana de recursos naturales y espacio para el desarrollo (Estrada et al., 2019). Debido a la alteración de la vegetación y el paisaje, las regiones biodiversas han sido aisladas y degradadas, resultando en un cambio en las características a nivel de la comunidad, como la riqueza de especies, estructura y composición. Como resultado de los cambios en las características de las comunidades, los servicios ambientales que proveen las especies pueden perderse, generando repercusiones para la gente local. Los resultados destacan las diferencias al nivel de comunidad a lo largo de un gradiente de perturbación humana y de vegetación en Palenque, Chiapas, México.

El área con los niveles de perturbación humana intermedia (área de transición TRA) presentó la diversidad de Simpson y de Rao más alta debido a la presencia de la mayoría de las especies de aves dominantes y comunes de ambas áreas en los extremos del gradiente de perturbación (el área conservada PRES y el área perturbada DIS). Esta tendencia tiene similitud con la hipótesis de disturbio intermedia, donde los niveles intermedios de disturbio conllevan niveles de diversidad más altas a lo largo de gradientes de perturbación (Connell, 1976).

Cada comunidad local fue distinta en composición de diversidad de especies y funcional, destacando el recambio de especies de aves en el área de estudio. Los rasgos funcionales de cada comunidad cambiaron a lo largo del gradiente de perturbación hacia especies más grandes, con mejor capacidad de dispersarse, y más gremios de forrajeo especializados en áreas abiertas (granívoros, omnívoros y carroñeros). Por lo anterior, los servicios ecosistémicos proporcionados por las especies de aves de cada comunidad local no se conservan, destacando las implicaciones de la pérdida de especies de aves de selva tropical (insectívoros pequeños del sotobosque, nectarívoros y frugívoros). La pérdida de hábitat incesante lleva a un aumento en el recambio de especies que pone en duda la conservación a largo plazo de las especies de aves y los servicios ambientales que brindan. Por esta razón, la conservación a largo plazo de las comunidades locales de aves del Parque Nacional Palenque y las áreas alrededores dependerán de la implementación de estrategias enérgicas de gestión de la tierra dedicadas a la conservación de las áreas selváticas alrededor del Parque Nacional Palenque.

Las tendencias en las características de las comunidades de aves a lo largo del gradiente de perturbación se reflejaron en la proporción de los tipos de cobertura de suelo (p. ej. selva tropical y pastizales introducidos para el ganado). En DIS, donde el pastizal introducido es la cobertura dominante, la comunidad de aves presentó los valores más bajos del índice de Simpson en relación con PRES y TRA. La comunidad de aves estaba dominada por aves especialistas de áreas abiertas, las cuales tienen la capacidad de resistir condiciones abióticas más extremas (p. ej. temperatura alta y aumento de luz solar) y usar vegetación con estructura y composición homogénea (Williams et al. 2020). Por ejemplo, DIS presentó abundancias más altas de insectívoros que forrajean en el suelo (*Turdus grayi*), omnívoros (*Quiscalus mexicanus*) y granívoros (*Volatinia jacarina* y *Columbina talpacoti*). Además, DIS proporcionó hábitat para una diversidad alta de especies migratorias (*Setophaga magnolia* e *Icterus spurius*), reflejando una tendencia observada en la que muchas especies de aves migratorias ocupan frecuentemente las áreas perturbadas y abiertas en el Neotrópico (McDermott et al. 2015). Los fragmentos remanentes de selva secundaria presentaron una riqueza alta de especies, ya que contuvieron puntos de conteo con los valores de diversidad taxonómica y funcional más altos de todo el paisaje. Las aves especialistas de selva secundaria estuvieron presentes en DIS, incluyendo el granívoro del suelo *Geotrygon montana* y el insectívoro del sotobosque *Habia fuscicauda*. Sin embargo, la selva secundaria en DIS está fragmentada y degradada, presentando abundancias relativamente bajas de un amplio rango de gremios de forrajeo (p. ej. insectívoros que forrajean en la corteza de los árboles y en la parte inferior y superior del dosel) que son comunes en PRES, generando una composición única de diversidad funcional.

TRA presentó una comunidad de aves con cualidades compartidas de PRES y DIS. Así mismo, presentó la riqueza de especies más alta de las especies dominantes y comunes que ocurren en todo el paisaje del estudio debido a la mezcla de selva secundaria conservada con baja presencia humana y hábitat abierto como pastizales introducidos para ganado. TRA presentó la mayor proporción de selva secundaria entre los extremos del gradiente de perturbación, lo que da lugar a una gran diversidad de especies que prosperan en la selva tropical. Además, la presencia de los pastizales introducidos atrajo aves especialistas residentes de áreas abiertas (*Icterus cucllatus* y *Tyrannus melancholicus*) y especies migratorias que prefieren hábitat abierto (*Vireo griseus* y *Dumetella carolinensis*). Es probable que la proximidad y conectividad de TRA con PRES y DIS permitiera la migración local de aves hacia TRA (Mayhew et al., 2019). La conectividad con PRES y DIS y la mezcla de tipos de cobertura de suelo en TRA son los posibles factores que atrajeron un rango amplio de especies de aves y gremios de forrajeo, causando una alta diversidad de especies y funcional. Estas características de TRA representan un valor de conservación alto al brindar recursos importantes para las especies de aves en riesgo de extirpación en el paisaje bajo estudio.

PRES presentó una comunidad de aves típica de las comunidades de aves conservadas del Neotrópico (p. ej. las áreas de selva tropical de la selva Lacandona; Patten et al., 2011). Las especies de aves comunes en PRES fueron especialistas de selva, las cuales utilizaron las características estructurales distintivas de selva primaria, incluyendo el suelo sombreado (*Crypturellus boucardi*, *Formicarius analis* y *Basileuterus culicivorus*) y el sotobosque denso (*Cercomacroides tyrannina* y *Henicorhina leucosticta*). Los insectívoros que forrajean en la corteza de los árboles (*Dendrocolaptes sanctithomae* y *Dendrocincla anabatina*) y que excavan la corteza (*Celeus castaneus* y *Dryobates fumigatus*) fueron más diversos y con mayores abundancias en PRES, relativo a TRA y DIS. Las especies de aves de dichos gremios de forrajeo generalmente prosperan en áreas donde la diversidad de especies de árboles es alta y la estructura de la vegetación es compleja (Kang et al. 2015), lo cual explica por qué esos gremios no están presentes en la selva secundaria joven y en las áreas agrícolas de TRA y DIS. Otras especies comunes de PRES fueron encontradas en menor número en TRA y DIS, incluyendo los insectívoros del dosel superior *Pachysylvia decurtata* y *Ornithion semifalvum*. Además, las diferencias drásticas en la estructura y composición de la vegetación entre PRES, TRA, y DIS ocasionaron que algunas especies de aves se localizaran únicamente en pequeñas áreas del paisaje de estudio. En general, 40 especies fueron encontradas solo en PRES, mientras que 20 y 9 fueron encontradas solo en TRA y DIS, respectivamente. La mayoría de las especies exclusivas en PRES fueron especialistas de selva, las cuales tienen requisitos de recursos y hábitat altamente específicos con una baja capacidad de dispersión (p. ej. el insectívoro del sotobosque *Xenops minutus*; Şekercioğlu et al., 2004). Con el tiempo, el aislamiento de PRES de TRA y DIS ha disminuido la probabilidad de que las aves especialistas de selva puedan dispersarse hacia el hábitat fuera de PRES, originando poblaciones de aves aisladas y la extirpación de especies, resultando en por lo menos 26 especies de aves extirpadas hasta 2009 (Patten et al., 2009).

El área de Palenque requiere un rango diverso de medidas de conservación para detener la pérdida y recambio de especies en las áreas selváticas. Estas acciones son más necesarias en DIS debido al mal estado de los parches de selva secundaria y a las áreas agrícolas homogéneas que conforman la matriz del paisaje. DIS es la comunidad más disimilar a PRES, con más especies de aves que se encuentran frecuentemente en las áreas urbanas del Neotrópico norte. Un mayor número de especies de aves enigmáticas, como la guacamaya roja (*Ara macao*), el hocofaisán (*Crax rubra*) y el manaquín cabeza roja (*Ceratopipra mentalis*), se encuentran en TRA y especialmente en PRES, por lo que el turismo, que se concentra en mayor medida dentro del PNP, presenta fuertes presiones para la comunidad de aves (Chun et al., 2020). La medida más efectiva para la conservación de las aves y su hábitat en Palenque será combatir la deforestación (incluyendo la práctica común de “limpiar” los sotobosques de selva) en todas las áreas del paisaje, aunada a la recuperación de las áreas perturbadas mediante su regeneración natural. Para restaurar el hábitat en DIS y proporcionar áreas nativas que puedan restar presión turística del PNP (Chun et al., 2020) se debe reducir el contraste entre los pastizales introducidos y los parches de vegetación remanentes a través de la preservación de la vegetación nativa aislada dentro de los pastizales y la sucesión natural de la vegetación (Le Roux et al., 2018). Una mayor cobertura de selva y mayor conectividad de la vegetación en los pastizales tendrán impactos positivos en las especies de aves y en los gremios de forrajeo que dependen de la selva secundaria de alta calidad para anidar y forrajear (McDermott et al., 2015). El aumento de conectividad con TRA facilitará la dispersión local de aves en un rango amplio de especies y favorecerá un nivel de diversidad funcional mayor, así como más servicios ambientales en TRA y DIS. En TRA, el aumento de conectividad con PRES es una prioridad importante para disminuir el riesgo de extirpación de las especies de aves susceptibles al aislamiento y degradación de hábitat (Kang et al., 2015; Mayhew et al., 2019). Las selvas secundarias maduras de TRA deben ser protegidas de la extracción de recursos naturales, de manera que se reestablezca una zona de amortiguamiento de alta calidad alrededor de PRES que proporcione hábitat para anidar y forrajear para las especies de aves que son susceptibles a la perturbación del hábitat.

Para lograr estos objetivos de manejo del uso de suelo, los oficiales locales deben ser informados del estado actual de las comunidades de aves y el riesgo de que PRES siga perdiendo especies de aves si se permite que continúe la deforestación en el paisaje de Palenque.

Los numerosos problemas logísticos con la implementación de ese tipo de estrategia de manejo del uso del suelo pueden resolverse con una campaña informativa que presente los principales problemas que enfrentan las comunidades de aves locales de Palenque. Tales como las repercusiones socioeconómicas de la deforestación y pérdida de especies de aves para el turismo y producción agrícola, así como las acciones de conservación necesarias para preservar las comunidades de aves y selva tropical. Unos modelos exitosos ya existen en DIS, incluyendo un centro de rehabilitación de vida silvestre que conserva un parche grande de selva secundaria y un humedal en sus terrenos. Otros centros públicos afuera de PRES que atraigan al público mientras contribuyen activamente a la conservación de la vida silvestre en Palenque serán cruciales para la conservación a largo plazo de la avifauna y el PNP. La reintroducción de la guacamaya roja (*Ara macao*) representa una medida de conservación exitosa que ayuda en la campaña informativa sobre el valor de conservar el hábitat y de poner fin a prácticas ilegales como la caza y captura de aves (Estrada 2014; Amaya-Villarreal et al. 2015). Se debe alentar la participación local en el monitoreo de las comunidades de aves al largo plazo a través de la ciencia ciudadana (aVerAves y Naturalista) para involucrar al público en la conservación de la vida silvestre y comenzar el desarrollo del aviturismo (Şekercioğlu, 2002). El monitoreo de aves realizado por la gente local permitirá la detección de diferencias en las comunidades de aves durante pausas de la intensa actividad humana, como la "Anthropause" originada después de la pandemia COVID-19 (Rutz et al., 2020). Finalmente, se necesita reconsiderar el uso de la carretera que conecta Palenque con el PNP para una aplicación más estricta de los límites de velocidad y multas por tirar basura. No se debe permitir que el tráfico ingrese al área protegida del PNP mediante el uso de infraestructura ya disponible (estacionamiento y edificios de admisión al parque) diseñada para limitar el tráfico vehicular dentro del PNP. Será necesario trabajar con empresas de transporte locales para implementar tal cambio de uso de la carretera principal en Palenque.

CONCLUSIONES

1. La conversión de selva a pastizales introducidos para el ganado ha resultado en la pérdida de especies de aves especializadas en selva y en el aumento de especies de aves especialistas de áreas abiertas.
2. A lo largo de la gradiente de perturbación humana, la diversidad de especies y funcional fue mayor en el área de transición debido a una alta riqueza de especies comunes y dominantes que utilizan áreas abiertas y selva secundaria.
3. Los rasgos funcionales de las aves cambiaron a lo largo del gradiente de perturbación hacia una mayor diversidad de aves grandes, aves con altas capacidades de dispersión, omnívoros, carnívoros y carroñeros en TRA y DIS; mientras que PRES presentó mayor diversidad de aves sedentarias, nectarívoras, insectívoras pequeñas e insectívoras del sotobosque.
4. En términos de composición comunitaria de diversidad de especies y funcional, cada comunidad local resultó distinta entre sí debido al recambio de especies de aves en respuesta a la conversión de selva a pastizales introducidos para el ganado y zonas urbanas.
5. El futuro de las comunidades de aves locales corre el riesgo de presentar una separación composicional si no se detiene la conversión de selva a pastizales introducidos para el ganado y zonas urbanas y la degradación y aislamiento de los parches de hábitat restantes en el paisaje antropogénico y en el PNP.
6. La conservación de las comunidades de aves locales en Palenque dependerá de una filosofía de gestión territorial que tenga como objetivo aumentar la conectividad del paisaje con el PNP a través del uso de plantas nativas en áreas no selváticas. Además, la salud de las comunidades de aves locales dependerá de la reducción de actividades humanas al dentro y alrededor de los parches de selva, particularmente en TRA y PRES, para evitar más aislamiento de los parches remanentes de selva y para disminuir los efectos adversos del ruido antropogénico y tráfico vehicular.

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APPENDICES

Table A1. List of bird species recorded and functional traits used in the data analysis. Scientific names follow the latest AOS supplement to the North and Middle American birds checklist (Chesser et al., 2020). Air forager = AiF, tree forager = TF, air hawker = AH, air hawker above canopy = AHAC, air hawker under canopy = AHUC, bark excavator = BE, bark gleaner = BG, freshwater forager = FF, ground hawker = GH, ground to lower canopy gleaner = GLCG, ground to undergrowth gleaner = GUG, lower canopy foliage gleaner = LCFG, upper canopy gleaner = UCG. The community column lists the local communities (P = PRES or preserved, T = TRA or transition, D = DIS or disturbed) that each species was detected in.

Common name	**Scientific name**	**Log body mass (g)**	**Diet category**	**Foraging stratum**	**Migratory status**	**Habitat breadth**	**Community**
Great Tinamou	*Tinamus major*	3.04	Frugivore	GLCG	sedentary	1	P
Little Tinamou	*Crypturellus soui*	2.37	Frugivore	GLCG	sedentary	2	P, T
Slaty-breasted Tinamou	*Crypturellus boucardi*	2.66	Frugivore	GLCG	sedentary	1	P
Black-bellied Whistling-Duck	*Dendrocygna autumnalis*	2.92	Herbivore	FF	sedentary	1	T, D
Muscovy Duck	*Cairina moschata*	3.35	Herbivore	FF	sedentary	1	T
Plain Chachalaca	*Ortalis vetula*	2.74	Frugivore	GLCG	sedentary	2	T, D
Great Curassow	*Crax rubra*	3.62	Frugivore	GLCG	sedentary	1	P
Spotted Wood-Quail	*Odontophorus guttatus*	2.48	Granivore	GUG	sedentary	1	P
Rock Pigeon	*Columba livia*	2.43	Granivore	GUG	sedentary	1	D
Pale-vented Pigeon	*Patagioenas cayennensis*	2.36	Frugivore	UCG	sedentary	1	P, T, D
Red-billed Pigeon	*Patagioenas flavirostris*	2.50	Frugivore	GLCG	sedentary	1	D
Eurasian Collared-Dove	*Streptopelia decaocto*	2.30	Granivore	GUG	sedentary	1	D
Ruddy Ground-Dove	*Columbina talpacoti*	1.60	Granivore	GUG	sedentary	2	P, T, D
Ruddy Quail-Dove	*Geotrygon montana*	2.15	Granivore	GUG	sedentary	1	P, D
White-tipped Dove	*Leptotila verreauxi*	2.18	Granivore	GUG	sedentary	2	P, T, D
Gray-chested Dove	*Leptotila cassinii*	2.20	Granivore	GUG	sedentary	2	P
Gray-headed Dove	*Leptotila plumbeiceps*	2.23	Granivore	GUG	sedentary	3	P, T
White-winged Dove	*Zenaida asiatica*	2.18	Granivore	GUG	sedentary	1	T, D
Groove-billed Ani	*Crotophaga sulcirostris*	1.93	Insectivore	GUG	sedentary	2	T, D
Squirrel Cuckoo	*Piaya cayana*	2.02	Insectivore	UCG	sedentary	2	P, T, D
Yellow-billed Cuckoo	*Coccyzus americanus*	1.81	Insectivore	LCFG	migrant	3	P, T, D
White-collared Swift	*Streptoprocne zonaris*	2.40	Insectivore	AHAC	sedentary	3	P, T, D
Vaux's Swift	*Chaetura vauxi*	1.23	Insectivore	AHAC	sedentary	3	T, D
Lesser Swallow-tailed Swift	*Panyptila cayennensis*	1.32	Insectivore	AHAC	sedentary	2	P, T, D
White-necked Jacobin	*Florisuga mellivora*	0.87	Nectarivore		sedentary	2	P, T
Long-billed Hermit	*Phaethornis longirostris*	0.80	Nectarivore		sedentary	2	P, T, D

Stripe-throated Hermit	*Phaethornis striigularis*	0.48	Nectarivore		sedentary	2	P, T, D
Green-breasted Mango	*Anthracothorax prevostii*	0.75	Nectarivore		sedentary	2	T, D
Long-billed Starthroat	*Heliomaster longirostris*	0.82	Nectarivore		sedentary	2	P, T, D
Ruby-throated Hummingbird	*Archilochus colubris*	0.51	Nectarivore		migrant	6	P, T, D
Canivet's Emerald	*Cynanthus canivetii*	0.40	Nectarivore		sedentary	1	T
Wedge-tailed Sabrewing	*Pampa curvipennis*	0.78	Nectarivore		sedentary	3	P, T
Violet Sabrewing	*Campylopterus hemileucurus*	1.04	Nectarivore		sedentary	2	P, T
Rufous-tailed Hummingbird	*Amazilia tzacatl*	0.66	Nectarivore		sedentary	4	P, T, D
White-bellied Emerald	*Chlorestes candida*	0.58	Nectarivore		sedentary	3	P, T, D
Russet-naped Wood-Rail	*Aramides albiventris*	2.60	Carnivore	FF	sedentary	2	T, D
Ruddy Crake	*Laterallus ruber*	1.65	Herbivore	FF	sedentary	1	P
Neotropic Cormorant	*Phalacrocorax brasilianus*	3.08	Carnivore	FF	migrant	1	T
Bare-throated Tiger-Heron	*Tigrisoma mexicanum*	3.11	Carnivore	FF	sedentary	1	T, D
Great Blue Heron	*Ardea herodias*	3.46	Carnivore	FF	migrant	1	D
Great Egret	*Ardea alba*	2.94	Carnivore	FF	migrant	1	D
Cattle Egret	*Bubulcus ibis*	2.53	Insectivore	GUG	sedentary	1	T, D
Green Heron	*Butorides virescens*	2.32	Carnivore	FF	sedentary	1	T, D
King Vulture	*Sarcoramphus papa*	3.53	Scavenger	AiF	sedentary	1	P
Black Vulture	*Coragyps atratus*	3.30	Scavenger	AiF	sedentary	4	P, T, D
Turkey Vulture	*Cathartes aura*	3.26	Scavenger	AiF	sedentary	3	P, T, D
Lesser Yellow-headed Vulture	*Cathartes burrovianus*	2.97	Scavenger	AiF	sedentary	1	T, D
Osprey	*Pandion haliaetus*	3.20	Carnivore	FF	migrant	1	D
Hook-billed Kite	*Chondrohierax uncinatus*	2.45	Carnivore	GH	sedentary	2	P
Double-toothed Kite	*Harpagus bidentatus*	2.28	Insectivore	UCG	sedentary	2	P, T
Plumbeous Kite	*Ictinia plumbea*	2.41	Insectivore	AHAC	migrant	1	P
Common Black Hawk	*Buteogallus anthracinus*	2.98	Carnivore	FF	sedentary	2	P
Roadside Hawk	*Rupornis magnirostris*	2.44	Insectivore	GUG	sedentary	2	P, T, D
White Hawk	*Pseudastur albicollis*	2.87	Carnivore	GH	sedentary	1	P
Gray Hawk	*Buteo plagiatus*	2.73	Carnivore	GH	sedentary	2	T, D
Broad-winged Hawk	*Buteo platypterus*	2.59	Carnivore	GH	migrant	2	P
Short-tailed Hawk	*Buteo brachyurus*	2.62	Carnivore	AH	sedentary	2	T, D
Zone-tailed Hawk	*Buteo albonotatus*	2.91	Carnivore	GH	migrant	1	T
Ferruginous Pygmy-Owl	*Glaucidium brasilianum*	1.85	Insectivore	AHUC	sedentary	2	D
Slaty-tailed Trogon	*Trogon massena*	2.16	Frugivore	UCG	sedentary	1	P
Black-headed Trogon	*Trogon melanocephalus*	1.95	Frugivore	UCG	sedentary	3	P, T, D
Gartered Trogon	*Trogon caligatus*	1.71	Frugivore	UCG	sedentary	3	P, T, D
Collared Trogon	*Trogon collaris*	1.81	Frugivore	UCG	sedentary	1	P, T
Lesson's Motmot	*Momotus lessonii*	2.12	Insectivore	AHUC	sedentary	3	P, T, D
Ringed Kingfisher	*Megaceryle torquata*	2.49	Carnivore	FF	sedentary	1	T, D
Amazon Kingfisher	*Chloroceryle amazona*	2.08	Carnivore	FF	sedentary	1	T, D
American Pygmy Kingfisher	*Chloroceryle aenea*	1.17	Carnivore	FF	sedentary	2	P

Green Kingfisher	*Chloroceryle americana*	1.56	Carnivore	FF	sedentary	1	P, T
Rufous-tailed Jacamar	*Galbula ruficauda*	1.42	Insectivore	AHUC	sedentary	3	P, T
Collared Aracari	*Pteroglossus torquatus*	2.36	Frugivore	UCG	sedentary	3	P, T, D
Keel-billed Toucan	*Ramphastos sulfuratus*	2.64	Frugivore	UCG	sedentary	2	P, T, D
Black-cheeked Woodpecker	*Melanerpes pucherani*	1.82	Insectivore	BE	sedentary	3	P, D
Golden-fronted Woodpecker	*Melanerpes aurifrons*	1.91	Insectivore	BE	sedentary	2	P, T, D
Ladder-backed Woodpecker	*Dryobates scalaris*	1.48	Insectivore	BE	sedentary	1	T, D
Smoky-brown Woodpecker	*Dryobates fumigatus*	1.56	Insectivore	BE	sedentary	2	P
Golden-olive Woodpecker	*Colaptes rubiginosus*	1.75	Insectivore	BE	sedentary	3	P, T, D
Chestnut-colored Woodpecker	*Celeus castaneus*	1.93	Insectivore	BE	sedentary	1	P, T
Lineated Woodpecker	*Dryocopus lineatus*	2.29	Insectivore	BE	sedentary	3	P, T, D
Pale-billed Woodpecker	*Campephilus guatemalensis*	2.38	Insectivore	BE	sedentary	3	P, T
Laughing Falcon	*Herpetotheres cachinnans*	2.77	Carnivore	GH	sedentary	2	P, T, D
Crested Caracara	*Caracara cheriway*	3.00	Scavenger	AiF	migrant	1	D
Merlin	*Falco columbarius*	2.28	Carnivore	AH	migrant	1	T
Bat Falcon	*Falco rufigularis*	2.11	Carnivore	AH	sedentary	2	P, T, D
Olive-throated Parakeet	*Eupsittula nana*	1.89	Frugivore	UCG	sedentary	4	P, T, D
Scarlet Macaw	*Ara macao*	3.08	Frugivore	UCG	sedentary	1	P, D
Brown-hooded Parrot	*Pyrilia haematotis*	2.17	Frugivore	UCG	sedentary	2	P
White-crowned Parrot	*Pionus senilis*	2.33	Frugivore	UCG	sedentary	2	P, T
White-fronted Parrot	*Amazona albifrons*	2.30	Frugivore	UCG	sedentary	4	P, T, D
Red-lored Parrot	*Amazona autumnalis*	2.68	Frugivore	UCG	sedentary	3	T, D
Great Antshrike	*Taraba major*	1.77	Insectivore	LCFG	sedentary	2	P
Barred Antshrike	*Thamnophilus doliatus*	1.51	Insectivore	LCFG	sedentary	2	P, T, D
Dusky Antbird	*Cercomacroides tyrannina*	1.26	Insectivore	GUG	sedentary	2	P, T
Black-faced Antthrush	*Formicarius analis*	1.75	Insectivore	GUG	sedentary	1	P
Scaly-throated Leaftosser	*Sclerurus guatemalensis*	1.53	Insectivore	GUG	sedentary	1	P
Olivaceous Woodcreeper	*Sittasomus griseicapillus*	1.16	Insectivore	BG	sedentary	3	P
Tawny-winged Woodcreeper	*Dendrocincla anabatina*	1.57	Insectivore	BG	sedentary	1	P, T
Wedge-billed Woodcreeper	*Glyphorynchus spirurus*	1.16	Insectivore	BG	sedentary	1	P, T, D
Northern Barred-Woodcreeper	*Dendrocolaptes sanctithomae*	1.83	Insectivore	BG	sedentary	1	P, T
Ivory-billed Woodcreeper	*Xiphorhynchus flavigaster*	1.67	Insectivore	BG	sedentary	3	P, T
Streak-headed Woodcreeper	*Lepidocolaptes souleyetii*	1.41	Insectivore	BG	sedentary	3	P, T, D
Plain Xenops	*Xenops minutus*	1.03	Insectivore	LCFG	sedentary	1	P
Rufous-breasted Spinetail	*Synallaxis erythrothorax*	1.23	Insectivore	LCFG	sedentary	3	P, T, D
Red-capped Manakin	*Ceratopipra mentalis*	1.18	Frugivore	UCG	sedentary	1	P
Masked Tityra	*Tityra semifasciata*	1.90	Insectivore	UCG	sedentary	4	P, T, D
Black-crowned Tityra	*Tityra inquisitor*	1.63	Insectivore	UCG	sedentary	2	P, T, D
Rose-throated Becard	*Pachyramphus aglaiae*	1.48	Insectivore	LCFG	sedentary	2	T, D
Royal Flycatcher	*Onychorhynchus coronatus*	1.15	Insectivore	AHUC	sedentary	1	P, T
Sulphur-rumped Flycatcher	*Myiobius sulphureipygius*	1.08	Insectivore	AHUC	sedentary	1	P

Stub-tailed Spadebill	*Platyrinchus cancrominus*	0.96	Insectivore	LCFG	sedentary	1	P
Ochre-bellied Flycatcher	*Mionectes oleagineus*	1.08	Insectivore	AHUC	sedentary	3	P, T
Sepia-capped Flycatcher	*Leptopogon amaurocephalus*	1.07	Insectivore	AHUC	sedentary	2	P, T, D
Northern Bentbill	*Oncostoma cinereigulare*	0.76	Insectivore	AHUC	sedentary	1	P
Slate-headed Tody-Flycatcher	*Poecilotriccus sylvia*	0.85	Insectivore	LCFG	sedentary	2	P, T, D
Eye-ringed Flatbill	*Rhynchocyclus brevirostris*	1.34	Insectivore	AHUC	sedentary	1	P
Yellow-olive Flycatcher	*Tolmomyias sulphurescens*	1.16	Insectivore	AHUC	sedentary	4	P, T, D
Yellow-bellied Tyrannulet	*Ornithion semiflavum*	0.82	Insectivore	AHUC	sedentary	2	P, T
Northern Beardless-Tyrannulet	*Camptostoma imberbe*	0.87	Insectivore	AHUC	sedentary	4	T
Greenish Elaenia	*Myiopagis viridicata*	1.09	Insectivore	AHUC	sedentary	3	P, T
Yellow-bellied Elaenia	*Elaenia flavogaster*	1.38	Insectivore	AHUC	sedentary	1	D
Bright-rumped Attila	*Attila spadiceus*	1.59	Insectivore	AHUC	sedentary	3	P, T
Rufous Mourner	*Rhytipterna holerythra*	1.57	Insectivore	AHUC	sedentary	1	P
Dusky-capped Flycatcher	*Myiarchus tuberculifer*	1.30	Insectivore	AHUC	sedentary	4	P
Great Crested Flycatcher	*Myiarchus crinitus*	1.53	Insectivore	AHUC	migrant	4	P, T, D
Brown-crested Flycatcher	*Myiarchus tyrannulus*	1.64	Insectivore	AHUC	sedentary	2	T, D
Great Kiskadee	*Pitangus sulphuratus*	1.78	Insectivore	AHUC	sedentary	3	P, T, D
Boat-billed Flycatcher	*Megarynchus pitangua*	1.85	Insectivore	AHUC	sedentary	3	P, T, D
Social Flycatcher	*Myiozetetes similis*	1.45	Insectivore	AHUC	sedentary	4	P, T, D
Streaked Flycatcher	*Myiodynastes maculatus*	1.63	Insectivore	AHUC	migrant	2	P, T
Sulphur-bellied Flycatcher	*Myiodynastes luteiventris*	1.66	Insectivore	AHUC	migrant	3	P, T, D
Piratic Flycatcher	*Legatus leucophaius*	1.42	Insectivore	AHUC	migrant	2	T
Tropical Kingbird	*Tyrannus melancholicus*	1.60	Insectivore	AHUC	sedentary	1	T, D
Couch's Kingbird	*Tyrannus couchii*	1.63	Insectivore	AHUC	sedentary	1	T, D
Fork-tailed Flycatcher	*Tyrannus savana*	1.46	Insectivore	AHUC	sedentary	1	D
Olive-sided Flycatcher	*Contopus cooperi*	1.51	Insectivore	AHUC	migrant	2	D
Eastern Wood-Pewee	*Contopus virens*	1.15	Insectivore	AHUC	migrant	4	P, T, D
Tropical Pewee	*Contopus cinereus*	1.06	Insectivore	AHUC	sedentary	2	P, D
Yellow-bellied Flycatcher	*Empidonax flaviventris*	1.06	Insectivore	AHUC	migrant	3	P, T, D
Acadian Flycatcher	*Empidonax virescens*	1.11	Insectivore	AHUC	migrant	3	T, D
Least Flycatcher	*Empidonax minimus*	1.01	Insectivore	AHUC	migrant	5	P, D
Vermilion Flycatcher	*Pyrocephalus rubinus*	1.16	Insectivore	AHUC	sedentary	1	D
Lesser Greenlet	*Pachysylvia decurtata*	0.94	Insectivore	UCG	sedentary	2	P, T, D
White-eyed Vireo	*Vireo griseus*	1.06	Insectivore	LCFG	migrant	2	P, T, D
Yellow-throated Vireo	*Vireo flavifrons*	1.26	Insectivore	LCFG	migrant	3	P, T, D
Blue-headed Vireo	*Vireo solitarius*	1.20	Insectivore	LCFG	migrant	2	D
Philadelphia Vireo	*Vireo philadelphicus*	1.08	Insectivore	LCFG	migrant	4	P, T, D
Warbling Vireo	*Vireo gilvus*	1.08	Insectivore	LCFG	migrant	3	P, T, D
Red-eyed Vireo	*Vireo olivaceus*	1.23	Insectivore	LCFG	migrant	3	T, D
Yellow-green Vireo	*Vireo flavoviridis*	1.26	Insectivore	LCFG	migrant	2	P, D
Brown Jay	*Psilorhinus morio*	2.30	Omnivore	TF	sedentary	4	P, T, D

Mangrove Swallow	*Tachycineta albilinea*	1.15	Insectivore	AHAC	sedentary	1	D
Northern Rough-winged Swallow	*Stelgidopteryx serripennis*	1.20	Insectivore	AHAC	sedentary	1	T, D
Barn Swallow	*Hirundo rustica*	1.28	Insectivore	AHAC	migrant	1	D
House Wren	*Troglodytes aedon*	1.04	Insectivore	LCFG	sedentary	1	P, T, D
Band-backed Wren	*Campylorhynchus zonatus*	1.54	Insectivore	LCFG	sedentary	2	P
Spot-breasted Wren	*Pheugopedius maculipectus*	1.21	Insectivore	LCFG	sedentary	3	P, T, D
White-breasted Wood-Wren	*Henicorhina leucosticta*	1.17	Insectivore	LCFG	sedentary	1	P
Long-billed Gnatwren	*Ramphocaenus melanurus*	1.04	Insectivore	LCFG	sedentary	2	P, T, D
Blue-gray Gnatcatcher	*Polioptila caerulea*	0.78	Insectivore	LCFG	migrant	4	P, T, D
Tropical Gnatcatcher	*Polioptila plumbea*	0.79	Insectivore	LCFG	sedentary	1	P
Swainson's Thrush	*Catharus ustulatus*	1.49	Insectivore	LCFG	migrant	3	T, D
Wood Thrush	*Hylocichla mustelina*	1.67	Insectivore	GUG	migrant	2	P, T, D
Clay-colored Thrush	*Turdus grayi*	1.87	Insectivore	GUG	sedentary	5	P, T, D
Gray Catbird	*Dumetella carolinensis*	1.57	Insectivore	GUG	migrant	3	P, T, D
Tropical Mockingbird	*Mimus gilvus*	1.73	Insectivore	GUG	sedentary	1	D
Scrub Euphonia	*Euphonia affinis*	1.11	Frugivore	GLCG	sedentary	4	P, T, D
Yellow-throated Euphonia	*Euphonia hirundinacea*	1.23	Frugivore	GLCG	sedentary	5	P, T, D
Olive-backed Euphonia	*Euphonia gouldi*	1.08	Frugivore	GLCG	sedentary	2	P
Green-backed Sparrow	*Arremonops chloronotus*	1.49	Granivore	GUG	sedentary	2	P, T, D
Orange-billed Sparrow	*Arremon aurantiirostris*	1.54	Granivore	GUG	sedentary	1	P
Yellow-breasted Chat	*Icteria virens*	1.40	Insectivore	LCFG	migrant	3	P, T, D
Eastern Meadowlark	*Sturnella magna*	1.95	Insectivore	GUG	sedentary	1	D
Yellow-billed Cacique	*Amblycercus holosericeus*	1.73	Insectivore	LCFG	sedentary	2	P, T
Chestnut-headed Oropendola	*Psarocolius wagleri*	2.35	Frugivore	UCG	sedentary	2	P
Montezuma Oropendola	*Psarocolius montezuma*	2.72	Frugivore	UCG	sedentary	3	P, D
Orchard Oriole	*Icterus spurius*	1.28	Insectivore	UCG	migrant	2	T, D
Hooded Oriole	*Icterus cucullatus*	1.38	Insectivore	LCFG	sedentary	2	T, D
Yellow-tailed Oriole	*Icterus mesomelas*	1.85	Insectivore	LCFG	sedentary	1	T
Altamira Oriole	*Icterus gularis*	1.76	Insectivore	LCFG	sedentary	3	T, D
Baltimore Oriole	*Icterus galbula*	1.52	Insectivore	UCG	migrant	4	P, T, D
Bronzed Cowbird	*Molothrus aeneus*	1.79	Granivore	GUG	sedentary	2	T, D
Melodious Blackbird	*Dives dives*	2.00	Insectivore	LCFG	sedentary	3	T, D
Great-tailed Grackle	*Quiscalus mexicanus*	2.28	Omnivore	GUG	sedentary	3	T, D
Ovenbird	*Seiurus aurocapilla*	1.29	Insectivore	GUG	migrant	3	P, T, D
Worm-eating Warbler	*Helmitheros vermivorum*	1.11	Insectivore	LCFG	migrant	3	P, T
Louisiana Waterthrush	*Parkesia motacilla*	1.31	Insectivore	GUG	migrant	2	P, T, D
Northern Waterthrush	*Parkesia noveboracensis*	1.26	Insectivore	GUG	migrant	2	P, T, D
Golden-winged Warbler	*Vermivora chrysoptera*	0.94	Insectivore	LCFG	migrant	2	P, T
Blue-winged Warbler	*Vermivora cyanoptera*	0.93	Insectivore	LCFG	migrant	2	P, T, D
Black-and-white Warbler	*Mniotitla varia*	1.03	Insectivore	BG	migrant	5	P, T, D
Tennessee Warbler	*Leiothlypis peregrina*	1.00	Insectivore	LCFG	migrant	3	T, D

Kentucky Warbler	*Geothlypis formosa*	1.15	Insectivore	LCFG	migrant	3	P, T, D
Common Yellowthroat	*Geothlypis trichas*	1.00	Insectivore	LCFG	migrant	1	P, D
Hooded Warbler	*Setophaga citrina*	1.02	Insectivore	LCFG	migrant	3	P, T, D
American Redstart	*Setophaga ruticilla*	0.92	Insectivore	AHUC	migrant	4	P, T, D
Northern Parula	*Setophaga americana*	0.93	Insectivore	LCFG	migrant	3	P, T, D
Magnolia Warbler	*Setophaga magnolia*	0.94	Insectivore	LCFG	migrant	5	P, T, D
Bay-breasted Warbler	*Setophaga castanea*	1.10	Insectivore	LCFG	migrant	2	P
Blackburnian Warbler	*Setophaga fusca*	0.99	Insectivore	LCFG	migrant	2	P
Yellow Warbler	*Setophaga petechia*	0.98	Insectivore	LCFG	migrant	3	P, T, D
Chestnut-sided Warbler	*Setophaga pensylvanica*	0.98	Insectivore	LCFG	migrant	3	P, D
Yellow-throated Warbler	*Setophaga dominica*	0.97	Insectivore	LCFG	migrant	2	D
Black-throated Green Warbler	*Setophaga virens*	0.94	Insectivore	LCFG	migrant	2	P, T, D
Golden-crowned Warbler	*Basileuterus culicivorus*	1.02	Insectivore	LCFG	sedentary	1	P
Wilson's Warbler	*Cardellina pusilla*	0.89	Insectivore	LCFG	migrant	4	P, T, D
Summer Tanager	*Piranga rubra*	1.46	Insectivore	UCG	migrant	4	P, T, D
Scarlet Tanager	*Piranga olivacea*	1.45	Insectivore	UCG	migrant	4	D
Red-crowned Ant-Tanager	*Habia ribica*	1.53	Insectivore	LCFG	sedentary	1	P
Red-throated Ant-Tanager	*Habia fuscicauda*	1.61	Insectivore	LCFG	sedentary	3	P, T, D
Rose-breasted Grosbeak	*Pheucticus ludovicianus*	1.65	Insectivore	UCG	migrant	4	T, D
Blue-black Grosbeak	*Cyanoloxia cyanoides*	1.51	Granivore	GUG	sedentary	2	P
Blue Bunting	*Cyanocompsa parellina*	1.18	Granivore	GUG	sedentary	1	D
Indigo Bunting	*Passerina cyanea*	1.16	Granivore	GUG	migrant	3	T, D
Painted Bunting	*Passerina ciris*	1.19	Granivore	GUG	migrant	2	T
Blue-gray Tanager	*Thraupis episcopus*	1.54	Frugivore	UCG	sedentary	3	T, D
Yellow-winged Tanager	*Thraupis abbas*	1.65	Frugivore	UCG	sedentary	2	P, T, D
Golden-hooded Tanager	*Stilpnia larvata*	1.30	Frugivore	UCG	sedentary	2	P, T
Green Honeycreeper	*Chlorophanes spiza*	1.28	Frugivore	UCG	sedentary	2	P
Blue-black Grassquit	*Volatinia jacarina*	0.97	Granivore	GUG	sedentary	2	P, T, D
Crimson-collared Tanager	*Ramphocelus sanguinolentus*	1.61	Insectivore	LCFG	sedentary	2	P, T, D
Scarlet-rumped Tanager	*Ramphocelus passerinii*	1.51	Frugivore	UCG	sedentary	3	P, T, D
Red-legged Honeycreeper	*Cyanerpes cyaneus*	1.15	Nectarivore		sedentary	3	P, T, D
Bananaquit	*Coereba flaveola*	0.98	Nectarivore		sedentary	3	P, T
Thick-billed Seed-Finch	*Sporophila funerea*	1.13	Granivore	GUG	sedentary	2	P, T, D
Variable Seedeater	*Sporophila corvina*	1.04	Granivore	GUG	sedentary	2	P, T, D
Morelet's Seedeater	*Sporophila morelleti*	0.95	Granivore	GUG	sedentary	2	P, T, D
Black-headed Saltator	*Saltator atriceps*	1.90	Frugivore	GLCG	sedentary	3	P, T, D
Buff-throated Saltator	*Saltator maximus*	1.67	Frugivore	GLCG	sedentary	3	P, T, D
Grayish Saltator	*Saltator coerulescens*	1.74	Frugivore	GLCG	sedentary	3	T, D

Figure A1. Percentage of each land cover type (primary forest, secondary forest, pasture/grassland, and concrete surface) in each local community in the study landscape. Percent cover values were determined with a land cover classification using the semi-classification plugin (Congedo, 2013) with the QGIS software platform version 3.8 Zanzibar (QGIS Development Team, 2020).

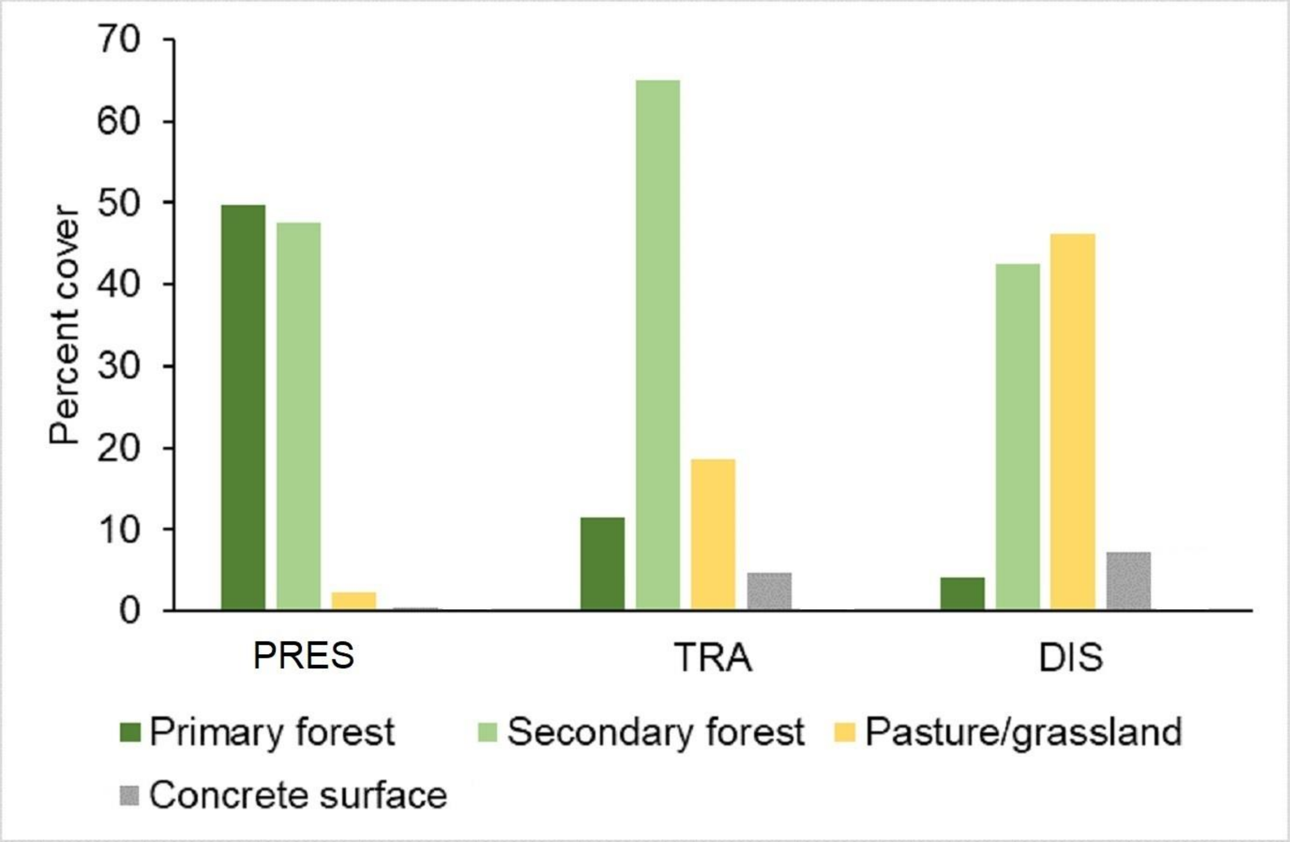

Figure A2. Photo mosaic of vegetation cover and disturbance in each area of the vegetation disturbance gradient. (**A**) Cattle pasture with isolated trees in DIS. (**B**) Secondary forest in TRA. (**C**) Primary forest in PRES. (**D**) Deforested area in DIS. Secondary forest was converted to cattle pasture. (**E**) Deforested area in TRA underneath a powerline. (**F**) Treefall gap in primary forest in PRES. Photo credit: DRL.

Figure A3. Estimated species diversity curves for (**a**) overall species, (**b**) Shannon, and (**c**) Simpson diversity for the preserved, transition, and disturbed local communities from the iNEXT analysis. Each graph shows the interpolated and extrapolated (extrapolated to twice the number of individuals as the original sample size) estimated species diversity curves and 95% confidence intervals (represented by shaded regions surrounding the curves) for the number of individuals detected in each sample. Separation of 95% confidence intervals represent significant difference among local communities.

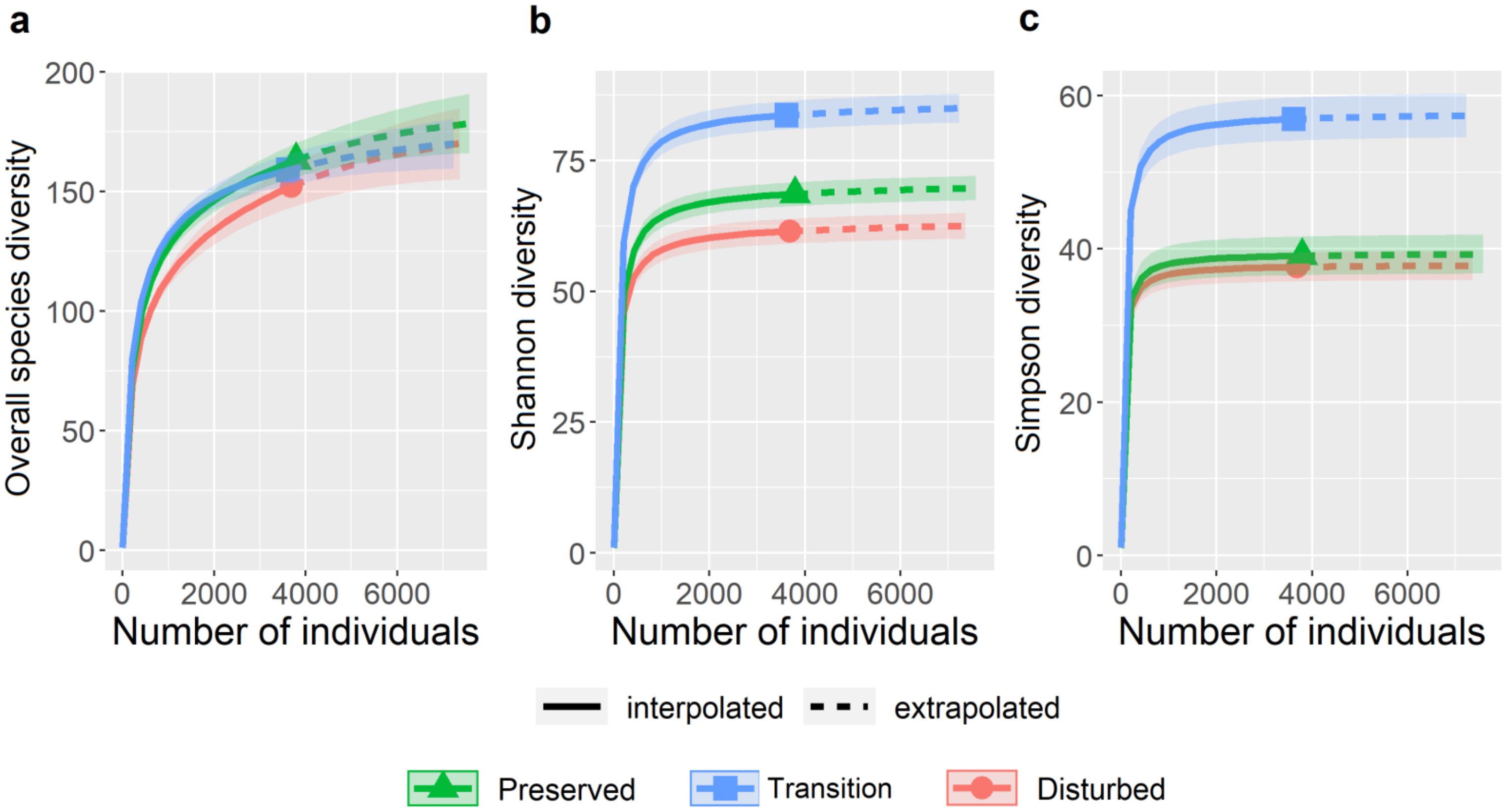

Figure A4. Sample completeness curves for (**a**) estimated species diversity (overall, Shannon, and Simpson) relative to sample coverage (the proportion of the total number of individuals that pertain to the species detected in each sample) and (**b**) sample coverage relative to the total number of interpolated and extrapolated number of individuals (twice the number of individuals as the original sample size) from the iNEXT analysis.