UNIVERSIDAD NACIONAL AUTÓNOMA DE MÉXICO

LICENCIATURA EN ECOLOGÍA

Escuela Nacional de Estudios Superiores,
Unidad Morelia

Estructura de metacomunidades de vertebrados terrestres tropicales en etapas sucesionales tempranas de un bosque tropical seco

TESIS

QUE PARA OBTENER EL TÍTULO DE

LICENCIADA EN ECOLOGÍA

PRESENTA

ORIANA RAMÍREZ SÁNCHEZ

DIRECTOR DE TESIS: DR. LUIS DANIEL ÁVILA CABADILLA
CO-DIRECTORA DE TESIS: DRA. MARIANA YÓLOTL ÁLVAREZ AÑORVE

MORELIA, MICHOACÁN **JULIO, 2021**

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UNIVERSIDAD NACIONAL AUTÓNOMA DE MÉXICO
ESCUELA NACIONAL DE ESTUDIOS SUPERIORES, UNIDAD MORELIA
SECRETARÍA GENERAL
SERVICIOS ESCOLARES

MTRA. IVONNE RAMÍREZ WENCE
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DIRECCIÓN GENERAL DE ADMINISTRACIÓN ESCOLAR
PRESENTE

Por medio de la presente me permito informar a usted que en la **sesión ordinaria 04** del **H. Consejo Técnico** de la Escuela Nacional de Estudios Superiores (ENES) Unidad Morelia celebrada el día **21 de abril del 2021**, acordó poner a su consideración el siguiente jurado para la presentación del Trabajo Profesional del alumno (a) **Oriana Ramírez Sánchez** adscrito a la Licenciatura en Ecología con número de cuenta **313093728,** quien presenta la tesis titulada: "Estructura de metacomunidades de vertebrados terrestres tropicales en etapas sucesionales tempranas de un bosque tropical seco", bajo la dirección como **tutor** del Dr. Luis Daniel Ávila Cabadilla y como **co-tutora** la Dra. Mariana Yólotl Álvarez Añorve

El jurado queda integrado de la siguiente manera:

Presidente:	Dr. Alberto Ken Oyama Nakagawa
Vocal:	Dra. Julieta Benítez Malvido
Secretario:	Dr. Luis Daniel Ávila Cabadilla
Suplente 1:	Dra. Ireri Suazo Ortuño
Suplente 2:	Dr. Carlos Alberto Yáñez Arenas

Sin otro particular, quedo de usted.

Atentamente
"POR MI RAZA HABLARA EL ESPIRITU"
Morelia, Michoacán a 28 de julio del 2021.

DRA. YESENIA ARREDONDO LEÓN
SECRETARIA GENERAL

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Índice

Resumen

Las actividades antropogénicas, como el cambio de uso de suelo, están transformando los bosques en paisajes dominados por etapas sucesionales tempranas (EST). El objetivo de esta tesis fue identificar los mecanismos y estructuras que moldean a las metacomunidades de vertebrados terrestres (anuros, lagartijas, serpientes, aves, roedores y murciélagos) en un bosque tropical seco. Para este propósito, se realizaron muestreos de vertebrados en 13 sitios que representaban bosques secundarios y primarios. Encontramos una alta diversidad beta en todos los grupos, con valores bajos de anidamiento que indican que la mayor contribución a la diversidad beta es la del recambio de especies. Los vertebrados se distribuyeron a lo largo de un gradiente de acuerdo con los análisis basados en el marco conceptual de los elementos de la estructura de la comunidad. Las metacomunidades de anuros, lagartijas, serpientes y aves migratorias mostraron una estructura quasi-Gleasoniana, mientras que las aves residentes y los murciélagos se una estructura quasi-Clementsiana; los roedores presentaron una estructura Gleasoniana. En general, los grupos fueron afectados por atributos del paisaje y la vegetación, esto sugiere que el efecto de masa y “species sorting” son los mecanismos estructurando las metacomunidades en el bosque secundario. Asimismo, observamos que: 1) se pueden encontrar varias especies en las EST, incluyendo especies exclusivas de bosques maduros, probablemente por el uso de los bosques secundarios como corredores biológicos; 2) el bosque maduro actúa como una fuente de especies que se dispersan hacia los remanentes de bosque que permiten la colonización de estos; 3) la conectividad del paisaje, la cobertura forestal y la composición de la vegetación son las variables ambientales más importantes que afectan a las metacomunidades de vertebrados en el bosque tropical seco de Chamela.

Abstract

Anthropogenic activities such as land-use change are converting forests to landscapes dominated by early successional stages (ESS). This study aimed to identify the mechanisms and structures that shape metacommunities of terrestrial vertebrates (anurans, lizards, snakes, birds, rodents, and bats) in a tropical dry forest. For this purpose, we sampled the vertebrates in 13 sites representing secondary and old-growth forests. We found a high beta diversity in all groups, with low values of nestedness indicating that turnover contributed the most to beta diversity. All groups were distributed along a latent gradient according to the analyses using the “elements of metacommunity structure” framework. Some vertebrate metacommunities showed a quasi-Gleasonian structure (anurans, lizards, snakes, and migratory birds); in contrast, bats and migratory birds showed a quasi-Clementsian structure and rodent group a Gleasonian one. In general, groups were affected by landscape and vegetation attributes, suggesting that species sorting and mass effects are structuring the metacommunities in secondary forests. In addition, we observed that: 1) various species are found in ESS, including some species exclusive of mature forests, probably because secondary forests are used as stepping stones and corridors; 2) old-growth forest is acting as a source of species that disperse to forest remnants and colonize them; 3) landscape connectivity, forest cover, and vegetation composition are the most important environmental variables affecting vertebrate metacommunities in Chamela dry forest.

Capítulo 1

Introducción

La pérdida del hábitat y su fragmentación actualmente son fenómenos comunes que han tenido repercusión sobre la biodiversidad del planeta. De acuerdo con la FAO (2006, 2007), el 3% de los bosques son perturbados cada año en todo el mundo. En el caso de la fragmentación, un hábitat que ha pasado por este proceso se transforma en un paisaje compuesto por varios fragmentos o parches aislados entre sí y embebidos en una matriz de hábitat diferente al original (Franklin et al., 2002). La fragmentación puede tener tanto efectos adversos como beneficiosos sobre la abundancia, interacciones ecológicas y dinámicas poblacionales de diferentes especies, (Fahrig, 2003; Wiegand et al., 2005).

Como resultado de la fragmentación y la pérdida del hábitat, se espera que los paisajes de bosques perturbados se encuentren dominados por etapas sucesionales tempranas. Por ejemplo, en el caso de los bosques tropicales secos en México, en el año 2002, el 62% de la cobertura de este tipo de vegetación ya era secundaria con diferentes grados de perturbación (Challenger & Dirzo, 2009). Esto resalta la importancia de estudiar los estadios sucesionales tempranos.

Uno de los efectos de la fragmentación y degradación de los hábitats es la pérdida inmediata y a largo plazo de la biodiversidad (Krauss et al., 2010; Solé et al., 2004). La biodiversidad de los vertebrados terrestres en particular (anfibios, reptiles, aves y mamíferos), está declinando como consecuencia de distintas amenazas como la alteración del hábitat, la presencia de especies invasivas, el cambio climático, la sobreexplotación, entre otras. Sin embargo, la alteración y destrucción del hábitat es la principal amenaza (Ducatez & Shine, 2017). En México los vertebrados terrestres con mayor número de especies en alguna categoría de riesgo son los reptiles (443 especies), seguidos por las aves (392), mamíferos (291) y anfibios (194), (Semarnat, 2019). En este sentido, resulta urgente comprender las respuestas de las comunidades de vertebrados terrestres ante los disturbios antropogénicos.

Dado que gran parte de los bosques están constituidos por fragmentos que anteriormente conformaron un continuo y que podrían estar potencialmente comunicados por procesos de dispersión en la actualidad (Hagen et al., 2012), el marco conceptual de las metacomunidades puede ser útil para comprender los mecanismos y procesos del ensamblaje de estas comunidades de vertebrados terrestres durante las etapas sucesionales tempranas en los bosques tropicales (Holyoak et al., 2005).

Bosques tropicales secos

El bosque tropical seco (BTS), también conocido como selva seca, selva baja o bosque tropical caducifolio, es considerado como uno de los ecosistemas tropicales más amenazados del mundo (Janzen, 1988; Olson & Dinerstein, 1998), y se encuentra desapareciendo a tasas alarmantes por presiones tanto naturales como antropogénicas, por ejemplo: cambio climático, incremento en el tamaño poblacional, cambio de uso de suelo, fragmentación del bosque, entre otras (FAO, 2019). Estos bosques son de suma importancia para las comunidades rurales debido a que les proporcionan servicios ecosistémicos y diferentes recursos (Balvanera et al., 2011; Siyum, 2020). El cambio de uso de suelo de los BTS se debe a las condiciones favorables que tienen para que estos puedan ser aprovechados como sitios de extracción de recursos maderables y no maderables, áreas para pastoreo de ganado (cuando el bosque es convertido a pastizales), agricultura, pesca e incluso caza (Burgos & Maass, 2004; Monroy-Sais et al., 2020).

Este ecosistema se encuentra distribuido en África, América y Asia, representando casi el 40% de los bosques a nivel mundial (FAO, 2019; Miles et al., 2006; Murphy & Lugo, 1986). De acuerdo con Miles et al. (2006), el 54% de los bosques tropicales secos se encuentra en Latinoamérica. En el caso de México, el BTS se distribuye en la vertiente del Pacífico desde Sonora hasta Chiapas, en el Atlántico al sur de Tamaulipas y en la Península de Yucatán; también es posible encontrarlo al sureste de San Luis Potosí, al norte y centro de Veracruz y en parte de la Huasteca (Rzedowski, 2006).

Los BTS se caracterizan por la marcada estacionalidad entre épocas de lluvia y épocas secas, que tiene como consecuencia la pérdida de las hojas de los árboles (Meave et al., 2012; Rzedowski, 2006). Su precipitación varía entre los 600 a 1800 mm anuales en promedio y su altura se encuentra entre los 7 y 15 metros (Murphy & Lugo, 1986). Asimismo, este tipo de ecosistema es muy importante en términos de diversidad biológica, debido a los altos niveles de endemismos y de diversidad beta tanto de especies vegetales como de especies animales (Durán et al., 2006; Janzen, 1988; Pennington et al., 2009).

En México, los BTS han experimentado tasas de deforestación del 2% anual desde 1980 (Masera et al., 1997), mientras que los bosques distribuidos a lo largo de la costa del Pacífico se encuentran con altos grados de fragmentación y de deforestación (Sánchez-Azofeifa & Portillo-Quintero, 2011). Esto ha tenido como consecuencia cambios en la presencia y abundancia de diferentes especies de vertebrados, reduciendo la diversidad de forma alarmante y poniendo en peligro a especies y grupos vulnerables a la perturbación (Torres et al., 2014). De igual forma, la degradación de estos ecosistemas puede tener efecto sobre algunos procesos ecológicos como la polinización y reproducción de plantas (Quesada et al., 2011), o el ensamblaje de las comunidades que habitan los sitios perturbados y fragmentados (Fraga-Ramírez et al., 2017; Morales-Díaz et al., 2019; Ruiz-García & Avila-Cabadilla, 2016).

Etapas sucesionales tempranas

De acuerdo a la FAO (2006), más del 60% de los bosques del mundo se están recuperando de un disturbio pasado. Después de un disturbio, los bosques inician un proceso de sucesión ecológica secundaria que comienza con las etapas sucesionales tempranas (EST). Estas han sido nombradas como las “etapas olvidadas de la sucesión ecológica” (Swanson et al., 2011) debido a los pocos estudios que se han realizado en torno a los procesos ecológicos que ocurren durante estos estadios.

Las condiciones iniciales de los bosques secundarios dependen del tipo de disturbio, pero comparten algunos atributos en común. En aras de dilucidar los procesos, mecanismos y características de las EST, Swanson et al. (2011) realizaron una revisión donde se resumen los principales atributos y procesos de estas etapas. Cabe señalar en este punto, que en ecología el término “proceso” se refiere al conjunto de las fases sucesivas de un fenómeno natural (RAE, 2020) y describe *cómo* surgen los patrones que percibimos, mientras que los “mecanismos” explican *por qué* ocurren estos patrones (Anand, 1994).

Atributos de los EST

- **Condiciones ambientales:** el microclima se ve afectado al remover el dosel de los árboles. Los regímenes de luz cambian y como consecuencia las temperaturas son más extremas, y la humedad del aire y del suelo disminuye.
- **Supervivientes:** los organismos que sobreviven a la perturbación son cruciales para los procesos de repoblación y el restablecimiento de funciones ecológicas.
- **Complejidad estructural:** los remanentes de madera, como troncos o ramas caídas, facilitan el desarrollo de la recuperación del sistema al proporcionar un hábitat a los colonizadores y supervivientes.
- **Heterogeneidad espacial:** los sitios perturbados generalmente resultan en ambientes heterogéneos.

Procesos de los EST

- **Recarga de fuentes de nutrientes:** adición de nitrógeno principalmente por la presencia de plantas leguminosas; aumento de tasas de mineralización de materia orgánica como resultado del incremento de la temperatura en estos sitios.
- **Modificación de regímenes hidrológicos y geomórficos:** reducción de la transpiración; mayor contribución al flujo del agua durante eventos hidrológicos de una magnitud pequeña. Cambios en las tasas y patrones de erosión y lixiviación de nutrientes, generalmente un aumento en estas.

Además de los atributos anteriores, los bosques secundarios pueden albergar una gran diversidad y riqueza de especies animales a pesar de no tener la diversidad de bosques maduros. Esto se debe a que la vegetación de las EST provee de recursos como alimento (frutas, semillas) o sitios de refugio a diferentes especies, (Blake & Loiselle, 2001; Fraga-Ramírez et al., 2017).

Metacomunidades

La ecología de comunidades se enfoca generalmente en una escala y asume que las comunidades locales se encuentran cerradas y aisladas (Leibold et al., 2004). Sin embargo, algunos autores han reconocido la importancia del papel de las dinámicas espaciales y temporales, la escala, la heterogeneidad y el proceso de dispersión en este campo (Holyoak et al., 2005; Verhoef & Morin, 2009). De esta forma, se propuso que la interacción entre especies puede ocurrir dentro de una red de comunidades locales potencialmente comunicadas por procesos de dispersión, llamada metacomunidad (Hubbell, 2001; Leibold & Mikkelson, 2002) y que diferentes factores tanto regionales e históricos, como bióticos, influyen en la estructura de esta (Heino et al., 2015; Josefson, 2016).

La distribución espacial de las especies dentro de las metacomunidades se puede analizar de dos formas: una aproximación se enfoca en los mecanismos que explican la variación composicional de las especies en las comunidades (Leibold et al., 2004), mientras que la otra se enfoca en los patrones de distribución espacial de las especies a través de gradientes ambientales (Leibold & Mikkelson, 2002; Presley et al., 2010).

Por un lado, los mecanismos que determinan la estructura y composición de las metacomunidades, mejor conocidos como los paradigmas de la teoría de metacomunidades son: dinámica de parche, “species sorting”, efecto de masa y la perspectiva neutral (Cottenie, 2005; Leibold et al., 2004). A continuación, se explicará brevemente en qué consiste cada uno:

- **Dinámica de parche:** considera que los parches de una metacomunidad son homogéneos, estos sufren extinciones tanto por procesos determinísticos como estocásticos y pueden estar influidos por interacciones interespecíficas que se contrarrestan por medio de la dispersión. La coexistencia es posible en este paradigma gracias al compromiso ecológico entre la habilidad competitiva y la tasa de dispersión de las especies, (Leibold et al., 2004; Leibold & Chase, 2018; Levins & Culver, 1971).
- **“Species sorting”:** en este mecanismo la heterogeneidad ambiental es muy importante, ya que se asume que las comunidades cambian a lo largo de gradientes ambientales. Asimismo, se consideran los efectos de los elementos abióticos sobre las tasas de vida de las poblaciones y las interacciones de las especies. Este paradigma se enfoca en compromisos ecológicos de las especies que permiten sus especialización en diferentes condiciones locales (o tipos de parche), (Chase & Leibold, 2003; Leibold et al., 2004).

- **Efecto de masa:** se enfoca en los efectos de la emigración y de la inmigración sobre las dinámicas de las poblaciones locales, que son afectadas por estos eventos de dispersión. Similar al paradigma de “species sorting”, el efecto de masa requiere de una heterogeneidad ambiental entre parches y de conectividad entre estos para garantizar la existencia de relaciones fuente-sumidero entre las poblaciones de diferentes parches. Si las tasas de dispersión son muy altas, el efecto de masa puede reducir la coexistencia en la metacomunidad a nivel regional, resultando en una homogeneización de las comunidades locales (Leibold et al., 2004; Mouquet & Loreau, 2003).
- **Paradigma neutral:** este paradigma asume que las especies dentro de una metacomunidad son idénticas y que la coexistencia de estas solamente está influida por procesos estocásticos de demografía, colonización, extinción y limitación de la dispersión. Si no existe especiación e inmigración desde fuera de la metacomunidad, el modelo neutral tenderá lentamente a perder todas las especies competitivas, excepto a una, por un proceso lento de extinción. Es considerado como una hipótesis nula a comparar con los paradigmas anteriores y es contrario al mecanismo de “species sorting”, (Hubbell, 2001; Leibold et al., 2004; Leibold & Chase, 2018).

En el caso de los patrones, entendidos como el arreglo espacial de las especies que percibimos, para determinar la estructura de una metacomunidad se deben analizar los “elementos de la estructura de la metacomunidad” (EMS por sus siglas en inglés) a través de matrices de presencia-ausencia entre las especies y los sitios de colecta, estos elementos son: coherencia, recambio de especies o “turnover” y “boundary clumping”. Según el marco conceptual propuesto por Leibold y Mikkelson (2002), la coherencia se mide al contar las interrupciones en las distribuciones de especies o en las composiciones de los sitios; cuando una matriz no es coherente, significa que las especies de la metacomunidad no responden al mismo gradiente ambiental. Por otro lado, el recambio de especies o “turnover” es una medida del reemplazo de una especie por otra a lo largo del eje de ordenación o gradiente ambiental. Finalmente, el “boundary clumping” mide el grado en el que los bordes de los rangos de las especies son coincidentes, es decir, si ocurren o no en el mismo sitio.

Una vez realizados los análisis de EMS, se pueden identificar cinco estructuras o patrones de metacomunidades: tablero de ajedrez, anidado, “evenly spaced”, Gleasoniano, Clementsiano, o un patrón aleatorio (Presley et al., 2010). En seguida, se describirán brevemente las características de cada uno de los patrones mencionados:

- **Clemenstiano:** es una metacomunidad idealizada, basada en una historia evolutiva compartida y con rangos de bordes que coinciden; las especies están distribuidas a lo largo de un gradiente ambiental en forma de comunidades discretas que se reemplazan entre sí como grupos (Clements, 1916; Leibold & Mikkelson, 2002).
- **Gleasoniano:** las especies se distribuyen a lo largo de un gradiente, sin embargo, cada especie responde de forma individualista a las condiciones ambientales. La coexistencia de las especies es consecuencia de una similitud entre los requerimientos y tolerancias de las diferentes especies (Gleason, 1926; Leibold & Mikkelson, 2002; Presley et al., 2010).
- **“Evenly spaced”:** los gradientes resultan en comunidades que no son discretas, sin embargo, los rangos de las especies se encuentran arreglados de una forma más espaciada que la esperada por el azar. En las metacomunidades con esta estructura existe una fuerte competencia interespecífica (Leibold & Mikkelson, 2002; Tilman, 1982).
- **Tablero de ajedrez:** los pares de especies tienen distribuciones mutuamente excluyentes, no obstante, esos pares ocurren de forma independiente a otros pares de especies (Diamond, 1975; Leibold & Mikkelson, 2002).
- **Anidado:** las especies de diferentes sitios conforman un conjunto formal de subconjuntos anidados. Generalmente se observa que las especies de los sitios menos diversos son un sobconjunto de todas las especies que están presentes en los sitios más diversos. La pérdida de especies en los conjuntos menos diversos está asociada a las características especie específicas (Leibold & Mikkelson, 2002; Patterson & Atmar, 1986).
- **Aleatorio:** la distribución de las especies no responde a ningún gradiente u otro patrón detectable (Simberloff, 1983).

Es importante mencionar que Presley et al., (2010) propusieron el uso de quasi estructuras (p. ej., quasi Clementsiana, quasi Gleasoniana) cuando el valor del recambio de especies de los análisis no es significativo; en este caso, las quasi estructuras tienen las mismas características que las estructuras reales pero las fuerzas que las estructuran son más débiles comparadas con aquellas que afectan a las estructuras reales. Asimismo, las quasi estructuras pueden surgir ante dos situaciones: cuando la amplitud del nicho de la especie es mayor que el gradiente ambiental existente, o cuando solo una parte del gradiente empírico es muestreado (Ochoa-Ochoa & Whittaker, 2014).

Antecedentes

Los estudios que se han realizado sobre los mecanismos que estructuran las metacomunidades son principalmente sobre invertebrados, en su mayoría en sistemas acuáticos (Brasil et al., 2017; Heino et al., 2015; Urban, 2004; Willig et al., 2011). Sin embargo, recientemente esta perspectiva ha cobrado fuerza también en estudios de vertebrados terrestres en el continente americano, por ejemplo en comunidades de: anfibios y serpientes en Brasil (Cavalheri et al., 2015; Delatorre et al., 2015; Provete et al., 2014), aves en Cuba, las islas Galápagos y Chile (García–Quintas & A., 2017; Lawson et al., 2019; Meynard & Quinn, 2008), roedores en Estados Unidos, México y Argentina (López-González & Lozano, 2015; Massa et al., 2020; Stevens & Tello, 2009, 2012), o murciélagos en México, Paraguay y Brasil (López-González et al., 2012, 2015; Presley et al., 2009; Stevens et al., 2020).

No obstante, a la fecha existen pocos estudios que investiguen metacomunidades de vertebrados en ambientes antropogénicos o perturbados anteriormente por el humano. Un estudio recientemente presentado en la plataforma bioRxiv (Dalmolin et al., 2020) identificó los efectos de los caminos y monocultivos de pinos sobre las metacomunidades de anfibios. Otros estudios en el Desierto Chihuahuense, Estados Unidos, se enfocaron en encontrar los patrones y mecanismos que estructuran una metacomunidad de lagartijas en un paisaje fragmentado (Leavitt & Fitzgerald, 2013; Ryberg & Fitzgerald, 2016). En el caso de mamíferos pequeños no voladores, de la Sancha et al. (2014) analizaron los efectos de la deforestación sobre la estructura una metacomunidad en un bosque fragmentado en el Bosque Atlántico y sus patrones biogeográficos históricos.

Asimismo, en Costa Rica, se estudiaron los efectos de la modificación antropogénica del paisaje sobre la estructura de una metacomunidad de murciélagos (Cisneros et al., 2015).

En México pocas veces se ha empleado análisis de metacomunidades para comprender los procesos y mecanismos que estructuran a las comunidades del país en ambientes con perturbación antropogénica y en proceso de regeneración. Por un lado, dos investigaciones realizadas en Chiapas estudiaron: 1) los mecanismos que estructuran a las metacomunidades de anfibios en la Selva Lacandona en un gradiente de sucesión ecológica (Hernández-Ordóñez et al., 2019), y 2) la variación espacial y temporal (entre temporadas) de la estructura de la metacomunidades en un bosque tropical húmedo en sitios con diferentes grados de perturbación (Ochoa-Ochoa & Whittaker, 2014). El otro grupo estudiado desde el marco conceptual de comunidades en México es el de las aves; en la región de la Sierra Tarahumara se compararon la composición y tamaño de las metacomunidades entre sitios manejados (ejidos) y no manejados (parque nacional), (Carrillo-Rubio et al., 2014); además, Leyequién-Abarca et al. (2006) estudiaron a las metacomunidades de aves de una zona agroecológica donde se practica el cultivo tradicional de café de sombra. Por otro lado, una serie de trabajos en el BTS de Chamela, Jalisco, estudió las respuestas de las comunidades de herpetofauna (Fraga-Ramírez et al., 2017), murciélagos y sus ectoparásitos (Hernández-Martínez et al., 2019; Martínez-Ferreira et al., 2020), roedores (Morales-Díaz et al., 2019) y aves (Ruiz-García & Avila-Cabadilla, 2016) en etapas sucesionales tempranas.

En general, en estos estudios se ha encontrado que las comunidades responden a gradientes ambientales relacionados con los atributos del paisaje (por ejemplo: conectividad o configuración de los parches), así como atributos de la vegetación (por ejemplo: cobertura del dosel). Estos resultados sugieren que el efecto de masa y “species sorting” son unos de los principales mecanismos que actúan sobre las metacomunidades de vertebrados terrestres en ambientes perturbados.

No obstante, existen escasos trabajos de metacomunidades de carácter comparativo (multitaxa) que permitan entender, por ejemplo, los factores y procesos que estructuran las metacomunidades de diferentes grupos de vertebrados en un mismo sistema. Entre los pocos que existen, uno de ellos compara las estructuras las metacomunidades de murciélagos, aves y roedores en un gradiente de elevación en Perú (Presley et al., 2012); mientras que otro consiste en una revisión en la que se analizan la biodiversidad y la estructura de metacomunidades, tanto vertebrados como invertebrados, a lo largo de gradientes de altitud en bosques de niebla (Willig & Presley, 2016). En México en particular, no hay trabajos que integren la información de las respuestas de las metacomunidades de diferentes grupos de vertebrados terrestres y mucho menos enfocados en los estadios tempranos de la sucesión en un paisaje antropogénico. En este sentido, hasta donde sabemos, este sería el primer trabajo en evaluar y comparar el efecto de la variación de la vegetación y del paisaje a diferentes escalas sobre diferentes grupos de vertebrados durante las etapas sucesionales tempranas de un bosque tropical.

De manera general, el objetivo de este trabajo es identificar y contrastar entre diferentes grupos de vertebrados terrestres (anuros, lagartijas, serpientes, aves, roedores y murciélagos) los factores y procesos que potencialmente estructuran sus metacomunidades en etapas iniciales de la sucesión ecológica de un bosque tropical seco. Nos enfocamos en sitios que representan las etapas iniciales de la sucesión, debido a que: 1) es el tipo de cobertura predominante en una gran proporción de los paisajes tropicales, 2) el entendimiento de los factores y procesos que estructuran las metacomunidades de vertebrados en estas etapas de la sucesión es de vital importancia para la conservación, el manejo y la restauración de este ecosistema y 3) los atributos de las comunidades asociadas a estos estadios pueden determinar en gran medida el curso de proceso sucesional que subyace a la regeneración natural y, con ello, el grado de resiliencia de este ecosistema.

El resultado de este trabajo se encuentra reflejado en el artículo científico “Vertebrate metacommunities along anthropogenic gradients in a tropical dry forest region”, que se someterá a publicación en una revisa indizada. Este trabajo se realizó en el marco de los proyectos financiados por el “Programa de Apoyo a Proyectos de Investigación e Innovación Tecnológica” de la Universidad Nacional Autónoma de México (L.D.A.C., IA-

203413), (M.Y.A.A., IA-204014); y por el Consejo Nacional de Ciencia y Tecnología (L.D.A.C., CB-222202). Mi contribución al artículo en particular fue, bajo la dirección de mis tutores, integrar la información de los diferentes grupos de vertebrados y analizarla utilizando el marco conceptual de las metacomunidades para responder la pregunta planteada en esta tesis. En este sentido, participé activamente en el diseño y redacción del manuscrito y también estuve a cargo del análisis e interpretación de los datos.

Capítulo 2

VERTEBRATE METACOMMUNITIES ALONG ANTHROPOGENIC GRADIENTS IN A TROPICAL DRY FOREST REGION

Ramírez-Sánchez, Oriana [a]; Suazo-Ortuño, Ireri [b]; Benitez-Malvido, Julieta [c]; Alvarado-Díaz, Javier [b]; Lobato-García, Juan Manuel [c]; Zamora-Espinosa, Mayra Edith [b]; Fraga-Ramírez, Yesenia[b]; Ruiz-García, Sole Yered [d]; Morales-Díaz, Sharon Patricia [d]; Oyama, Ken [a]; Alvarez-Añorve, Mariana Yolotl [e*]; Avila-Cabadilla, Luis Daniel [e*].

[a] *Escuela Nacional de Estudios Superiores, Unidad Morelia, Universidad Nacional Autónoma de México, Antigua Carretera a Pátzcuaro No. 8701, Col. Ex Hacienda de San José de la Huerta, C.P. 58190, Morelia, Michoacán, Mexico.*

[b] *Instituto de Investigaciones sobre los Recursos Naturales, Universidad Michoacana de San Nicolás de Hidalgo, Av. San Juanito Itzicuaros/n, Col. Nueva Esperanza, Morelia, Michoacán, México.*

[c] *Instituto de Investigaciones en Ecosistemas y Sustentabilidad, Universidad Nacional Autónoma de México, Antigua Carretera a Pátzcuaro No. 8701, Col. Ex Hacienda de San José de la Huerta, C.P. 58190, Morelia, Michoacán, Mexico.*

[d] *Facultad de Estudios Superiores Zaragoza, Universidad Nacional Autónoma de México, Ciudad de México, México, Campus II Batalla 5 de mayo s/n esquina Fuerte de Loreto, Col. Ejército de Oriente, Iztapalapa, C.P. 09230, Ciudad de México, México.*

[e] *Escuela Nacional de Estudios Superiores, Unidad Mérida, Universidad Nacional Autónoma de México, Carretera Mérida-Tetiz km. 4.5, C.P. 97357, Ucú, Yucatán, Mexico.*

Corresponding authors: avila@enesmerida.unam.mx (ACLD); malvarez@enesmerida.unam.mx (AAMY)

Abstract

Anthropogenic activities such as land-use change are converting forests to landscapes dominated by early successional stages (ESS). This study aimed to identify the mechanisms and structures that shape metacommunities of terrestrial vertebrates (anurans, lizards, snakes, birds, rodents, and bats) in a tropical dry forest. For this purpose, we sampled the vertebrates in 13 sites representing secondary and old-growth forests. We found a high beta diversity in all groups, with low values of nestedness indicating that turnover contributed the most to beta diversity. All groups were distributed along a latent gradient according to the analyses using the "elements of metacommunity structure". Some vertebrate metacommunities showed a quasi-Gleasonian structure (anurans, lizards, snakes, and migratory birds); in contrast, bats and migratory birds showed a quasi-Clementsian structure and rodent group a Gleasonian one. In general, groups were affected by landscape and vegetation attributes, suggesting that species sorting and mass effects are structuring the metacommunities in secondary forests. Nevertheless, we observed that: 1) various species are found in ESS, including some species exclusive of mature forests, probably because secondary forests are used as stepping stones and corridors; 2) old-growth forest is acting as a source of species that disperse to forest remnants and colonize them; 3) landscape connectivity, forest cover, and vegetation composition are the most important environmental variables affecting vertebrate metacommunities in Chamela dry forest.

Key Words

Metacommunity, terrestrial vertebrates, beta diversity, turnover, tropical dry forest, early successional stages

Introduction

The anthropogenic transformations of natural landscapes have caused that today almost the 60% of the remaining forest regions show low landscape-level integrity (Grantham et al. 2020). This significantly impacts not only on the species abundance and distribution, but also on the ecological processes in which they are involved, with consequences for ecosystems resilience, ecosystem services and human health (Betts et al. 2017, Watson et al. 2018). This is particularly evident in the tropics, the most biodiverse and threatened regions around the world, containing over 50% of terrestrial species, while 50% of its coverage has been degraded globally (Stork et al. 2009, Hansen et al. 2013, Betts et al. 2017, FAO and UNEP 2020). In these regions, vegetation continuums are being rapidly replaced by complex mosaics of farmlands, cattle pastures, logging forests and human settlements, therefore, the vegetation is increasingly embedded in anthropogenic matrices, increasingly represented by young secondary forests, and tends to occur in smaller and more isolated patches, displaying a higher edge effect (Chazdon et al. 2009, Haddad et al. 2015).

In this way, human disturbance results in substantial transformation of the environmental conditions, resources availability and biodiversity distribution in tropical forest regions, reducing the functional landscape connectivity and altering the spatial heterogeneity that characterizes old-growth landscapes, the ones which the biota has a closer evolutionary relationship with (Givnish 1999). Given this scenario, it is necessary to address local-scale processes structuring single communities, restricted to a certain portion of emerging anthropogenic gradients, but it is also necessary to address the structuration of the metacommunities, by simultaneously analyzing the species distributional patterns across sets of communities potentially connected through dispersal, which together cover larger portions of emerging gradients (Leibold and Chase 2018, Presley et al. 2019). This will allow us to gain a broader understanding about the consequences of habitat shift in amount, quality, and distribution, which is particularly relevant for those very diverse *taxa* playing critical roles in ecosystems. For example, until now just a few studies have evaluated the structure and mechanisms underlying vertebrates metacommunities along anthropogenic landscape gradients; this topic is an open question today and is considered one of the great challenges of the 21st century (Cisneros et al. 2015, Presley et al. 2019). Addressing these questions is especially important since vertebrates play important ecological roles, by influencing nutrient recycling, ecosystem productivity, and other processes such as mycorrhizal dispersal, herbivory, pollination, and seed dispersal, which determine the biophysical properties of ecosystems (Dirzo et al. 2014).

In general, the combination of species ecological traits and requirements (defining species dispersal capability and habitat affinity), with the characteristics of anthropogenic disturbance (defining environmental heterogeneity and landscape connectivity), determine the species distribution along the anthropogenic gradients as well as the extent of spatial change in species composition (β-diversity) (Ewers and Didham 2006). For example, on one hand, a reduction in environmental heterogeneity and the proliferation of disturbance-adapted species could result in a reduction of β-diversity – a metacommunity species composition homogenization –, whereas, on the other hand, an increase in environmental heterogeneity or spatial constrains and the environmental sorting due to species affinity by patches differing in their biotic and abiotic environment could result in an increase of β-diversity – a species composition differentiation – (Cisneros et al. 2015, Morante-Filho et al. 2016). Additionally, it has been expected that metacommunities present nested structures in human-modified landscapes, that is, less speciose communities are composed by a nested subset of species found in the more specious ones, because of a non-random pattern of species loss by interspecific differences in competitive ability and dispersal capacity (Atmar and Patterson 1993). However, contrary to the expectations, most vertebrates metacommunity (i.e., small non volant mammals and different phyllostomid bats ensembles) evaluated to date were never nested along a richness gradient, since they have exhibited Gleasonian (individualistic responses of species along gradients), Clementsian (bundles of species forming cohesive units that are exchanged along gradients) or chequerboard (mutually exclusive species pair) structures. Such structures were associated to local habitat (i.e., fragment size) and landscape attributes (distance between forest patches, edge density, proportion of pasture, forest patch density), as well as to seasonality and historical factors (i.e., vicariance events associated to natural barriers (Clements 1916, Gleason 1926, Diamond 1975, de la Sancha et al. 2014, Cisneros et al. 2015).

Taking into consideration the described scenario, this study aimed to characterize cross-*taxa* patterns in vertebrates metacommunities along anthropogenic gradients to identify potential mechanisms and factor shaping such metacommunities. For this study we focus on a set of quite diverse *taxa*, from the taxonomic and functional point of view: anurans (for amphibians), lizards and snakes (for reptiles), resident and migratory passerines (for birds), and rodents and noctilionids bats (for mammals). Specifically, we first characterized the spatial β-diversity for each study *taxa*, evaluating the contribution of species replacement and species loss to such change (Baselga 2010). Second, we employed a patterns-based approach looking for potential mechanisms underlying the structuring of vertebrates metacommunities (Leibold and Mikkelson 2002, Holyoak et al. 2005, Presley et al. 2010). Specifically, we performed the hierarchical analysis of three elements of metacommunities (coherence, range turnover, and boundary clumping), to discriminate among six idealized patterns of species distribution: Clementsian, Gleasonian, checkerboard, evenly spaced, nested, and random distribution, as well as among their quasi-structures (Clements 1916, Gleason

1926, Diamond 1975, Tilman 1982, Patterson and Atmar 1986, Presley et al. 2010). Finally, we evaluated for patches (i.e., floristic composition and vegetation structure) and landscape attributes (landscape composition and configuration), influencing species distribution.

To our knowledge, very few studies have simultaneously evaluated various vertebrate metacommunities (Acevedo-Charry and Aide 2019), but none of them offer an integrated view of the metacommunities structure and its structuring mechanisms on anthropogenic landscapes. As some studies have demonstrated that different *taxa* have differential responses to human disturbances, it is important to account for such differences by carrying out cross-*taxa* studies (Torres et al. 2014). With this study we look to expand the traditional empirical community ecology approach, focused on local processes, to a metacommunity approach, to generate an integrated and wider understanding on the effect of anthropogenic transformation of tropical landscapes over fauna.

As the location for this study, we selected a tropical dry forest (TDF) region mainly transformed by agricultural and cattle ranging. Globally, TDFs are characterized by a high level of endemism and by a high alfa and beta diversity. However, they are experiencing high rates of deforestation and disturbance, being some of the most threatened ecosystems in the world (Olson and Dinerstein 1998, Miles et al. 2006, Rzedowski 2006, Pennington et al. 2009, Meave et al. 2012). For this study we focused on young secondary forests because: 1) they are the main type of coverage in a great proportion of tropical forests (Miles et al. 2006), 2) the understanding of the factors and processes that structure vertebrate metacommunities during early successional stages (ESS) is crucial to conservation, restoration, and management of dry forests, and there is a lack of information to this respect (Thompson and Donnelly 2018), 3) the attributes of the communities associated to early successional stages can determine the path of the successional process underlying natural regeneration, and, consequently, the resilience degree of the ecosystem. To date, the study of the fauna in young secondary forests has generally received little scientific attention, and the early successional stage has been recognized as “the forgotten stage of forest succession” (Swanson et al. 2011).

In general, we expect that the structure of vertebrates metacommunities and the factors that determine such structure along anthropogenic gradients are largely determined by the species life history traits prevalent in metacommunities, such as, movement behavior (i.e., resident or migratory), diel time partitioning strategy, home range, feeding guild, type of roost, as well as by other factors such as the proportion of invasive species or the degree of evolutionary relatedness among species. Specifically, regarding the β-diversity patterns, we expect that *taxa* with higher dispersal abilities (i.e., birds and bats) will display less spatial species turnover and will be less sensible to habitat modification (i.e., simplification of vegetation structural complexity, changes in plant communities composition, reduction in the original vegetation coverage) than *taxa* with lower dispersal abilities (i.e., anurans, lizards, rodents), as a high dispersal rate contributes to the "rescue effect", which favors the species persistence in disturbed habitats due to the continuous flow of individuals between patches (Brown and Kodric-Brown 1977, Hames et al. 2001). In addition, we expect that metacommunities with a higher proportion of invasive or disturbance-adapted native species will display a low β-diversity, due to a process of biotic homogenization resulting from the loss of species with high habitat specialization requirements and from the ubiquity of disturbance-tolerant species (McKinney and Lockwood 1999). Regarding the metacommunity structure, we expect that all vertebrate *taxa* show a significant coherence and deviate from random species distribution, because the study metacommunities are composed by a set of horizontal communities, where the species tend to be similar in their ecological requirements and, consequently, should respond to common environmental gradients. Indeed, we expect this to be more marked in those metacommunities composed of more related species, as a consequence of phylogenetic conservatism. In addition, we expect that metacommunities composed by species similar in their ecological requirements and with a low dispersal capacity or restricted to environmental conditions (i.e., less modified, or highly forested sites) will display a chequerboard pattern, as a consequence of competitive exclusion between pairs of species. We also expect that metacommunities where species with a high dispersal capacity dominate will display a Clementsian pattern, as the mobility reduce the interaction strengths (Cisneros et al. 2015). Finally, regarding the effect of vegetation patches and landscape attributes on species occurrence, we expect that all study metacommunities will be modulated by changes in vegetation structure complexity because they are composed of species with different degrees of habitat specialization. This could be more marked for those metacommunities dominated by diurnal species, which are exposed to high variation in environmental conditions, such as radiation level, temperature, humidity, and water availability; these conditions are tightly associated to changes in vegetation structure and can act as environmental filters on species composition (Alvarez-Añorve et al. 2012, Fraga-Ramírez et al. 2017). Finally, we expect that metacommunities composed predominantly by species with low vagility will be less sensible to changes at landscape scale than those composed predominantly by high vagility species, but more sensible to changes in vegetation composition and structure. In this sense, we also expect to find that metacommunities composed of native species are more sensitive to the loss of the original vegetation cover than migratory species, due to their closer evolutionary relationship with such vegetation.

Methods

Study area

The study was conducted in the Chamela region, around the Chamela-Cuixmala Biosphere Reserve (CCBR), located on the west coast of Mexico in the state of Jalisco, Mexico (19°22′–19°35′N, 104°56′–105°03′W). The region is characterized by a markedly seasonal rainfall pattern, with a dry season lasting approximately seven months (from November to May). The average annual rainfall is 915 ± 311 (S.D.) mm, and the average annual temperature is 24.6°C (Chamela Biological Station: http://www.ibiologia.unam.mx/ebchamela/www/clima.html). This area is dominated by tropical dry forest vegetation (56.1% of the Jalisco coast) and some patches of riparian forest (RF) (3.7% of the Jalisco coast), followed by other types of vegetation (Lott 2002, Lott and Atkinson 2006, Sánchez-Azofeifa et al. 2009).

As a consequence of forest use, the landscape surrounding the CCBR is fragmented and composed of a complex mosaic of patches representing different successional stages, cattle pastures, or agricultural fields (Burgos and Maass 2004, Castillo et al. 2005).

Study system

For this study, we selected 11 permanent sites outside of the CCBR that represented the early successional stages (from 3 to 9 years of abandonment) of the TDF and two sites inside the reserve representing advanced successional stages (more than 50 years of abandonment) (Fig. 1). The sites location and abandonment age were determined with the help of classified ASTER (Advanced Spaceborne Thermal Emission and Reflection Radiometer) satellite images generated for the region, high-resolution satellite images (Google Earth website: http://earth.google.com), and information from interviews with farmers and landowners (Sánchez-Azofeifa et al. 2009, Avila-Cabadilla et al. 2012). Finally, sites with the following characteristics were selected: 1) accessible

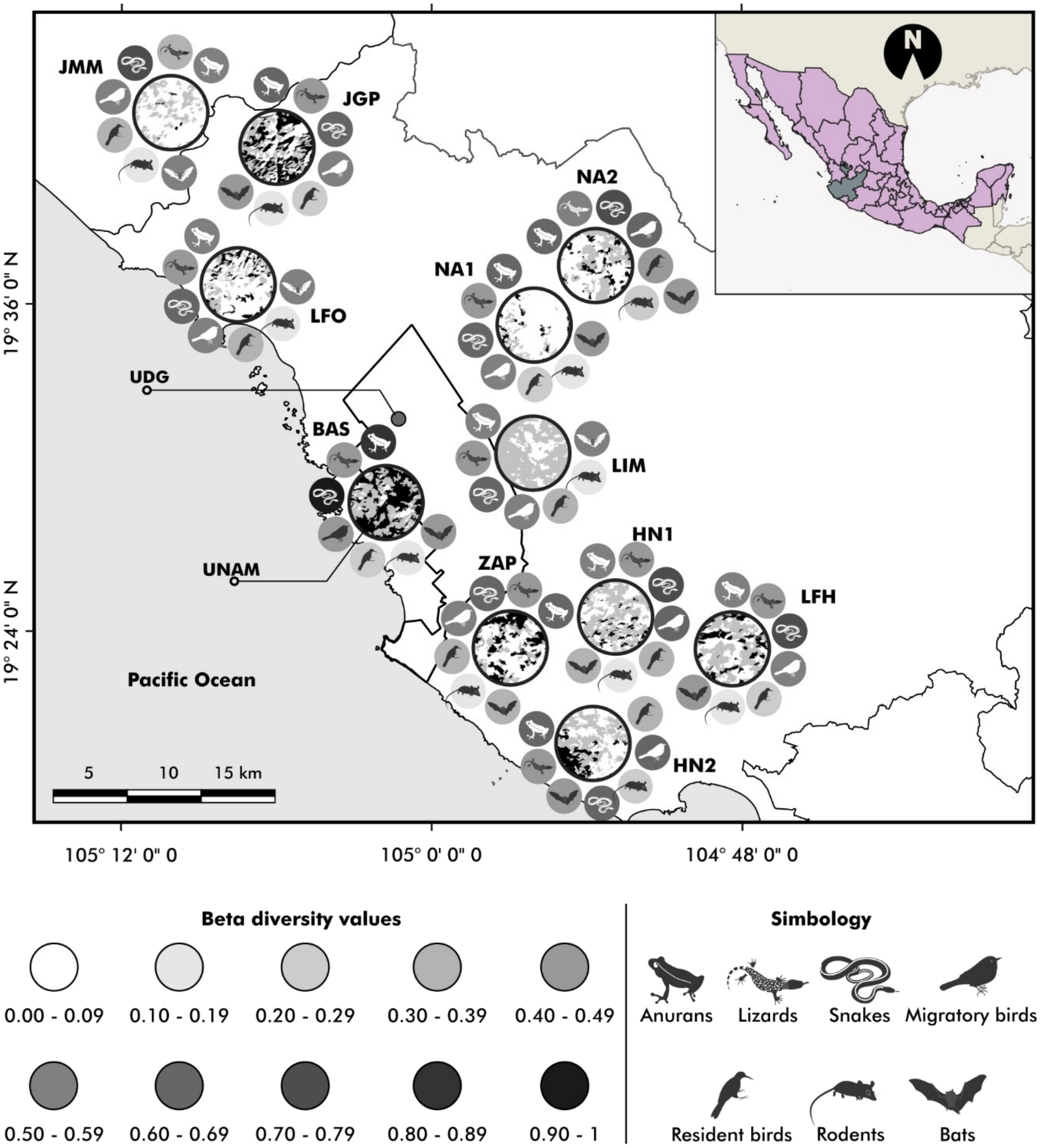


Figure 1. Distribution of sampling sites along the Jalisco coast, Mexico and their corresponding buffers (circles) representing the maximum focal scale (3000 m) considered and the type of land cover around the study sites. Land cover classes are: 1) tropical dry forest (gray), 2) riparian forest (black), and 3) other types of coverage (white). Circles with animals and different shading represent values of total beta diversity for each taxon in each site.

by road, 2) area of at least 200 x 200 m, 3) minimum distance of 3000 m between each other, 4) representing a gradient in the percentage of dry and riparian forest coverage, and 5) slope < 20°. This design avoids common problems of landscape ecology, such as pseudoreplication, spatial autocorrelation, unappropriated spatial scales for the species and processes studied and minimizes the likelihood of incurring in the Type I error in the statistical analyses (Eigenbrod et al. 2011).

Vegetation characterization

We established five transects of 2 × 100 m (1000 m^2) separated from each other 25 m and at 50 m (at least) from other vegetation types in each site. Vegetation sampling was conducted during the rainy season, when most of the plants in the region have leaves and fruits, facilitating taxonomic identification. All individuals of plant woody species with a diameter at breast height (DBH -1.30 m-) ≥ 2.5 cm were marked. In addition, we measured the following vegetation attributes: 1) the number of species, 2) the number of individuals, 3) the DBH, 4) the number of branches, 5) the total basal area, and 6) the average height of the ten highest trees. We also measured the Plant Area Index (PAI) during the rainy season using an LAI-2000 Plant Canopy Analyzer (LI-COR, USA). The PAI is the projected plant area per unit of a horizontal plane and is considered a helpful indicator of the vegetation structure and canopy structure; its value increases in sites with a higher number of strata (Fournier et al. 2003).

Understory density was quantified by taking photographs of the vegetation against a white background of 3 x 3 m located at 10 m from the camera at eight random points in every sampling site (adapted from Marsden et al., 2002). This measure estimates the structural complexity of the understory.

For further details about PAI and understory density estimation in the study sites, see Fraga-Ramírez et al. (2017) and Morales-Díaz et al. (2019) studies.

Landscape characterization

The landscape characterization of the vegetation cover adjacent to each site within a ratio of 3000 m was based on classified SPOT-5 images with the following characteristics: 1) a nominal spatial resolution of 10 m, 2) corresponding to the dry season, which facilitates the discrimination of the main types of vegetation in the region (i.e., dry forest, riparian forest, and pasturelands) (Sánchez-Azofeifa et al. 2009, Avila-Cabadilla et al. 2012), 3) free of clouds, 4) projected on the

WGS84/UTM coordinate system, 5) atmospherically corrected, and 6) formed by the first four bands of the SPOT-5 sensor (B1: green, B2: red, B3: near-infrared, B4: infrared medium), plus two additional bands produced by the calculation of the spectral vegetation indexes "Normalized Difference Vegetation Index" (NDVI) and "Single Ratio" (SR), both increasing the discriminant power of the main types of vegetation. Land cover classification included: 1) dry forests, 2) riparian forests, and 3) other types of cover (i.e., crop fields, water, bare soil, and grasslands).

Besides, we calculated two independent landscape metrics: 1) the percentage of landscape coverage (PLAND) as a measure of the availability of TDF and RF, and 2) the effective mesh size (m_{eff}, connectivity), as a measure of the degree of fragmentation of each habitat. The indices were calculated as: $PLAND = (A_1 + A_2 + \ldots A_i + \ldots A_n) / A_{total}$, and the effective mesh size was calculated as $m_{eff} = 1/A_{total} (A_1^2+A_2^2 + \ldots A_i^2 + \ldots A_n^2)$, where n = number of patches, A_{total} = total area of the landscape, and A_i = size of patch i (I = 1, … , n) (Jaeger 2000, McGarigal 2002). The effective mesh size can be interpreted from an ecological perspective as two animals' ability, with a random location in a region, to find each other when moving through a certain type of cover (Jaeger 2000).

For each study site, we estimated the percentage of coverage of TDF and RF at six different spatial scales; this was assessed by using buffers defined by the area comprised between two concentric circumferences centered on the plot of each sampling site, except for the smallest scale, which was defined as a disc-based buffer. The focal scales analyzed included: 500, 1000, 1500, 2000, 2500, and 3000 m radius.

Image classification and the landscape metrics estimation were measured with the software QGIS (v. 2.6.1-Brighton, QGIS Development Team, 2015) and the modules and complements Orfeo, SAGA, GRASS, and LecoS (Landscape Ecology Statistics) implemented in this software.

Sampling of vertebrate groups

Anurans, lizards and snakes: the sampling of herpetofauna was conducted by the same team of four biologists familiar with the local herpetofauna. The method used for the sampling was the Visual Encounter Survey (VES) (Crump and Scott 1994), in which search for animals is on trees, herbs, shrubs, under rocks, logs and ground litter, and on the ground. The search for animals was time-constrained: two hours in the morning, 09:00-11:00, and two hours at night, 22:00-00:00. All detected individuals were captured, and we registered the following attributes: 1) the species, 2) the sex, 3) the relative age, and 4) the reproductive condition. The toes of lizards and frogs as well as the ventral scales of snakes were clipped to avoid counting the same individual more than once. All animals were released on the same site they were captured.

Sites were sampled six times from January 2014 to May 2015, and a total search effort of 1344 person-hours was completed. More details about herpetofaunal sampling can be found on Fraga-Ramírez et al (2017) work.

Birds: the present study is focused on birds of the Passeriformes order, the largest order of birds, which includes more than half of all living bird species (Lovette and Fitzpatrick 2016). Birds sampling was carried out in each study site using eight mist nets (12 x 2.5 m and 30 mm mesh size), covering a total sampling area of 240 m^2. Nets were arranged at ground level within each plot and separated from each other at least 30 m. Additionally, two point counts of a fixed radius were used (time: 10 min, radius: 30 m, distance between point counts: 50 m), following Ralph et al. (1993) methods. Each sampling session lasted 5 hours, and nets were activated at dawn to cover bird activity's main peak (Ralph et al. 1993). During sampling sessions, the nets were checked every 15-30 minutes, and captured individuals were removed and deposited in cloth bags and processed *in situ* later. The following attributes were measured for each bird: 1) the species, 2) the sex, 3) the relative age, and 4) the reproductive condition, *sensu* Ralph et al. (1993). Species identification was determined with the help of Howell and Webb (1995), and NGS (2002) field guides and taxonomic nomenclature used was based on the checklist of the American Ornithologists' Union, including the fifty-fourth supplement (AOU 1998, Chesser et al. 2013). Individuals were released after registering their attributes.

Sites were sampled eight times from July 2013 to June 2015, covering both the dry and the rainy seasons. Further information about birds' sampling can be found in Ruiz-García (2016).

Rodents: rodent sampling was conducted using a standardized sampling unit composed of 100 large folding Sherman traps (https://www.shermantraps.com) set inside a 100 x 100 m grid with a spacing of 10 m. The bait used for the traps was made with vanilla essence, oats, and peanut butter, and the traps remained open from dusk to dawn (11 h). Sampling sessions were carried out during the non-rainy and moonless nights to reduce variation in capture success. Captured individuals were deposited in cloth bags for processing. The following attributes were registered for each rodent: 1) the species, 2) the sex, 3) the relative age, and 4) the reproductive condition. Species determination was carried out with the help of dichotomous keys (Ceballos and Miranda 2000), and taxonomic designation of species follows Reeder and Wilson (2005) and includes modifications presented by (Ceballos 2014). Finally, all individuals were released at the place of capture.

All sites were sampled approximately every 96 ± 4 (SD) days, from July 2013 to February 2015, and 8 sampling sessions per site were carried out, four during the rainy season and four during the dry season. More details about rodent sampling on these sites can be found on Morales-Díaz et al. (2019).

Bats: this study focuses on bats of the Noctilionoidea superfamily, specifically on the Phyllostomidae and Moormopidae families, distributed only on the Neotropic (Jones et al. 2002). The sampling was carried out using in each site a standardized sampling unit composed of six mist nets (12 x 2.6 m and 30 mm mesh size), with a total sampling area of 187 m^2. The nets' arrangement was across potential flight corridors and at ground level within each plot; they were separated from each other by at least 50 m. The nets remained open for 6 hours, being activated one hour before sunset to cover bat activity's main peak (Fenton and Kunz 1977, Williams-Guillén and Perfecto 2011). To evade variation in capture success associated with environmental conditions, we avoided sampling during the full moon and rainy and windy nights (Saldaña-Vázquez and Munguía-Rosas 2013). The nets were checked every 15-30 minutes, and captured individuals were stored in cloth bags and processed *in situ*. For each captured bat, it was registered: 1) the species, 2) the sex, 3) the relative age, and 4) the reproductive condition. Species identification was carried out with the help of the field guide by Medellín et al. (2007), and the reproductive condition was found using the method by Racey (2009). After the register was made, individuals were released at the place of capture.

Sites were sampled approximately every 96 ± 4 (SD) nights for three years, and eight sampling sessions were carried out, covering both the dry and rainy seasons. More details about bat sampling on these sites can be found in Hernández-Martínez et al. (2019) and Martínez-Ferreira et al. (2020).

Data analysis

All statistical analyses were performed in R 4.0.0 (R Core Team, 2020); we excluded the old forest sites from all the analyses and used them only as a reference of preserved forests.

Sampling completeness and spatial autocorrelation test: the percentage of sampled species in relation to the estimated species richness was estimated for all sampling sites; we estimated the species richness by using the rarefaction and extrapolation with Hill numbers estimator; this analysis was performed using the *iNEXT* R package (Hsieh et al. 2016). This estimator facilitates the comparison of biodiversity data as it standardizes samples based on sampling size or sample completeness (Chao et al. 2014). Additionally, we tested the data for spatial autocorrelation using the Spearman correlation-based Mantel test (999 permutations) and the *vegan* R package (Oksanen et al. 2019). We tested the correlation between ecological (Jaccard distance) and geographic distance matrices (Euclidean distance). We considered a $p < 0.05$ value as a significant result for this test.

Beta diversity and partition into its components (turnover and nestedness): this study aimed to understand the mechanisms driving ESS vertebrates metacommunities; thus, rather than just studying a total beta diversity alone, we partitioned it into its components (spatial turnover and nestedness), in order evaluate the contribution of species replacement and species loss to such β-diversity (Baselga 2010, Baselga and Orme 2012, Soininen et al. 2018).

The analyses were performed using the *betapart* R package (Baselga and Orme 2012), which receives as an input a site-by-species incidence matrix (for each group) and calculates the percentage of the turnover and the nestedness that contributes to the total of the beta value quantified by Jaccard distance coefficient. Two analyses were performed per group: 1) the beta multiple comparison, a computation between the 11 ESS sites resulting in a unique value, and 2) the beta pair comparison, based on paired comparisons among all the 11 sites, resulting in a matrix of distances with the values of the comparisons. We used the average of beta pair analysis per site per group to quantify the species composition differentiation of each community with respect to the other communities, while the beta multiple analysis was used to compare the contribution of species replacement and loss to the observed beta diversity in each group.

Elements of metacommunity structure: to detect the best-fit metacommunity structure for anurans, lizards, snakes, bats, rodents, migratory passerines, and resident passerines on the ESS sites of a TDF, we used the Elements of Metacommunity Structure (EMS) approach proposed by Leibold and Mikkelson (2002) and the conceptual framework of Presley et al. (2010). This analysis is divided into three phases, each one refers to a different aspect of the metacommunity structure:

coherence, species turnover, and boundary clumping. Before analysis, site-by-species incidence matrices were ordinated via reciprocal averaging, which extracts the first ordination axis and reduces the number of interruptions in species' ranges, provides a basis for judging whether a metacommunity is nested or dominated by species turnover, and defines the boundaries for species' ranges in relation to the primary axis of compositional variation (Leibold and Mikkelson 2002). The degree of coherence is indicated by the number of embedded absences (an interruption in a range or community) within the axis; to test significance, embedded absences are compared with a null distribution. A non-significant result suggests a random assembly; a negative coherence suggests a checkerboard distribution. Both non-significant and negative results stop the analysis, but if a metacommunity is positively coherent, we must examine the species turnover and the boundary clumping metrics to find its structure (Leibold and Mikkelson 2002, Leibold and Chase 2018).

The turnover analyzes the number of times that a species is replaced by another between two sites in an ordinated matrix (number of replacements) and refers to the changes in species composition across sites. As coherence, results are compared with a null model of replacement values created from 1000 matrices containing randomly shifted species ranges. When turnover is significantly less than expected by chance, a nested distribution is suggested for the metacommunity. If the result is significantly equal or higher than expected by chance, a Clementsian, Gleasonian or evenly spaced structure can be found after boundary clumping analysis (Leibold and Mikkelson 2002). Metacommunities with a non-significant turnover have quasi-structures, that have the same basic characteristics as their idealized structures (Clementsian, evenly spaced, Gleasonian or nested distributions), differing only on the turnover, which is indistinguishable from random (Presley et al. 2010).

The third metric to calculate is the boundary clumping, that tests if the boundaries of the ranges of a given metacommunity coincide more or less than expected by chance. It is measured using Morisita's index; when the result is non-significant, the metacommunity has a Gleasonian or quasi-Gleasonian structure, because community boundaries are randomly distributed. If the index is significantly greater than 1, it suggests a Clementsian or quasi-Clementsian distribution with clumped boundaries; if the value is significantly less than 1, the test indicates over-dispersed boundaries, consistent with evenly spaced, quasi-evenly spaced distributions or hyper-dispersed species loss in nested distributions (Leibold and Mikkelson 2002, Presley et al. 2010, Leibold and Chase 2018).

The ordination via reciprocal averaging and analyses of coherence, turnover, and boundary clumping were conducted using the "Metacommunity" function of the R package *metacom* (Dallas 2014).

Parameters characterizing vegetation attributes: for evaluating the study site variation in specific composition of the vegetation, we carried out Non-Metric Multidimensional Scaling ordinations (NMDS), based on a dissimilarity matrix calculated with the Bray-Curtis coefficient (McCune et al. 2002). The Bray-Curtis coefficient reflects the intuitive ordering of sites by the assignment of the same maximum distance to all pairs of non-taxon-sharing sites. We transformed the species abundance data using the square-root transformation before the analysis for minimizing the influence on the coefficient of those species showing the largest difference in abundance (Kindt and Coe 2005). The scores of the sampling sites in the resulting NMDS axes were used as continuous synthetic variables summarizing site variation regarding the vegetation composition for assessing vertebrate responses to such vegetation attributes (Appendix Table A1). Analysis was conducted using the "metaMDS" function of the R package *vegan* (Oksanen et al. 2019).

Vertebrate groups responses to vegetation and landscape attributes: we evaluated the responses of each metacommunity to environmental variables performing three canonical correspondence analyses (CCA) for each group: 1) one for vegetation attributes, including seven attributes of the vegetation structure and the three synthetic variables summarizing the site composition obtained via the NMDS, 2) one for landscape attributes of dry forest (coverage and connectivity) for all the scales, and 3) one for landscape attributes of riparian forest (coverage and connectivity) for all the scales. We associated a site-by-species incidence matrix for each group and an environmental matrix (vegetation matrix, dry forest landscape matrix, or riparian forest landscape matrix) through CCA (McCune et al. 2002).

After performing the CCA, we identified the important variables and the best model for the CCA (Noble et al. 2004). For model selection, we used the stepwise method based on the Akaike Information Criterion (AIC_c) and we performed an ANOVA on the model selected to test the significance of models and predictors (Burnham and Anderson 2002). We used a CCA because the reciprocal averaging methods agree with metacommunity analysis. The CCA analysis was performed with the R package *vegan*.

Results

Spatial autocorrelation test

Mantel test's results indicated no evidence of spatial structure in the set of data used for hypothesis testing in six taxonomic groups (anurans $r = -0.105$, $p = 0.748$; lizards $r = -0.02798$, $p = 0.516$; snakes $r = -0.2468$, $p = 0.974$; migratory birds $r = 0.05611$, $p = 0.315$; resident birds $r = -0.07636$, $p = 0.668$; rodents $r = 0.1422$, $p = 0.143$). In contrast, bats' data set exhibited evidence of spatial structure according to the Mantel test ($r = 0.3179$, $p = 0.017$).

Completeness

Anurans: we recorded a total of 17 species, 13 genera, and 7 families on the ESS sites, the most speciose family was Hylidae with 7 species (41.17%), 3 species were conspicuous and 2 were restricted (Appendix Table A2). On the OGF sites we registered 10 species, none of them was exclusive of this stage, but 7 species were exclusive of ESS (Appendix Table A2). Our sampling effort reached a sampling completeness average value of 59%, ranging from 4% in an ESS site (JGP) to 86% in another ESS site (LFO). We captured 17 of the 19 registered species of anurans for the region (García and Ceballos 1994).

Lizards: lizards count was of 18 species, 14 genera, and 8 families on the ESS sites, the most speciose family was Phrynosomatidae with 5 (27.77%), 4 species were conspicuous an only 2 were restricted species (Appendix Table A2). On the OGF 13 species were registered and one was exclusive of this stage (*Gerrhonotus liocephalus*). In this sense, 6 species were ESS exclusive (Appendix Table A2). The sampling effort reached a sampling completeness average value of 93%, ranging from 87% in an ESS site (ZAP) to 98% in two ESS sites (JMM and BAS). We captured 19 of the 22 registered species for the region (García and Ceballos 1994).

Snakes: we recorded 20 species of snakes, 18 genera, and 5 families on the ESS sites. The most speciose family was Colubridae with 15 (75%) and the most conspicuous species was *Oxybelis* *aeneus* (10 sites). Five species were present only in one site (Appendix Table A2). On the OGF 11 species were registered and 4 were exclusive of OGF (Appendix Table A2). We found 13 exclusive species of ESS sites (Appendix Table A2). Our sampling effort reached a sampling completeness of 55%, ranging from 6% in an ESS site (NA2) to 93% in an ESS site (JMM). We captured 24 of the 35 species registered for the region (García and Ceballos 1994).

Migratory birds: we found 30 species of migratory birds, 21 genera, and 10 families on the ESS sites. The most speciose family was Parulidae with 9 (30%) and 4 species were conspicuous (Appendix Table A2). Eight species were restricted to only one site (Appendix Table A2). On the OGF 15 species were registered and 1 was exclusive of these sites (*Basileuterus lachrymosus*), whilst 16 species were ESS exclusive (Appendix Table A2). Our sampling effort reached a sampling completeness of 67% ranging from 25% in an ESS site (HN2) to 84% in an ESS site (LFH).

Resident birds: we registered 36 species of resident birds, 31 genera, and 14 families on the ESS sites. The most speciose family was Tyrannidae with 12 (33%) and 10 species were conspicuous (Appendix Table A2). There were 5 restricted species to one site (Appendix Table A2). On the OGF we found 26 species and none of them was exclusive of these sites. The ESS exclusive species were 11 (Appendix Table A2).

Our sampling effort for birds reached sampling completeness of 93% ranging from 86% in an ESS site (JMM) to 100% in an OGF site (UDG). In total we captured 67 of the 118 passerine birds registered for the region (Arizmendi et al. 1990).

Rodents: we found 8 species, 7 genera, and 2 families on the ESS sites. The most speciose family was Cricetidae with 7 (87.5%) and 6 species were conspicuous (Appendix Table A2). On the OGF we registered 6 species, none of them was exclusive of these sites. We found 2 species exclusive of ESS sites (Appendix Table A2). Additionally, we recorded in two ESS sites individuals of *Mus musculus*, we excluded this species from the analyses. The sampling effort reached sampling completeness of 95% ranging from 89% in two ESS sites (LFH and HN1) to 100% in three ESS sites (HN2, JMM, and ZAP) and in an OGF site (UDG). We captured 8 of the 9 terrestrial rodents reported for the region (Ceballos and Miranda 2000).

Bats: for the Mormoopidae family, we found 2 species and 1 genus and for the Phyllostomidae family, we found 12 species of bats and 8 genera on the ESS sites. There were 3 conspicuous species (Appendix Table A2). On the other hand, 4 species were restricted (Appendix Table A2). On the OGF sites, we found 12 species, one of them exclusive of OGF sites (Appendix Table A2). We found 3 ESS exclusive species (Appendix Table A2). Our sampling effort reached sampling completeness of 90% ranging from 73% in an ESS site (JMM) to 100% in an ESS site (LFO). We captured 3 of the 4 Mormoopidae bats registered for the region and 12 of the 15 Phyllostomidae bats registered for the region (Ceballos and Miranda 2000).

Beta diversity: turnover and nestedness

Average values of beta diversity per site per taxon were measured; anurans' and snakes' composition at site BAS showed the highest beta values, while BAS, HN1, JGP, JMM, LFH, LFO, LIM, NA1, and ZAP sites for rodents evinced the lowest beta values (Fig. 1).

The highest values of beta diversity were found in snakes (0.89), anurans (0.85), and migratory passerines (0.84), whereas the lowest values were found in resident passerines (0.69) and rodents (0.54) (Fig. 2). After dividing beta diversity into its components, it was found that spatial turnover contributed the most to beta diversity in all the taxonomic groups studied (Fig. 2), contributing more than 75% in all groups. Bats were the group with the highest value of nestedness, which contributed 22.85% to beta diversity.

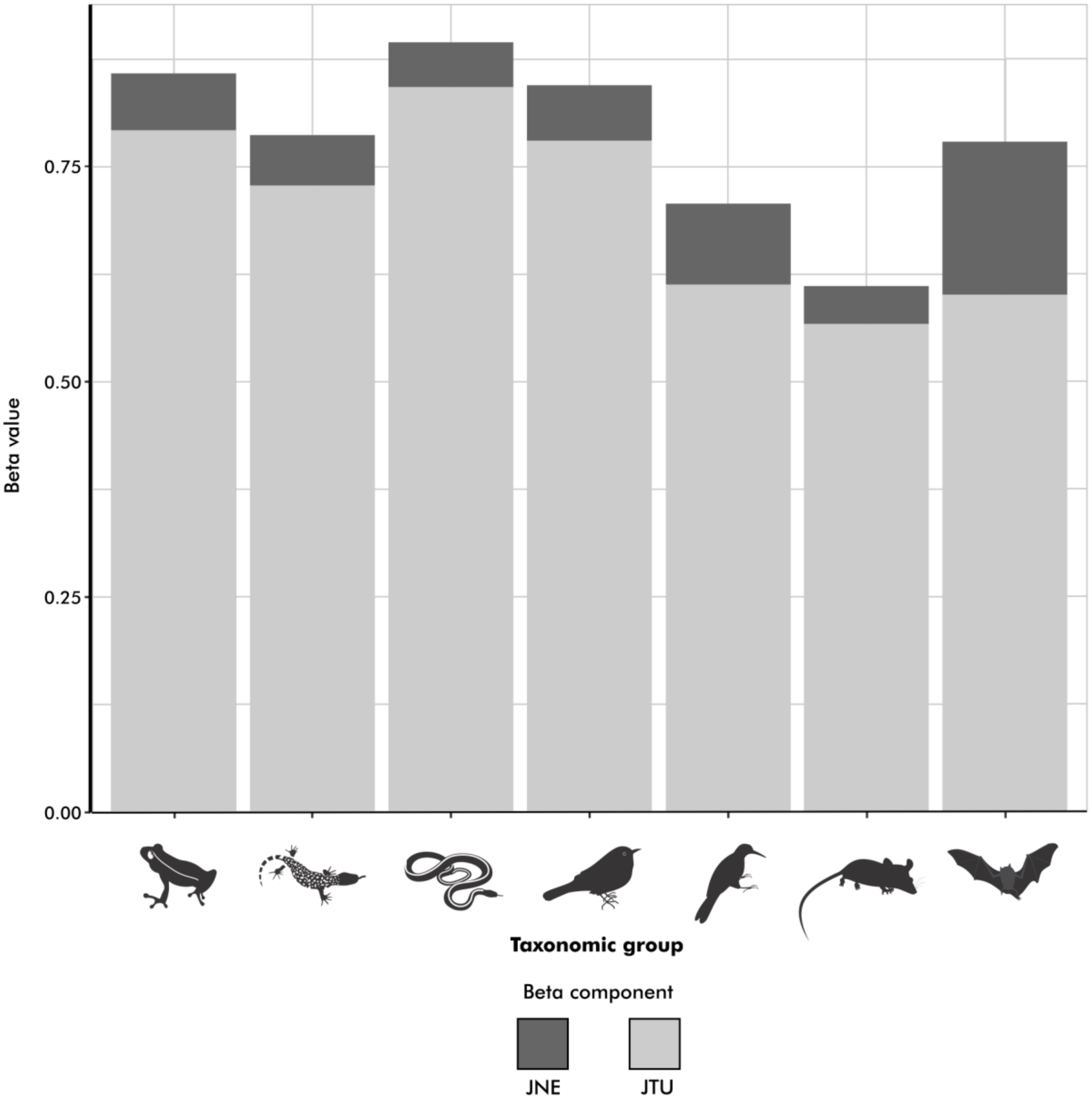


Figure 2. Values of beta partition for anurans, lizards, snakes, migratory birds, resident birds, rodents, and bats showing the contribution of nestedness (JNE) and turnover (JTU).

Metacommunity structure

The occurrences and matrix fill for each group were (Fig. 3): anurans' occurrences = 78, matrix fill = 42%; lizards' occurrences = 106, matrix fill = 54%; snakes' occurrences = 65, matrix fill = 30%; migratory birds' occurrences = 131, matrix fill = 40%; resident birds' occurrences = 246, matrix fill = 62%; rodents' occurrences = 76, matrix fill = 86%; bats' occurrences = 82, matrix fill = 53%.

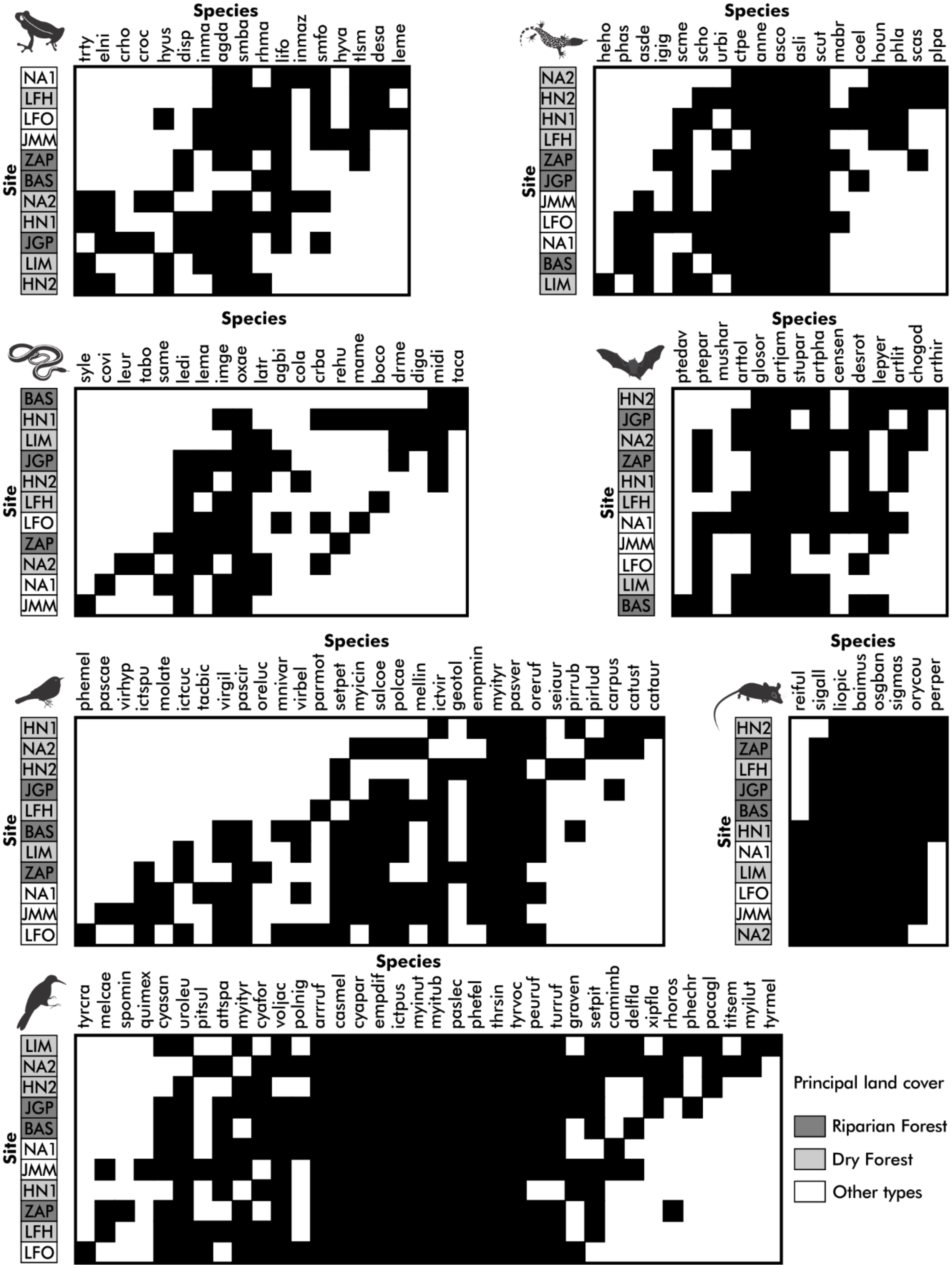
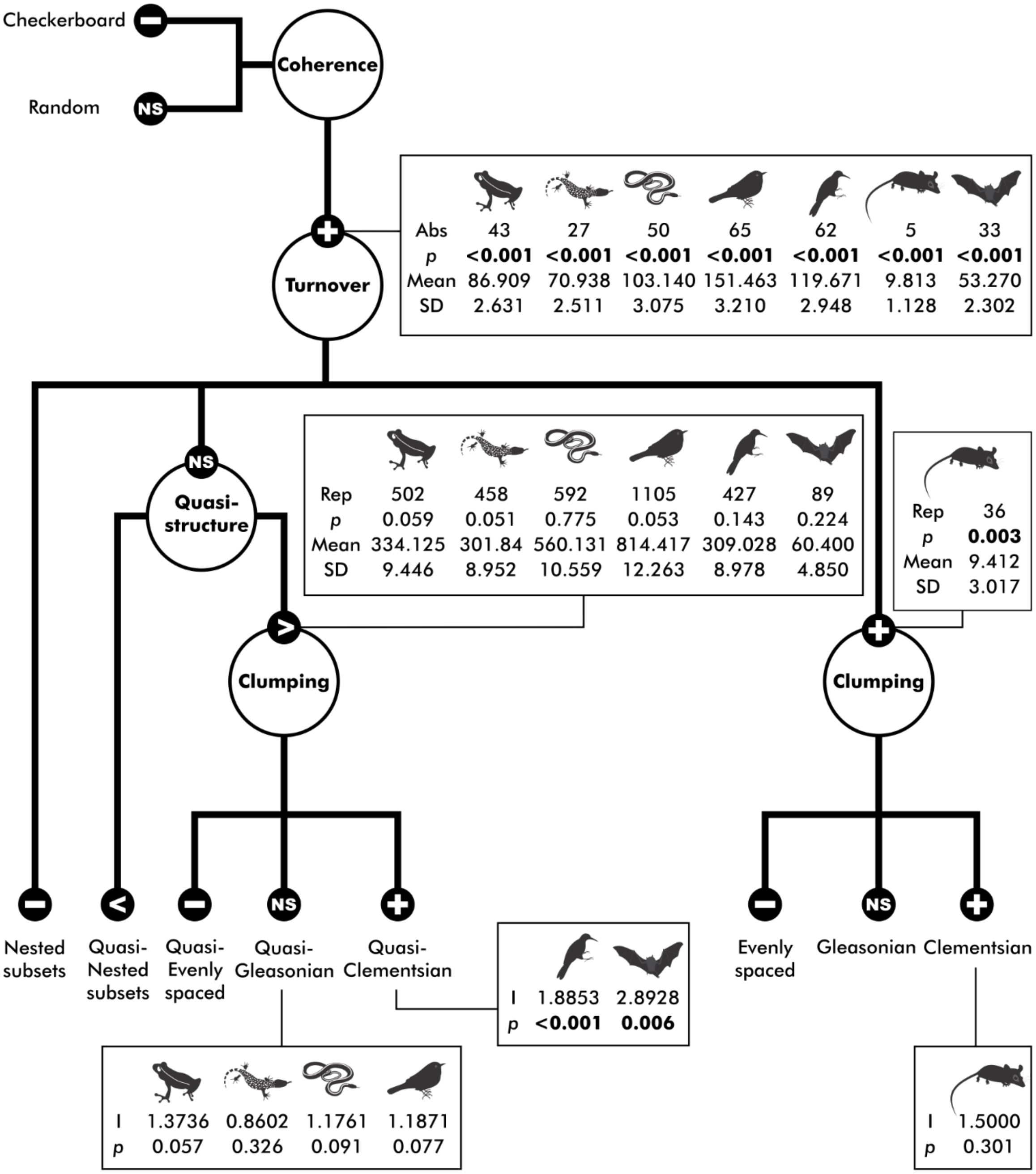


Figure 3. Distributional profiles of species (black squares) as ordered via reciprocal averaging for each taxonomic group of metacommunities. The order of sites (rows) and species (columns) is different among communities. Abbreviations of all species are given in Appendix A.



Abs	43	27	50	65	62	5	33
p	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**
Mean	86.909	70.938	103.140	151.463	119.671	9.813	53.270
SD	2.631	2.511	3.075	3.210	2.948	1.128	2.302

Rep	502	458	592	1105	427	89
p	0.059	0.051	0.775	0.053	0.143	0.224
Mean	334.125	301.84	560.131	814.417	309.028	60.400
SD	9.446	8.952	10.559	12.263	8.978	4.850

Rep	36
p	**0.003**
Mean	9.412
SD	3.017

I	1.8853	2.8928
p	**<0.001**	**0.006**

I	1.3736	0.8602	1.1761	1.1871
p	0.057	0.326	0.091	0.077

I	1.5000
p	0.301

Figure 4. Theoretical framework of the analytical method of Elements of Metacommunity Structure (after Presley et al. 2010) and results of analyses of coherence, species range turnover and range boundary clumping for anurans, lizards, snakes, migratory birds, resident birds, rodents, and bats, in the Chamela region. Significant values (p = <0.05) are represented with numbers in bold.

The metacommunity of each taxonomic group exhibited significant positive and strong coherence (Fig. 4). The value for spatial turnover for rodents was significant and positive, and boundary clumping was non-significant; these values are characteristic of a Gleasonian structure. However, all the other groups evinced non-significant positive results for spatial turnover analysis. In bats and resident birds, boundary clumping was significant and positive, consistent with quasi-Clementsian structure. Anurans, lizards, snakes, and migratory birds evinced non-significant boundary clumping, consistent with quasi-Gleasonian structure.

Vegetation composition

For the NMDS used for creating a synthetic variable summarizing the vegetational variation in composition, we just considered three axes because an additional dimension did not substantially diminish the stress values. The low stress (5.02 on a scale of 0 to 100) indicates no real risk of drawing false inferences from ordination (McCune et al. 2002). The NMDS indicates differences among sites according to vegetation composition (Appendix Table A1).

Responses of vertebrate groups to environmental variables

Anurans: the changes in the specific composition of the communities that are part of the metacommunity were associated with the variation on vegetation attributes and landscape attributes on dry and riparian forests. The resultant model for vegetation attributes ($F(2,8)=2.3191$, $p = 0.001$) explained 36% of the variation in specific composition, including the PAI and the axis MDS2 of the vegetation composition (Fig. 5 and Appendix Fig. A1). The variation associated with the dry forest landscape attributes was explained in 32% by the obtained model ($F(2,8)=1.9597$, $p=0.007$), including connectivity and coverage at the scale of 1000 m (Fig. 6 and Appendix Fig. A2). Finally, the resulting model for landscape attributes of riparian forest ($F(1,9)=1.8449$, $p=0.24$) explained the 17% of the variation in anurans' communities, including the coverage at 1500 m scale (Fig. 6 and Appendix Fig. A3).

Lizards: vegetation attributes were found to explain the 24% of the variation on the metacommunity assemblage of lizards in the resultant model ($F(1,9)$, $p=0.004$), including the height of woody individuals (Fig. 5 and Appendix Fig. A4).

Snakes: we found that none of the variables regarding vegetation and landscape attributes was associated with variation in species composition of metacommunities of snakes.

Migratory birds: we found that the variation on the metacommunity of migratory birds was influenced by the Stem Basal Area (SBA) of trees (Fig. 5 and Appendix Fig. A5), a composition vegetation attribute. The model we obtained ($F(1,9)$, $p=0.004$) explained 18% of the species' variation.

Resident birds: the variation on the metacommunity assemblage of resident birds was only associated with landscape attributes of dry forest, the obtained model ($F(1,9)=1.9651$, $p=0.033$) explained 17% of the species data variability, the variable connectivity at 3000 m was found to be the only variable explaining our model (Fig. 6 and Appendix Fig. A6).

Rodents: the variation on the metacommunity assemblage of rodents was associated with landscape attributes of riparian forest, the resultant model ($F(1, 9)=9.843, p=0.003$) explained 52% of the specific variation, including connectivity at the 2500 m scale (Fig. 6 and Appendix Fig. A7). We found that the obtained model for vegetation attributes could be potentially associated with the variation on rodents' communities ($F(1,9)=3.5539$, $p=0.087$), potentially explaining 28% of the variation by the axis MDS2 of the composition of vegetation (Fig. 5 and Appendix Fig. A8).

Bats: the specific variation on bats' communities comprising the metacommunity was associated with vegetation attributes. The resulting model ($F(7,3)=1.7487$ $p=0.021$) explained 80% of the variation, including the number of woody individuals and the MDS1 and MDS3 axes of vegetation composition (Fig. 5 and Appendix Fig. A9).

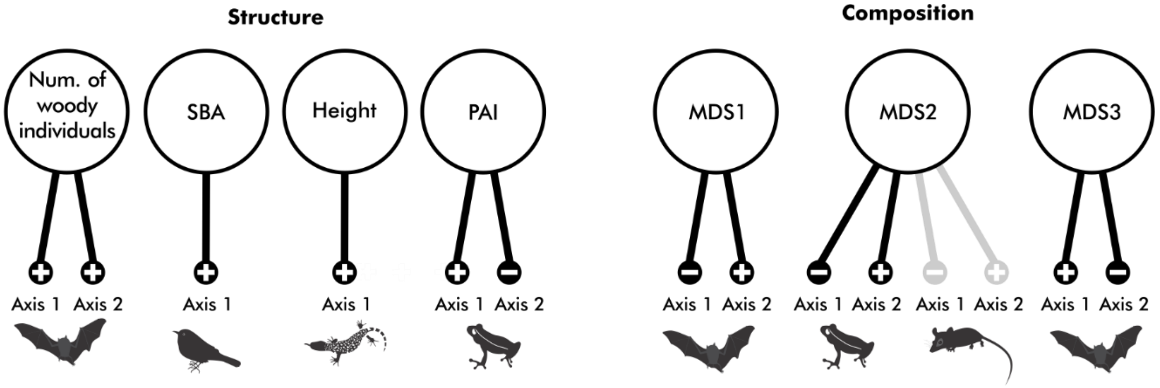


Figure 5. Resume of the CCA analyses performed showing the significant variables of vegetation attributes explaining variation in anurans, lizards, resident birds, rodents, and bats. The lines explain the positive (lines with a plus sign) or negative (lines with a minus sign) relation with the axis 1 and 2 of the CCA; grey lines represent a non-significant variable but potentially associated with variation in rodent species. SBA = Stand Basal Area, PAI = Plant Area Index, MDS1 = scores for the first axis of the non-Metric Multidimensional Scaling (MDS) ordination for vegetation composition, MDS2 = scores for the second axis of the MDS for vegetation composition, MDS3 = scores for the third axis of the MDS for vegetation composition.

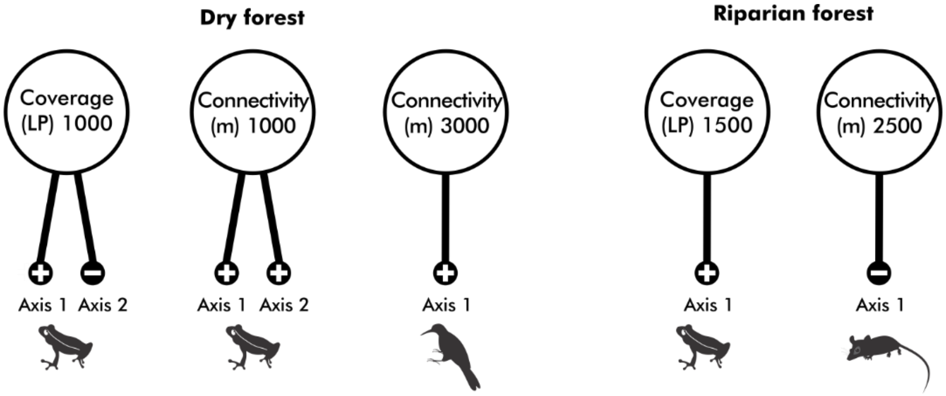


Figure 6. Resume of the CCA analyses performed showing the significant variables of landscape attributes of dry and riparian forest explaining variation in anurans and resident birds. The lines explain the positive (lines with a plus sign) or negative (lines with a minus sign) relation with the axis 1 and 2 of the CCAs.

Discussion

Sampling completeness varied among surveyed vertebrate groups from 55% to 93%. The lowest values for completeness corresponded to snakes, which are considered a rare group in herpetological surveys (e.g. Suazo-Ortuño et al. 2008, Fraga-Ramírez et al. 2017). The range of completeness values for our vertebrate groups fall within the range reported in other studies for each group (Gómez de Silva and Medellín 2001, de la Peña-Cuéllar et al. 2015, Flores-Peredo and Vázquez-Domínguez 2016, Marroquín-Páramo et al. 2021).

The most conspicuous species in ESS sites in all groups were generalist species, capable of tolerating diverse habitats and some degree of disturbance and living in young or disturbed forests' climatic and vegetation conditions. Anurans *Agalichnys dacnicolor, Lithobates forreri* and *Smilisca fodiens* have major plasticity in environments associated with disturbed sites such as secondary forests (García and Ceballos 1994, Suazo-Ortuño et al. 2008, Soto-Sandoval et al. 2017). Lizards species *Anolis nebulosus, Aspidoscelis communis, Aspidoscelis lineatissima,* and *Sceloporus utiformis* are known to be dominant in disturbed places; size, diet, and activity are traits that could allow them to use these sites (Berriozabal-Islas et al. 2017). The high prey density (e.g., lizards, anurans, rodents) could explain the high richness of snakes on ESS sites (Luiselli 2006); for example, *Oxybelis aeneus* was the most conspicuous snake, and its preferred prey is the anole *A. nebulosus,* the most conspicuous species of lizards in the region (Henderson 1974). The habitat of conspicuous species of migratory and resident birds (*Icteria virens* and *Myiarchus tyrannulus; Arremonops rufivirgatus*, *Cassiculus melanicterus* and *Thryophilus sinaloa*) consists of disturbed or cleared forests and edges on tropical dry forests (Bent 1963, Cadman et al. 2007, Cardiff and Dittmann 2020, Soberanes-González et al. 2020, Ammon and Gilbert 2020, Brush 2020, Collar 2020, Eckerle and Thompson 2020, Fraga 2020). Rodent generalists species, such as the two ESS exclusive species *Baiomys musculus* and *Reithrodontomys fulvescens*, are favored in perturbed or secondary forests because of the open canopy and the high presence of shrubs that enhance habitat heterogeneity by increasing the microhabitat diversity (Packard and Montgomery 1978, Spencer and Cameron 1982, Vázquez et al. 1999, 2004, Schnell et al. 2008, Flores-Peredo and Vázquez-Domínguez 2016, Benedek and Sîrbu 2018, Arce-Peña et al. 2019, Bovendorp et al. 2019). The presence of bat species such as *Artibeus jamaicensis*, *Artibeus phaoetis* and *Glossophaga soricina* in almost all the ESS sites can be due to their generalists roosting and feeding habits (Lemke 1984, Alvarez et al. 1991, Ortega and Castro-Arellano 2001).

The high species richness of flying groups such as migratory birds, resident birds, and bats could be explained by the high vagility and mobility of them and by the proximity of these sites to old-growth forest patches in the CCBR, which can be considered as the source habitat of several species. These groups could use ESS sites as pathways between forest fragments (Nassar et al. 2013); in this sense, some species may temporarily move to early forests searching for available resources such as fruits (Blake and Loiselle 2001). For migratory birds, early forests are sites with resources, like fruits with seeds, that are important to reunite energy for returning to the north (Blake and Loiselle 2001, Ramos-Ordoñez and Arizmendi 2011, Nassar et al. 2013, Latta et al. 2018).

Beta diversity: turnover and nestedness

We found high levels of beta diversity in all local communities for all taxa except for rodents and migratory birds. The same result was found in vegetation in early successional stages in Chamela tropical dry forest (Durán et al. 2006, Alvarez-Añorve et al. 2012). When partitioning the beta diversity, we found that the contribution of turnover to beta diversity was high, ranging from 77% in bats to 94% in snakes, compared to the low percentage of nestedness contributing in all groups; this means beta diversity is mainly caused by variation in species composition, instead of differences in species richness among local communities (Baselga and Orme 2012). In this sense, it has been proposed that turnover is a consequence of historical spatial constraints or a degree of species sorting (Baselga 2010). The tendency found across our metacommunities has been reported in numerous studies; according to the meta-analysis performed by Soininen et al. (2018), in most of the local studies using beta partitioning, turnover contributes the most to beta diversity.

When comparing beta diversity between the taxa studied, we found some similarities across some of the metacommunities. For example, ectotherms (lizards, anurans, and snakes) showed high levels of biodiversity, probably because the ectotherm group is constrained by environmental variables like temperature, moisture and depend on environmental sources for heat gain (sun and warm surfaces) and heat loss (shade, water, and cool surfaces) (Vitt and Caldwell 2014). On the other hand, volant groups (migratory and resident birds and bats) showed lower beta diversity values than ectotherms, except for the migratory birds. The high vagility of these taxa might allow the movement between patches of species, resulting in more similar communities.

The high beta diversity and high levels of turnover in the anurans metacommunity were expected as a result of the low mobility of the group (Qian 2009, Dobrovolski et al. 2012, da Silva et al. 2014) and because of their dependence on specific environmental conditions for dispersal and reproduction (e.g. water bodies, environmental moisture, cooler temperatures, rainfall) (Wells 2010, Vitt and Caldwell 2014, Thompson and Donnelly 2018). In addition, the formation of ephemeral habitats in ESS (e.g. temporary ponds) could increase the microhabitat availability for some species of anurans, leading to high diversity in different sites (Hernández-Ordóñez et al. 2015, Acevedo-Charry and Aide 2019). Finally, coverage of dry and riparian forests and attributes of vegetation structure (PAI and composition) were important in determining the presence of some species in our metacommunity of anurans, which will be discussed later.

Lizards also depend on light, sun exposure, humidity, and temperature for regulating temperatures; they have a lower vagility than bats and birds, restricting their dispersal capacity and enhancing beta diversity in the metacommunity. In addition to this, ESS have a high structural complexity of vegetation (Huang et al. 2013), which may lead to higher diversity and the co-occurrence of various species of lizards with different requirements as a result of the availability of more habitats: different strata for perching, availability of gaps for thermoregulation, or litter layer (Genet et al. 2001, Gienger et al. 2002, González-Sánchez 2012). Thus, the environmental heterogeneity is crucial for allowing the coexistence of different species of lizards, leading to higher diversity when the heterogeneity is higher; this result has been found in desert lizards (Pianka 1966), in lizards inhabiting coffee crops (Macip-Ríos and Muñoz-Alonso 2008), and in lizards of TDF (Berriozabal-Islas et al. 2017).

Snakes showed the highest beta diversity of all groups, as seen with anurans and lizards; snakes are ectotherms more restricted by environmental variables. For example, Soininen et al. (2018) found that taxa occupying high trophic positions, such as carnivores specialists, have a higher beta diversity because of the spatial distribution of the food availability. Other studies on beta diversity on snakes have found that snake assemblages are affected by environmental variables, such as soil texture and variation in tree cover that generates mosaics (Moura et al. 2017, de Fraga et al. 2018), and prey availability, like high abundances of rodents, lizards, and amphibians (Akani et al. 2008, Soininen et al. 2018, Zipkin et al. 2020).

Migratory birds showed a high beta diversity; this result was not expected for a group with high vagility; however, migrants from different species can show differential responses to variation in landscape (Hutto 1989), and the structural heterogeneity in the landscape may increase the diversity of migrants (Hovick et al. 2014, Ke et al. 2018). Some studies have demonstrated that many neotropical migrants take advantage of different habitats in a landscape perturbed by anthropogenic disturbance and that live fences in landscapes are very important to these species (Estrada and Coates-Estrada 2005). The tropical dry forest could be either a habitat for staying or a stopover for some species; thus, this could explain the dissimilarity between sites. In the case of species that use Chamela tropical dry forest as a stopover, some species may use the habitat differently: individuals with different levels of fuel stores (energy) might have different demands for the habitats, some will be searching for safer places that protect them from predation, while others will be searching for sites with resources, this might vary between individuals from the same species (Moore and Aborn 2000, Petit 2000, Chernetsov 2012).

Compared to migratory birds, resident birds evinced lower beta diversity values; this group could be considered less sensitive to variation in landscape structure (Flather and Sauer 1996, Trzcinski et al. 1999). We expected this result because birds are vagile and volant, and dispersion between patches at the landscape level is high. As stated before, the sharing species between sites might be a consequence of the resources present in these patches that birds use for feeding or as stepping stones, but not necessarily as sites for residing (Estrada et al. 1997). The slight dissimilarity between sites could be due to a different input of species depending on the matrix of each forest fragment in which the communities are embedded; MacGregor-Fors and Schondube (2011) found that bird communities in agricultural habitats, cattle pastures, and orchards were different.

Bats diversity was higher than the ones of resident birds and rodents but lower than the ectotherms and migratory birds, indicating that the metacommunity of this group shares some species because of its vagility, yet also responds to some environmental constraints like availability and abundance of food resources that causes the replacement of bat species (García-Estrada et al. 2006). A study in Chamela dry forest showed that communities became more homogeneous after hurricane disturbance (Sil-Berra et al. 2021); thus, we could expect a similar response to human disturbance.

The number of woody individuals and the vegetation composition were the two variables explaining the bat diversity in our study.

Finally, rodents showed the lowest total and site values of beta diversity. However, the low turnover values were significant according to the EMS analysis; this must be due to the ubiquitous presence of almost all species in all local communities and the few species number (eight) compared with the number of species in other groups. Generalist species of rodents are favored by habitat degradation. They are abundant and diverse during early successional stages (García-Estrada et al. 2002, Arce-Peña et al. 2019) because of the microhabitats proportioned by shrubs and trees that offer shelter to these species (Flores-Peredo and Vázquez-Domínguez 2016, Benedek and Sîrbu 2018). Another plausible explanation of the widespread distribution of all rodent species in our metacommunity is the reduction of the competitors and predators as a consequence of forest fragmentation (Morales-Díaz et al. 2019, Bovendorp et al. 2019). We found connectivity of riparian forest at high scales was important to rodent metacommunity and that there might be an effect on vegetation composition.

Metacommunity structure

The metacommunity approach is helpful for testing species that inhabit gradients or latent gradients and test if those species in metacommunities are distributed along the gradient. For example, vertebrate metacommunities in Chamela early successional forests presented a significant and positive coherence, which means species respond to the same latent environmental gradient and that their structure is different from the expected from random (Leibold and Mikkelson 2002).

Most of the studies analyzing the patterns and structure of vertebrate metacommunities have found Clementsian patterns (López-González et al. 2012, Ochoa-Ochoa and Whittaker 2014, Leibold and Chase 2018); however, four of our metacommunities showed a Gleasonian or quasi-Gleasonian pattern. These structures are more common to appear at small or local scales when species show an individualistic response to gradients, while Clementsian structures are expected at regional or continental scales when higher shifts in species composition occur (Leibold and Chase 2018).

The rodent group was the only metacommunity showing a real structure in this study: the Gleasonian pattern. It occurs in metacommunities with randomly distributed boundaries, which indicates that species are structured along a gradient. Species responses are independent in this pattern (Gleason 1939, Leibold and Mikkelson 2002, Presley et al. 2010), and their coexistence results from chance similarities in their environmental requirements (Gleason 1926). The rodent metacommunity was structured along the latent gradient (Fig. 3), with the species *R. fulvescens* associated to one side of the gradient in sites with low proportions of forest cover and sites dominated by dry forests. This species is opportunistic and more common in disturbed sites than conserved ones (Spencer and Cameron 1982, Vázquez et al. 1999, Flores-Peredo and Vázquez-Domínguez 2016). At the end of the gradient, we found *Peromyscus perfulvus*, associated with sites with a higher cover of dry and riparian forests. The distribution of this species is restricted to the coastal region of Jalisco, Colima, Cuenca del Balsas in Guerrero and Michoacán states, in Mexico (Ramírez-Pulido et al. 2001) and is an arboreal species found in sites with dry forests (Sánchez-Hernández et al. 2009). The other species were equally distributed along the gradient (e.g. *Liomys pictus*, *Osgoodomys banderanus*, *B. musculus*); these species are generalists and favored by the vegetation of early forests. Studies in San Pedro-Mezquital River and the Mojave Desert in the United States showed a Gleasonian and quasi-Gleasonian structure, with relationships to environmental conditions like humidity or vegetation and edaphic features (Stevens and Tello 2009, López-González and Lozano 2015). However, studies in the Atlantic Forest and the Peruvian Andes showed a Clementsian structure in rodent metacommunity, associated with gradients of temperature seasonality and elevation (Presley et al. 2012, de la Sancha et al. 2014). According to the analyses regarding the responses of rodents to habitat variation, we could suggest the rodent metacommunity is structured by landscape variables regarding riparian forest and by a gradient in the composition of vegetation; similarly, Stevens and Tello (2012) found that rodent metacommunity was associated with the spatial configuration and environmental conditions in the Mojave Desert.

Anurans, lizards, snakes, and migratory birds showed a quasi-Gleasonian structure; in this pattern, the responses to the latent gradient and environment are also species-specific, but the metacommunities have larger niche breadths and weaker structuring forces than Gleasonian metacommunities, which have a significant turnover (Presley et al. 2010).

Some of the species found in the anuran metacommunity were more related to one side in the latent gradient, including sites dominated by riparian forests and dry forests (Fig. 3); for example, *Trachycephalus typhonius*, *Eleutherodactylus nitidus, Craugastor hobartsmithi* and *Craugastor occidentalis*, are species associated with forested and wet areas (Reyna-Bustos et al. 2007, Peltzer et al. 2013, Rosas-Espinoza et al. 2013). Most of the species were present along the entire gradient, while species like *Hypopachus variolosus, Tlalocohyla smithii, Dendropsophus sartori* and *Leptodactylus melanonotus* were found at the end of the gradient, these species have in common they inhabit close to water bodies and muddy soils (Caldwell 1986, García and Ceballos 1994, Lee 1996, Bartlett and Bartlett 2006, Rosas-Espinoza et al. 2013). Although some of the sites are in a matrix with a low proportion of riparian forests, temporal ponds can be formed in perturbed sites and are important to species inhabiting sites with low canopy cover (Richter-Boix et al. 2007, Acevedo-Charry and Aide 2019). Other metacommunities of Mexican anurans have exhibited quasi-Gleasonian, Gleasonian, and Clementsian structures, describing a gradient from an open matrix to interior forest (Ochoa-Ochoa and Whittaker 2014). The anurans of our metacommunity may respond individually to a gradient in landscape features (e.g. connectivity) of dry and riparian forests and compositional changes of vegetation; similar results were found at Lacandona rainforest and north-east Spain, where the amphibian metacommunities were influenced by dispersal events and patch quality (Richter-Boix et al. 2007, Hernández-Ordóñez et al. 2019).

We also found that some species in lizards metacommunity were aggregated at one side of the latent gradient with lower proportions of forest cover (Fig. 3), for example, *Phrynosoma asio,* which inhabits open areas (García and Ceballos 1994). However, species occupying the end of the gradient like *Marisora brachypoda, Coleonyx elegans* or *Plestiodon parvulus*, depend on the amount of litter, surface debris, and moist sites (García and Ceballos 1994, Lee 1996); this side of the gradient was associated with larger proportions of dry forest or riparian forest. Many species were common along the whole gradient without showing a particular type of site preference. The latent gradient structuring lizard metacommunity could be associated with attributes of vegetation like the height of woody individuals; however, other attributes like the landscape configuration and quality have explained the assembly of lizard metacommunities in dune, pine forest, and lowland wet forest habitats (Leavitt and Fitzgerald 2013, Kurz et al. 2014, Johnson et al. 2016, Ryberg and Fitzgerald 2016).

Although there was a quasi-Gleasonian structure in snakes metacommunity, the latent gradient is less clear than the other groups analyzed, and many species were present only at one site. However, the conspicuous species (e.g., *Imantodes gemmistratus, Lampropeltis triangulum, O. aeneus*) occupied the entire gradient; these species are generalists and common in second forests and forests edges (Lee 1996). Other studies suggest some variables structuring snake communities, for example, multi-scale fluvial and geomorphic processes (e.g. particle size) that may lead to Clementsian or Gleasonian structures (Welsh Jr and Hodgson 2011); landscape attributes in insular systems like: distance to the mainland and area of the island (Burbrink et al. 2015), matrix surrounding forest remnants (Kurz et al. 2014), prey density (Naulleau 1994, Johnson et al. 2016), or coarse woody debris (Owens et al. 2008).

The metacommunity of migratory birds showed that species are distributed along a latent gradient but with individualistic responses; species of this group can vary in habitat requirements, some species require undisturbed habitats, while others are favored by second and disturbed forests (Finch 1991), this support the quasi-Gleasonian structure found in the study. In this respect, some species were present at the gradient side characterized by sites immersed in a heterogeneous matrix (Fig. 3), such as *Pheucticus melanocephalus*, *Icterus spurius* and *Tachycineta bicolor*, common in open areas and edges transitions (DeGraaf and Rappole 1995). However, most migratory species were distributed across the entire gradient, while six species were more associated with the end of the gradient, associated with sites dominated by dry forests. These species (e.g. *Seiurus aurocapilla*, *Piranga ludoviciana*, *Catharus ustulatus*) depend on mature or second growth dry forests, dense tall understory, and are vulnerable to deforestation (DeGraaf and Rappole 1995). The latent gradient found is coherent with other migratory bird communities in Mexico and South Africa shaped by landscape variables, like patch size and connectivity, and by attributes of the habitat, like vegetation cover (Leyequién-Abarca et al. 2006a, Ehlers Smith et al. 2018, 2019). In addition to this, environmental variables such as precipitation or water availability could contribute to differences in metacommunities of migrant birds because of their relation to abundance and availability of resources (e.g. insect density, fruit production), which are essential factors affecting winter survival of migrants (Cody 1981, Sherry and Holmes 1996, Brennan 2006).

The two metacommunities that exhibited quasi-Clementsian structures were bats and resident birds. Clementsian structures may reflect the effect of biogeographic processes and barriers, and species form discrete groups that replace each other along the gradient and share an evolutionary history (Clements 1916, Leibold and Mikkelson 2002, Dallas and Presley 2014). However, when a quasi-Clementsian pattern appears, the turnover is not significant, the range boundaries are coincident or quasi-coincident, and the majority of species cover a great part of the gradient, characterizing a metacommunity with a compositional unity along most of the gradient (Presley et al. 2010).

In the case of the resident birds, species such as *Tyrannus crassirostris, Melanotis caerulescens* and *Sporophila minuta* that inhabit secondary forests, riparian edges, and open areas (Rodríguez-Parga et al. 2012, Lowther et al. 2020, Rising and Jaramillo 2020), always occupied only one side of the gradient (Fig. 3); whereas species strongly related to dry forests, for example *Xiphorhynchus flavigaster, Tyrannus melancholicus, Tityra semifasciata, Myiodynastes luteiventris* (Vega-Rivera et al. 2003, Lowther and Stotz 2020, Marantz et al. 2020, Mobley and de Juana 2020, Stouffer et al. 2020), were present at the other side of the gradient. Furthermore, many species with generalist habits were common along the whole gradient. Landscape attributes, for example, connectivity or tree cover, may represent the gradient to which resident birds are responding; this association has been previously found in woodlands and grassland habitats in France in two Clementsian bird metacommunities, in a traditional shade coffee agro-ecological zone and in pine-oak forests, both in Mexico (Leyequién-Abarca et al. 2006b, Bonthoux et al. 2013, Carrillo-Rubio et al. 2014, Bonthoux and Balent 2015, Henckel et al. 2019). Moreover, Presley et al. (2012) also found a quasi-Clementsian structure in Peruvian passerines related to an elevational gradient, and they discuss that this structure may arise as a result of the high vagility of birds coupled with the use of presence-absence data and that metacommunity structure could be different for each guild.

The species of bats present at one side of the gradient (Fig. 3) were *Pteronotus davyi* and *Musonycteris harrisoni,* the first one is a species that inhabits in moist and warm caves and feeds on insects, specially moths (Adams 1989, Jiménez-Guzmán and Ceballos 2005); the second one is a nectarivore species endemic to the Pacific Coast of Mexico (Tellez and Ortega 1999). Both species are small-sized and cannot resist low temperatures (Bonaccorso et al. 1992, Tschapka et al. 2008). On the other side of the latent gradient, *Choeroniscus godmani* and *Artibeus hirsutus* were present; both species prefer undisturbed dry forests (Arita 2005, Téllez-Girón 2005, Avila-Cabadilla et al. 2009). Other species (e.g., *A. jamaicensis* and *G. soricina*) were common along the entire gradient. The quasi-Clementsian structure we found in Chamela region coincides with the Clementsian structures in other bats metacommunities at large scales in Mexican and

Paraguayan bats (Presley et al. 2009, López-González et al. 2012). Nonetheless, Gleasonian, quasi-Gleasonian and nested patterns have structured bats at local scales in San Pedro-Mezquital River, in the Caribbean lowlands of north-eastern Costa Rica, in Mount Nimba in Liberia and Guinea, and in Manu, Peru (Presley et al. 2012, Cisneros et al. 2015, López-González and Lozano 2015, Reardon and Schoeman 2017), responding to the gradients of elevation, humidity, and vegetation, the distance between forest patches and forest edge density. Our results coupled with the CCAs performed suggest that vegetation composition is related to the distribution of bats in the early forests of Chamela.

Responses of vertebrate groups to environmental variables

Anurans: coverage and connectivity of dry forest and coverage of riparian forest, both at small scales, explained the presence of anurans in the different metacommunities. Dry forests, even if disturbed, are habitats that favor some species, possibly with larger body size like *A. dacnicolor* or *S. fodiens*; these two species were found in 10 and six communities during this study (Fraga-Ramírez et al. 2017, Suazo-Ortuño et al. 2018a). Riparian forests provide shelter and resources to anurans, especially during the dry season, leading to greater species diversity and the establishment of anuran populations (García and Cabrera-Reyes 2008, Medina-Rangel 2011, Suazo-Ortuño et al. 2011). A change in anuran species' location between dry and riparian forests between dry and wet seasons has been studied (Suazo-Ortuño et al. 2011); the connectivity of dry forests must be an important variable because it allows individuals' movement during different seasons through the forest. We did not measure if species composition was related to each community's distance to the mature forest of the reserve; however, there might be an effect on species composition in communities with different distances to mature forests. Studies in insular systems have shown that the species richness of anurans decreases and changes when the distance from continuous forest increases (Watling and Donnelly 2008, da Silva et al. 2014). The following vegetation attributes were also significant for anurans' presence: Plant Area Index, which indicates the vegetation structural complexity (Fournier et al. 2003), and vegetation composition. Sites more complex in terms of vegetation have shown a greater number of microhabitats for anurans, which is very important for selecting sites to avoid evaporative water loss through the skin (Navas 1996, García and Cabrera-Reyes 2008, Rittenhouse et al. 2008, Wells 2010). Microhabitat selection and vegetation composition are also necessary for breeding purposes (Afonso and Eterovick 2007, Provete et al. 2014).

Lizards: the structural complexity of riparian and dry forests are variables that cause an effect on lizard assemblages. Usually, a higher structural complexity leads to higher levels of diversity and abundance (García and Cabrera-Reyes 2008, Suazo-Ortuño et al. 2011). The CCAs conducted showed that the height of woody individuals was the only variable explaining lizards' variation between communities. This result agrees with previous studies demonstrating a vertical differentiation of the habitat use between anoles' species (Moermond 1979, Ramírez-Bautista and Benabib 2001, Losos and Greene 2009). Lizards in tropical dry forests also indicate differential habitat utilization on the vertical plane. For instance, *A. nebulosus* and *Sceloporus melanorhinus* use low and high perches, while *S. utiformis* is predominantly a terrestrial species that uses leaf-litter; *Urosaurus bicarinatus* occupies higher perches (García 2008), and the beaded lizard *Heloderma horridum* uses the forest floor (Beck and Lowe 1991). The utilization of different strata could result from competition, prey availability, moisture, or thermoregulation requirements (Losos and Greene 2009). The lizards' ability to climb surfaces and occupy different strata and heights is related to running (sprinting), clinging and jumping, and morphological features such as the snout-vent length (Irschick and Losos 1999, Tulli et al. 2011), so species with different morphological features can use different strata. Besides, lizard assemblages of TDFs have shown a structure based on diet composition (de Pinho Werneck et al. 2009), which could be another variable structuring the metacommunity of lizards in Chamela.

Snakes: snakes metacommunity variation was not influenced by any of the variables we measured; the low capture rate for this group could limit our capacity to identify causal relationship (Gu and Swihart 2004). However, it has been hypothesized that snakes' distribution is determined principally by prey availability (Webb and Shine 1997, Barbo et al. 2011, Wasko and Sasa 2012). In addition, some studies have shown an effect of landscape and microhabitat characteristics on snakes diversity like the presence of edges, percentage of trees canopy and open habitats, and ground cover (Carfagno and Weatherhead 2006, de Fraga et al. 2011, França and Braz 2013).

Migratory birds: the stand basal area (SBA) was the only variable explaining the variation in the metacommunity of migratory birds, lower values of SBA are common in younger sites in a successional gradient, while higher values are representative of older forests (Kariuki and

Kooyman 2005). Most of the birds were associated with sites with low SBA values; in this respect, migrants are common in open areas and forest edges, probably because of the use of small insects and fruits that are not exploited by resident birds (Willis 1980); also, food availability could be four times greater in edge than in interior habitats. Some species might be favored by open areas because they provide access to the ground and foraging habitat for insectivorous species (Conner and Adkisson 1975). In this sense, abundance and availability of food resources are essential to migrants because they need enough food to store fat and survive during migration (Hutto 1980, 1985, Willis 1980, Greenberg et al. 1997). Compared to resident birds, migrants may not depend on specific habitat attributes (e.g., undisturbed dry forest) (Hutto 1989). Furthermore, these results show a similar pattern to the metacommunity ordenation and species related to more conserved forests and vulnerable to deforestation (e.g. *C. ustulatus*) were associated with sites with higher values of SBA, which are the sites dominated by dry forest cover.

Resident birds: the CCAs conducted for resident birds exhibited that connectivity of dry forest at 3000 m was an important variable when structuring the birds' metacommunity, probably because of the flight capability of the group. According to Taylor et al. (1993), landscape connectivity is the degree to which the landscape facilitates or impedes movement among resource patches; therefore, high connectivity could allow birds to use habitat fragments as stepping stones or corridors to avoid long flights crossing forest gaps. Besides, fragments provide sites where individuals can rest, feed, or shelter from predators (Clergeau and Burel 1997, Pearman 2002, Boscolo et al. 2008); corridors could also be used as breeding or roosting sites by some species and not only as foraging habitats (Faria et al. 2006). In this sense, connectivity can reduce the adverse effects of fragmentation by increasing the area and quality of habitat for birds when all the fragments are functionally connected (Andrén 1994, Martensen et al. 2008, Boscolo et al. 2008). For example, Lees and Peres (2008) found that connected corridors had higher structural integrity than remnants that had lost connectivity to source patches.

Rodents: we found connectivity of riparian forest at high scales was important to rodent metacommunity, explaining the low beta diversity in this group. Corridors of habitat allow rodent dispersal between patches, Garrido-Garduño et al. (2016) demonstrated that gene dispersal of rodents between localities in Chamela is usually associated with corridors of forested areas. The landscape connectivity of riparian forest is important to rodents because the movements across the habitat have a lower risk of predation than movements on an open matrix. Studies translocating rodents to patches with different degrees of isolation and connectivity have shown that individuals prefer connected habitats than isolated patches (Rizkalla and Swihart 2007, Büchner 2008, Mortelliti et al. 2011, 2013) and that rodents' populations establish and have higher population growth rates in connected habitats (Fahrig and Merriam 1985). Riparian forests show higher species richness of rodents (Ceballos 1990), this habitat may provide more resources such as food or shelter to rodent species, especially during the dry season, than dry forest (Zarazúa-Carbajal et al. 2017); species like *O. banderanus*, *P. perfulvus* are common in moist habitats associated with water bodies (Ceballos 1990).

The composition of vegetation potentially influenced rodent variation. For example, the most conspicuous plants present in our sites (*Caesalpinia coriaria, Jacquinia nervosa, Acacia farnesiana*) produce fruits and seeds consumed by rodent species like *L. pictus* (Janzen 1970, Traveset 1990, Sánchez-Rojas et al. 2004). Therefore, resource availability provided by these and other plant species may determine some rodent species' presence in this habitat (Mortelliti et al. 2014, Flores-Peredo and Vázquez-Domínguez 2016, Yang et al. 2018).

Bats: the plant species composition axes were the most important variables structuring bat metacommunity; plants' identity determines the availability of trophic resources, so vegetation composition will probably be an important predictor of bat variation (Chambers et al. 2016, Martínez-Ferreira et al. 2020). The early successional vegetation of dry forest and riparian forest could increase the abundance, diversity, and quality of flower resources (Avila-Cabadilla et al. 2009). Indeed, the number of woody individuals, which can be related to resource production (e.g. fruits, flowers, insects) and roosting or shelter sites (Hale et al. 2012, Kalda et al. 2015), was the other variable explaining bat variation. Plant species like *Acacia cochliacantha*, *Cordia alliodora,* and *J. nervosa* were conspicuous and abundant in our study sites; they all produce fruits and flowers (Janzen 1970, Johnson and Morales 1972, Seigler and Ebinger 1988, Chaves and Avalos 2006) that could be food for bats. This group forage selectively and prefer areas with high resource availability (Ripperger et al. 2015) probably because they spend less time flying when using sites with a high abundance of food and reduce flight distance between resources. Besides, the spatial use within the home range is correlated with food plant abundance (Rothenwöhrer et al. 2011).

Potential structuring mechanisms in vertebrate metacommunities in Chamela region

Based on all the analyses performed on the metacommunity structures obtained for each group, we propose the mechanisms shaping the vertebrate metacommunities during the early successional stages of the Chamela tropical dry forest.

Following the framework proposed by Leibold et al. (2004), we propose that the principal mechanisms operating over the vertebrate metacommunities in Chamela are in between mass effects and species sorting paradigms or archetypes (Leibold and Chase 2018). This result agrees with most studies searching for the mechanisms shaping metacommunities; a review made by Cottenie (2005) showed that species sorting was the principal mechanism, followed by the combination of species sorting and mass effects. Species sorting is the traditional "niche-based" mechanism, in which species specialize on different local conditions and dispersal is limited at the scale of the region; therefore, the communities change over environmental gradients (Leibold et al. 2004). On the other hand, mass effects include niche selection considering both dispersal and habitat heterogeneity; patches must have different conditions, and they must be connected in order to allow dispersal, this can result in source-sink dynamics (Mouquet and Loreau 2003, Leibold et al. 2004, Leibold and Chase 2018). For instance, mass effects could allow the arrival of OGF species to regenerating local communities, thus explaining the presence of those species (e.g., the rodent *P. perfulvus*, the lizards *H. horridum* and *Phyllodactylus lanei*, the frog *T. smithii,* the snake *I. gemmistratus*, the migratory bird *Passerina caerulea*) in the early forests in Chamela region.

Leibold and Chase (2018) and Cottenie (2005) indicate the importance of noting that the factors affecting the relative mechanisms of metacommunities are patch heterogeneity, the degree of connectivity, dispersal rates of individuals among those habitats and connectivity rates between habitats. Therefore, mechanisms can coexist, and metacommunities can land into a continuum among the patch dynamics, mass effects, species sorting and neutral processes. We propose that some of the vertebrate groups studied in this work are in different positions on the continuum (Fig. 7). The metacommunities shaped by species' sorting and mass effects suggest that some species are strongly affected by environmental conditions and processes, while dispersal processes influence the other set of species.

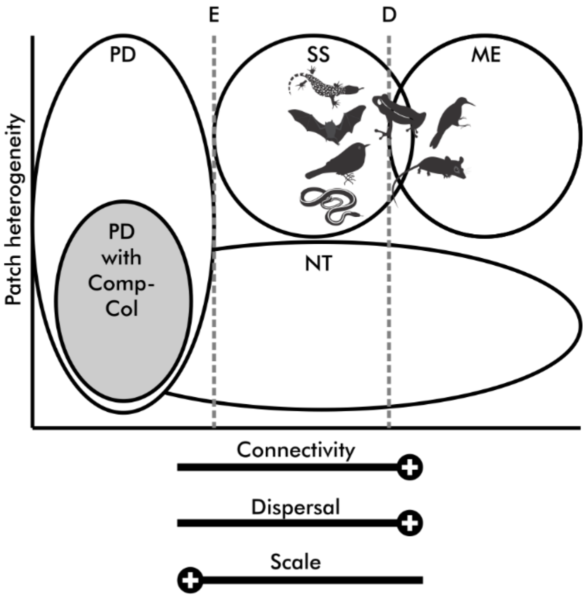


Figure 7. Mechanisms structuring metacommunities of anurans, lizards, snakes, migratory birds, resident birds, rodents, and bats, in the Chamela region. Populations are dispersal limited and extinctions are high compared to colonization to the left of line E. There is dispersal excess and high immigration compared with local death rates to the right of line D. E = local extinction rate, D = local death rate, PD = patch dynamics, SS = species sorting, ME = mass effects, NT = neutral model, Comp-Col = competition colonization models. Modified from Leibold 2011 and Leibold and Chase 2018.

Anurans: this group showed high turnover, but it was non-significant, resulting in a quasi-Gleasonian structure. The species-specific responses to environmental characteristics, such as the composition of the vegetation or understory cover, support that the anuran metacommunity is structured by species sorting. Besides, other species with increased dispersal abilities favored by landscape attributes, such as dry forest connectivity and riparian and dry forest cover, could be influenced by mass effects, indicating high dispersal rates and sink-source dynamics. Similar to our findings, other amphibian metacommunities in different places like a Mexican rainforest, an urban ecosystem, and water bodies in a Michigan reserve and Connecticut were structured by species-sorting and mass effects mechanisms. The species in these studies responded to the successional gradient of young, intermediate and old-growth forests (Hernández-Ordóñez et al. 2019), the gradient of the surface area of ponds (Parris 2006), the gradient of hydroperiod and forest canopy cover (Werner et al. 2007), and the gradient of vegetation structure and pond area (Urban 2004).

Lizards: similar to anurans, lizards showed high levels of turnover, but it was non-significant, leading to a quasi-Gleasonian structure. Each lizard species was associated with different local environmental conditions, consistent with the gradient related to vegetation attributes (height of woody individuals); this result agrees with a species sorting mechanism driving lizard metacommunity in this region. A reptile metacommunity in tallgrass prairies with different patch types resulting from disturbance (fire, grassland, cattle grazing) showed that species were responding to habitat variables such as food availability or physiological constraints (Larson 2014). In addition, communities of Amazonian lizards were separated due to different food preferences (Vitt et al. 1999). Ryberg and Fitzgerald (2016) found that lizards in a dune land ecosystem were also shaped by species sorting; however, when analyzing the metacommunity at higher scales, the most relevant mechanism was mass-effects, indicating regional factors were more important than environmental attributes.

Snakes: the quasi-Gleasonian structure coupled with the non-significant turnover in snake metacommunity suggest species-sorting as the structuring mechanism, each species respond individually to resources and environmental variables; although we did not find any variable suggesting the gradient to which snakes were responding, prey availability could explain the diversity in the metacommunity, as stated in previous sections in the discussion. Cavalheri et al. (2015) work in Brazil showed the importance of habitat type and habitat filtering on the phylogenetic structure of Neotropical snake metacommunities; in contrast, metacommunities in islands on the Eastern Nearctic were structured by neutral processes and not by habitat filtering (Burbrink et al. 2015). To our knowledge, the two mentioned works and this study are the only ones studying snakes with the metacommunity framework. Hence, the results and information derived from this work could shed some light on the mechanisms shaping snake metacommunities at local scales.

Migratory birds: this group showed high turnover that was non-significant and a quasi-Gleasonian structure, and the SBA was the variable explaining the species variation in the metacommunity. Evidence from other studies suggests that the metacommunities of migrant birds are shaped by the abundance and availability of food and resources (Lefebvre and Poulin 1996, Gram and Faaborg

1997). For example, Neotropical migrants in a fragmented forest and man-made habitats (e.g. shaded arboreal plantations, live fences, pastures) in Mexico take advantage of these landscapes by consuming the available resources (Estrada and Coates-Estrada 2005). A review by Cohen et al. (2017) summarizes that habitat quality (e.g. the shelter provided from predators, abundance, and spatial distribution of food resources) is crucial to determine the distribution of migrant species during migration. These results propose that the species sorting mechanism structures the migratory bird metacommunity.

Resident birds: the quasi-Clementsian structure of the metacommunity of the resident birds and the influence of connectivity at a large scale in species variation imply the operation of a mass effect; nonetheless, a supplementary role played by species sorting should not be discarded. Various studies have demonstrated that mass effects structure bird systems; for example, the composition of the landscape (e.g. the cover of pastures, crops, woodlands, and hedgerows) had shaped a metacommunity in southwest France in two different dates separated by 25 years (Bonthoux et al. 2013, Bonthoux and Balent 2015). Similarly, bird diversity in a Cuban archipelago was strongly determined by landscape attributes such as the area and shape of the fragments and minimum distance between cays and isle of Cuba (García–Quintas and A. 2017). Recent work by Morante-Filho et al. (2021) found that birds metacommunity was affected mainly by landscape composition metrics (i.e., forest cover amount and matrix quality); they discuss the possible relation between habitat amount and landscape connectivity and how this relation makes forest cover a key predictor for forest birds. Comparably, other bird metacommunities in the mountains in Turkey and in a temperate South American forest showed evidence of species sorting (related to habitat features like foliage density and understory cover) and mass effects shaping the bird assembly. However, in contrast to what we discovered, they found the strongest mechanism to be the one associated with niche processes, while the spatial factors played a weaker role (Meynard and Quinn 2008, Özkan et al. 2013).

Rodents: we propose that the most relevant mechanism structuring rodent metacommunity is mass effects related to connectivity of riparian forest at larger scales; however, we also suggest that species sorting mechanism plays a supplementary role in metacommunity assembly, these affirmations are based on the Gleasonian structure exhibited. The individualistic responses of rodents might be related not only to landscape attributes but also to food availability and resources derived from vegetation composition. Similar to our results, mass effects (colonization and extinction dynamics) and species sorting (niche characteristics) appeared to structure desert rodents in Arizona and Mexico (Ernest et al. 2008, López-González and Lozano 2015). In contrast, a Peruvian metacommunity was strongly influenced by local factors and did not show any effects related to landscape attributes (Presley et al. 2012). In particular, the seasonality of Chamela explains why dispersal processes are important for this metacommunity; rodents use riparian corridors during the dry season to find resources that are not available in dry forests but are present in riparian forests (Zarazúa-Carbajal et al. 2017). Mass effects have been reported in other rodent systems; for example, rodents in deserts in North America demonstrated the importance of spatial characteristics and events of colonization and extinction in structuring rodents metacommunities (Goheen et al. 2005, Stevens and Tello 2012).

Bats: the quasi-Clementsian structure and the moderate and non-significant turnover suggest that the species sorting mechanism is structuring bat metacommunity. The vegetation composition and number of woody individuals might be related to the abundance of food resources and roosting sites. Likewise, bats in Peru and Paraguay were strongly influenced by food distribution and abundance (e.g. fruit, nectar, insects) along an elevational gradient (Presley et al. 2012) and gradients representing precipitation and temperature (Presley et al. 2009); insectivores bats in an elevational gradient in West Africa and Mexican bats also seemed to be responding to niche characteristics (López-González et al. 2012, Reardon and Schoeman 2017). In this respect, a combination of species sorting and mass effects is suggested for a system in Costa Rica with different degrees of landscape modification, distances between patches and forest cover, and abundance of food resources in different patches seem to shape that bat metacommunity (Cisneros et al. 2015).

Concluding remarks

To our knowledge, this is the first work in Mexico using the EMS approach to study the vertebrate responses during early successional stages. Our results demonstrated that the analysis of metacommunities from the mechanism and pattern perspectives at different scales could unveil the mechanisms shaping animal communities after disturbance in secondary forests.

The most relevant highlights from these findings include:

First, the vertebrate metacommunities in the TDF studied are assembled by species sorting, mass effects, or a combination of both mechanisms. Thus, microhabitat variables, such as the composition of vegetation, height of trees, plant area index, or stand basal area, could be related to resource availability and are important to determine the presence of different species during ESS. In addition, landscape attributes like connectivity and dry and riparian forest cover are also important for the dispersal of species between forest fragments. The connectivity between forest fragments allows them to act as stepping-stones or corridors, and cover of dry and riparian forest provide resources to species in disturbed sites. However, García-Girón et al. (2020) highlight that biotic interactions should be integrated into the metacommunity framework; hence we do not discard that such interactions could play an important role in shaping the vertebrate metacommunities (e.g. snake group). In addition, it is important to emphasize that patterns and mechanisms structuring the metacommunities can change across time and scale, the former as a result of succession, human or natural disturbances (e.g. fragmentation, fires, hurricanes), and seasonality (Leibold et al. 2004, Alexander et al. 2012, Leavitt and Fitzgerald 2013, Ochoa-Ochoa and Whittaker 2014, Cisneros et al. 2015, Ryberg and Fitzgerald 2016). Thus, stochastic processes, patch dynamics or neutral processes could shape vertebrate metacommunities after a disturbance leading to identical forest fragments.

Second, the importance of the old-growth forests for various vertebrate groups. These may function as a source of species that disperse to the early forests, allowing the presence of species that are usually found in conserved forests in ESS and providing resilience to the metacommunities. In this sense, the CCBR acts as a buffer zone to different threatens occurring in the TDF, like human and natural disturbances. Recently, the Chamela region was impacted by two hurricanes: Jova (2011) and Patricia (2015); various studies in the region demonstrated the role of OGF on preserving vertebrate species and diversity after both hurricanes (Suazo-Ortuño et al. 2018a, 2018b, Marroquín-Páramo et al. 2021, Sil-Berra et al. 2021). Therefore, we must protect large continuums of old-growth forest to preserve the source of propagules that will disperse and colonize other patches, enhancing and maintaining species diversity after disturbances (e.g. change of land use, cattle grazing, logging, or hurricanes and fires).

Third, the high levels of beta diversity between ESS forests result from a high turnover between local communities. Therefore, the importance of preserving these forests to conserve different assemblages and greater diversity. Additionally, secondary forests provide habitats and resources to species in all the vertebrate groups (DeWalt et al. 2003) and might be used as corridors and stepping-stones, allowing species dispersal between fragments and the old-growth forest. Finally, the coexistence of species exclusive of OGF and generalist species in early forests could be due to an effect of the intermediate disturbance in ESS forests (Connell 1978).

Fourth, the different responses to landscape and vegetation attributes between vertebrate groups highlight the need for having a multi-taxa perspective when working on management and conservation plans and strategies in tropical dry forests; otherwise, ecological requirements by a specific group might be dismissed, leading to a potential loss of biodiversity in the system. In this sense, a metacommunity framework is an advantageous approach for biodiversity conservation because it provides tools when understanding distribution and abundance patterns of species and local communities of conservation interest, and it can predict the stability of the community (Chase et al. 2020).

Finally, assessing the responses of vertebrate groups after disturbance in ESS is crucial to understand the pathways of succession in TDF. Animals play an active role during succession (Swanson et al. 2011); for example, de la Peña-Domene et al. (2014) found two endangered plant species present in early successional habitats in Los Tuxtlas, Mexico, as a consequence of the presence of birds and bats. Moreover, fragmentation and disturbance can affect seed dispersal networks, changing the interactions between specialist plants and specialist animals that disperse seeds (Emer et al. 2020). In this respect, some examples of the processes that are affected and depend on the animal presence in ESS are seed dispersal, principally by frugivorous species of bats, birds, and some rodents (Tellería et al. 2005, Hilje et al. 2015); seed and plant recruitment, by predation from granivorous rodents (Velho et al. 2012); pollination, by nectarivores bats (Muscarella and Fleming 2007, Hilje et al. 2015); top-down effects and herbivory control, by predators such as snakes, lizards, and anurans (Dial and Roughgarden 1995, Heithaus et al. 2012, Cortés-Gómez et al. 2015).

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Appendix A. List of species and sites and their abbreviations.

A.1. Species and abbreviations of anurans:

Agalichnys dacnicolor (agda), *Craugastor hobartsmithi* (crho), *Craugastor occidentalis* (croc), *Dendropsophus sartori* (desa), *Diaglena spatulata* (disp), *Eleutherodactylus nitidus* (elni), *Hypopachus ustus* (hyus), *Hypopachus variolosus* (hyva), *Incilius marmoreus* (inma), *Incilius mazatlanensis* (inmaz), *Leptodactylus melanonotus* (leme), *Lithobates forreri* (lifo), *Rhinella marina* (rhma), *Smilisca baudini* (smba), *Smilisca fodiens* (smfo), *Tlalocohyla smithii* (tlsm), *Trachycephalus typhonius* (trty).

A.2. Species and abbreviations of lizards:

Anolis nebulosus (anne), *Aspidoscelis communis* (asco), *Aspidoscelis deppii* (asde), *Aspidoscelis lineatissima* (asli), *Coleonyx elegans* (coel), *Ctenosaura pectinata* (ctpe), *Gerrhonotus liocephalus* (geli), *Heloderma horridum* (heho), *Holcosus undulatus* (houn), *Iguana iguana* (igig), *Marisora brachypod*a (mabr), *Phrynosoma asio* (phas), *Phyllodactylus lanei* (phla), *Plestiodon parvulus* (plpa), *Sceloporus horridus* (scho), *Sceloporus melanorhinus* (scme), *Sceloporus utiformis* (scut), *Scincella assata* (urbi), *Urosaurus bicarinatus* (scas).

A.3. Species and abbreviations of snakes:

Agkistrodon bilineatus (agbi), *Boa constrictor* (boco), *Coniophanes lateritius* (cola), *Conophis vittatus* (covi), *Crotalus basiliscus* (crba), *Dipsas gaigeae* (diga), *Drymobius margaritiferus* (drma), *Drymarchon melanurus* (drme), *Imantodes gemmistratus* (imge), *Lampropeltis triangulum* (latr), *Leptophis diplotropis* (ledi) *Leptodeira maculata* (lema), *Leptodeira uribei* (leur), *Masticophis mentovarius* (mame), *Mastigodryas melanolomus* (masme), *Micrurus distans* (midi), *Oxybelis aeneus* (oxae), *Rena humilis* (rehu), *Salvadora mexicana* (same), *Sibon nebulatus* (sine), *Symphimus leucostomus* (syle), *Tantilla bocourti* (tabo), *Tantilla calamarina* (taca), *Trimorphodon biscutatus* (trbi).

A.4. Species and abbreviations of migratory birds:

Basileuterus lachrymosus (baslac), *Cardellina pusilla* (carpus), *Catharus aurantiirostris* (cataur), *Catharus ustulatus* (catust), *Empidonax minimus* (empmin), *Geothlypis tolmiei* (geotol), *Icteria virens* (ictvir), *Icterus cucullatus* (ictcuc), *Icterus spurius* (ictspu), *Melospiza lincolnii* (mellin), *Mniotilta varia* (mnivar), *Molothrus ater* (molate), *Myiarchus cinerascens* (myicin), *Myiarchus tyrannulus* (myityr), *Oreothlypis luciae* (oreluc), *Oreothlypis ruficapilla* (oreruf), *Parkesia motacilla* (parmot), *Passerina caerulea* (pascae), *Passerina ciris* (pascir), *Passerina versicolor* (pasver), *Pheucticus melanocephalus* (phemel), *Piranga ludoviciana* (pirlud), *Piranga rubra* (pirrub), *Polioptila caerulea* (polcae), *Saltator coerulescens* (salcoe), *Seiurus aurocapilla* (seiaur), *Setophaga petechia* (setpet), *Tachycineta bicolor* (tacbic), *Vireo bellii* (virbel), *Vireo gilvus* (virgil), *Vireo hypochryseus* (virhyp).

A.5. Species and abbreviations of resident birds:

Arremonops rufivirgatus (arrruf), *Attila spadiceus* (attspa), *Camptostoma imberbe* (camimb), *Cassiculus melanicterus* (casmel), *Cyanocompsa parellina* (cyapar), *Cyanocorax formosa* (cyafor), *Cyanocorax sanblasianus* (cyasan), *Deltarhynchus flammulatus* (delfla), *Empidonax difficilis* (empdif), *Granatellus venustus* (graven*), Icterus pustulatus* (ictpus), *Melanotis caerulescens* (melcae), *Myiarchus nuttingi* (myinut), *Myiarchus tuberculifer* (myitub), *Myiarchus tyrannulus* (myityr), *Myiodynastes luteiventris* (myilut), *Pachyramphus aglaiae* (pacagl), *Passerina leclancherii* (paslec), *Peucaea ruficauda* (peuruf), *Pheucticus chrysopeplus* (phechr), *Pheugopedius felix* (phefel), *Pitangus sulphuratus* (pitsul), *Polioptila nigriceps* (polnig), *Quiscalus mexicanus* (quimex), *Rhodinocichla rosea* (rhoros), *Setophaga pitiayumi* (setpit), *Sporophila minuta* (spomin), *Thryophilus sinaloa* (thrsin), *Tityra semifasciata* (titsem), *Turdus rufopalliatus* (turruf), *Tyrannus crassirostris* (tyrcra), *Tyrannus melancholicus* (tyrmel), *Tyrannus vociferans* (tyrvoc), *Uropsila leucogastra* (uroleu), *Volatinia jacarina* (voljac), *Xiphorhynchus flavigaster* (xipfla).

A.6. Species and abbreviations of rodents:

Baiomys musculus (baimus), *Liomys pictus* (lipoic), *Oryzomys couesi* (orycou), *Osgoodomys banderanus* (osgban), *Peromyscus perfulvus* (perper), *Reithrodontomys fulvescens* (reiful), *Sigmodon alleni* (sigall), *Sigmodon mascotensis* (sigmas).

A.7. Species and abbreviations of bats:

Artibeus hirsutus (arthir), *Artibeus jamaicensis* (artjam), *Artibeus lituratus* (artlit), *Artibeus phaeotis* (artpha), *Artibeus toltecus* (arttol), *Centurio cenex* (censen), *Choeroniscus godmani* (chogod), *Desmodus rotundus* (desrot), *Glossophaga soricina* (glosor), *Leptonycteris* *yerbabuenae* (lepyer), *Mormoops megalophylla* (mormeg), *Musonycteris harrisoni* (mushar), *Pteronotus davyi* (ptedav), *Pteronotus parnellii* (ptepar), *Sturnira parvidens* (stupar).

A.8. Sites and abbreviations

Road to the dump in Careyes town (BAS), Hidalgo Nuevo 1 (HN1), Hidalgo Nuevo 2 (HN2), Juan Gil Preciado (JGP), José María Morelos (JMM), Ley Federal Hidalgo (LFH), La Fortuna (LFO), Limoncitos (LIM), Nacastillo 1 (NA1), Nacastillo 2 (NA2), Zapata (ZAP), biological station of the UDG (UDG), biological station of the UNAM (UNAM).

Appendix Table A1. Plant communities scores in non-Metric Multidimensional Scaling axis summarizing site variations in vegetation species composition, stress % = 5.02.

Site	Axis 1	Axis 2	Axis 3
BAS	-1.4054	0.2266	-0.1389
HN1	0.5422	0.4480	-0.0365
HN2	0.6228	0.1117	-0.4534
JGP	-0.0240	0.0869	0.2823
JMM	-0.2545	0.1344	-0.1445
LFO	-0.3233	0.1746	-0.0297
LFH	-0.7156	-0.4562	0.3335
LIM	0.6986	0.1904	0.3380
NA1	0.0838	-0.4728	-0.4826
NA2	0.5949	-0.5815	0.1217
ZAP	0.1804	0.1378	0.2101

Appendix Table A2. List of conspicuous and restricted species in ESS sites, and exclusive species of ESS and OGF sites.

Taxa	Conspicuous species in ESS	Restricted species in ESS	Exclusive species of ESS	Exclusive species of OGF
Anurans	*Agalichnys dacnicolor (10 sites), Lithobates forreri (9 sitess), Smilisca baudini (10 sites)*	*Craugastor hobartsmithi (1 site), Hypopachus variolosus (1 site)*	*Craugastor hobartsmithi, Craugastor occidentalis, Eleutherodactylus nitidus, Hypopachus variolosus, Incilius marmoreus, Incilius mazatlanensis, Smilisca fodiens*	
Lizards	*Anolis nebulosus (11 sites), Aspidoscelis communis (11 sites), Aspidoscelis lineatissima (11 sites), Sceloporus utiformis (11 sites)*	*Heloderma horridum (1 site), Iguana iguana (2 sites), Plestiodon parvulus (2 sites)*	*Heloderma horridum, Iguana iguana, Marisora brachypoda, Phrynosoma asio, Phrynosoma parvulus, Urosaurus bicarinatus*	*Gerrhonotus liocephalus*
Snakes	*Oxybelis aeneus (10 sites)*	*Coniophanes lateritius (1 site), Conophis vittatus (1 site), Leptodeira uribei (1 site), Symphimus leucostomus (1 site), Tantilla bocourti (1 site)*	*Agkistrodon bilineatus, Boa constrictor, Coniophanes lateritius, Crotalus basiliscus, Drymarchon melanurus, Imantodes gemmistratus, Lampropeltis triangulum, Masticophis mentovarius, Micrurus distans, Rena humilis, Salvadora mexicana, Symphimus leucostomus, Tantilla calamarina*	*Drymobius margaritiferus, Mastigodryas melanolomus, Sibon nebulatus, Trimorphodon biscutatus*
Migratory birds	*Icteria virens (10 sites), Myiarchus tyrannulus (11 sites), Passerina versicolor (11 sites)*	*Catharus aurantiirostris (1 site), Oreothlypis luciae (1 site), Passerina caerulea (1 site), Pheucticus melanocephalus (1 site), Piranga ludoviciana (1 site), Seiurus aurocapilla (1 site), Tachycineta bicolor (1 site), Vireo hypochryseus (1 site)*	*Cardellina pusilla, Catharus aurantiirostris, Geothlypis tolmiei, Icterus cucullatus, Icterus spurius, Melospiza lincolnii, Mniotilta varia, Molothrus ater, Oreothlypis luciae, Passerina caerulea, Pheucticus melanocephalus, Piranga rubra, Polioptila caerulea, Setophaga petechia, Tachycineta bicolor, Vireo hypochryseus*	*Basileuterus lachrymosus*
Resident birds	*Arremonops rufivirgatus (11 sites), Cassiculus melanicterus (11 sites), Cyanocompsa parellina (11 sites), Empidonax difficilis (11 sites), Icterus pustulatus (11 sites), Myiarchus nuttingi (11 sites), Myiarchus tuberculifer (11 sites), Passerina leclancherii (11 sites), Pheugopedius felix (11 sites), Tyrannus vociferans (11 sites)*	*Quiscalus mexicanus (1 site), Sporophila minuta (1 site), Tityra semifasciata (1 site), Tyrannus crassirostris (1 site), Tyrannus melancholicus (1 site)*	*Camptostoma imberbe, Melanotis caerulescens, Myiodynastes luteiventris, Peucaea ruficauda, Pitangus sulphuratus, Quiscalus mexicanus, Saltator coerulescens, Sporophila minuta, Tyrannus crassirostris, Tyrannus melancholicus, Volatinia jacarina*	
Rodents	*Liomys pictus (11 sites), Baiomys musculus (11 sites), Oryzomys couesi (10 sites), Osgoodomys banderanus (11 sites), Sigmodon alleni (10 sites), Sigmodon mascotensis (11 sites)*		*Baiomys musculus, Reithrodontomys fulvescens*	
Bats	*Artibeus jamaicensis (11 sites), Artibeus phaeotis (10 sites), Glossophaga soricina (11 sites)*	*Pteronotus davyi (1 site), Musonycteris harrisoni (1 site), Artibeus hirsutus (1 site), Centurio senex (2 sites)*	*Pteronotus davyi, Musonycteris harrisoni, Centurio senex*	*Mormoops megalophylla*

Appendix Table A3. Incidence matrix and summary of richness for anuran species at each study site.

Family	Species	BAS	HN1	HN2	JGP	JMM	LFH	LFO	LIM	NA1	NA2	ZAP	UDG	UNAM
Bufonidae	*Incilius marmoreus*	0	1	0	1	1	0	1	1	0	0	0	0	0
	Incilius mazatlanensis	0	0	0	0	0	0	0	0	1	1	0	0	0
	Rhinella marina	1	1	1	0	1	1	1	0	0	0	0	1	1
Craugastoridae	*Craugastor hobartsmithi*	0	0	0	1	0	0	0	0	0	0	0	0	0
	Craugastor occidentalis	0	0	0	1	0	0	0	0	0	1	0	0	0
Eleutherodactylidae	*Eleutherodactylus nitidus*	0	1	1	1	0	0	0	0	0	1	0	0	0
Hylidae	*Agalichnys dacnicolor*	0	1	1	1	1	1	1	1	1	1	1	1	1
	Dendropsophus sartori	0	0	0	0	0	1	1	0	1	0	0	0	1
	Diaglena spatulata	1	1	0	1	0	0	0	0	0	0	1	1	0
	Smilisca baudini	0	1	1	1	1	1	1	1	1	1	1	1	0
	Smilisca fodiens	0	0	0	1	1	1	1	0	1	1	0	0	0
	Tlalocohyla smithii	0	0	0	0	1	1	1	0	1	0	1	0	1
	Trachycephalus typhonius	0	1	1	0	0	0	0	1	0	1	0	1	1
Leptodactylidae	*Leptodactylus melanonotus*	0	0	0	0	0	0	1	0	1	0	0	0	1
Microhylidae	*Hypopachus ustus*	0	0	1	0	0	0	1	1	0	1	0	0	1
	Hypopachus variolosus	0	0	0	0	1	0	0	0	0	0	0	0	0
Ranidae	*Lithobates forreri*	1	1	0	1	1	1	1	0	1	1	1	0	1
	Species richness	3	8	6	9	8	7	10	5	8	9	5	5	8

Appendix Table A4. Incidence matrix and summary of richness for lizard species at each study site.

Family	Species	BAS	HN1	HN2	JGP	JMM	LFH	LFO	LIM	NA1	NA2	ZAP	UDG	UNAM
Anguidae	*Gerrhonotus liocephalus*	0	0	0	0	0	0	0	0	0	0	0	1	0
Dactyloidae	*Anolis nebulosus*	1	1	1	1	1	1	1	1	1	1	1	1	1
Eublepharidae	*Coleonyx elegans*	0	1	1	1	0	0	0	0	0	0	0	0	1
Helodermatidae	*Heloderma horridum*	0	0	0	0	0	0	0	1	0	0	0	0	0
Iguanidae	*Ctenosaura pectinata*	1	1	1	1	1	0	1	1	1	1	1	1	0
	Iguana iguana	0	0	0	0	0	0	1	0	0	0	1	0	0
Phrynosomatidae	*Phrynosoma asio*	1	0	0	0	0	0	1	0	1	0	0	0	0
	Sceloporus horridus	0	1	1	0	0	0	1	1	1	0	0	0	1
	Sceloporus melanorhinus	1	1	0	1	1	1	1	1	0	0	1	1	1
	Sceloporus utiformis	1	1	1	1	1	1	1	1	1	1	1	1	1
	Urosaurus bicarinatus	0	0	1	0	0	0	0	0	0	1	1	1	0
Phyllodactylidae	*Phyllodactylus lanei*	0	1	1	0	0	1	0	0	0	1	0	1	1
Scincidae	*Marisora brachypoda*	0	1	0	0	0	0	1	0	0	0	1	0	0
	Plestiodon parvulus	0	0	1	0	0	0	0	0	0	1	0	0	0
	Scincella assata	1	0	1	1	1	1	1	0	1	0	0	0	0
Teiidae	*Aspidoscelis communis*	1	1	1	1	1	1	1	1	1	1	1	1	1
	Aspidoscelis deppii	1	0	0	0	1	0	1	1	1	0	0	0	1
	Aspidoscelis lineatissima	1	1	1	1	1	1	1	1	1	1	1	1	1
	Holcosus undulatus	0	1	1	1	0	1	0	0	0	1	1	1	1
	Species richness	9	11	12	9	8	8	12	9	9	9	10	10	10

Appendix Table A5. Incidence matrix and summary of richness for snake species at each study site.

Family	Species	BAS	HN1	HN2	JGP	JMM	LFH	LFO	LIM	NA1	NA2	ZAP	UDG	UNAM
Boidae	*Boa constrictor*	0	1	0	0	0	1	0	0	0	0	0	0	0
Colubridae	*Coniophanes lateritius*	0	0	1	0	0	0	0	0	0	0	0	0	0
	Conophis vittatus	0	0	0	0	0	0	0	0	1	0	0	0	1
	Dipsas gaigeae	0	1	0	0	0	0	0	1	0	0	0	1	1
	Drymobius margaritiferus	0	0	0	0	0	0	0	0	0	0	0	1	1
	Drymarchon melanurus	0	1	0	1	0	0	0	1	0	0	0	0	0
	Imantodes gemmistratus	0	1	0	1	1	1	1	0	1	0	1	0	0
	Lampropeltis triangulum	0	0	1	1	0	0	0	1	1	1	0	0	0
	Leptophis diplotropis	0	0	1	1	1	1	1	0	1	1	1	1	0
	Leptodeira maculata	0	0	1	1	0	0	1	0	0	1	1	0	1
	Leptodeira uribei	0	0	0	0	0	0	0	0	0	1	0	1	0
	Masticophis mentovarius	0	1	0	0	0	0	1	0	0	0	0	0	0
	Mastigodryas melanolomus	0	0	0	0	0	0	0	0	0	0	0	0	1
	Oxybelis aeneus	0	1	1	1	1	1	1	1	1	1	1	1	1
	Salvadora mexicana	0	0	0	0	0	0	0	0	1	0	1	0	0
	Sibon nebulatus	0	0	0	0	0	0	0	0	0	0	0	1	0
	Symphimus leucostomus	0	0	0	0	1	0	0	0	0	0	0	0	0
	Tantilla bocourti	0	0	0	0	0	0	0	0	0	1	0	0	1
	Tantilla calamarina	1	1	0	0	0	0	0	0	0	0	0	0	0
	Trimorphodon biscutatus	0	0	0	0	0	0	0	0	0	0	0	1	0
Elapidae	*Micrurus distans*	1	1	1	1	0	0	0	1	0	0	0	0	0
Leptotyphlopidae	*Rena humilis*	0	1	0	0	0	0	0	0	0	0	1	0	0
Viperidae	*Agkistrodon bilineatus*	0	0	0	1	0	0	1	0	0	0	0	0	0
	Crotalus basiliscus	0	1	0	0	0	0	1	0	0	1	0	0	0
	Species richness	2	10	6	8	4	4	7	5	6	7	6	7	7

Appendix Table A6. Incidence matrix and summary of richness for migratory bird species at each study site.

Family	Species	BAS	HN1	HN2	JGP	JMM	LFH	LFO	LIM	NA1	NA2	ZAP	UDG	UNAM
Cardinalidae	*Passerina caerulea*	0	0	0	0	1	0	0	0	0	0	0	0	0
	Passerina ciris	1	0	0	0	1	0	1	1	1	0	1	1	0
	Passerina versicolor	1	1	1	1	1	1	1	1	1	1	1	1	0
	Pheucticus melanocephalus	0	0	0	0	0	0	1	0	0	0	0	0	0
	Piranga ludoviciana	0	0	0	0	0	0	0	0	0	1	0	0	1
	Piranga rubra	1	1	1	0	0	0	0	0	0	0	0	0	0
Emberizidae	*Melospiza lincolnii*	0	0	0	0	1	1	0	0	1	1	0	0	0
Hirundinidae	*Tachycineta bicolor*	0	0	0	0	0	0	0	0	1	0	0	0	0
Icteridae	*Icterus cucullatus*	0	0	0	0	0	0	1	1	0	0	1	0	0
	Icterus spurius	0	0	0	0	1	0	1	0	1	0	1	0	0
	Molothrus ater	0	0	0	0	1	0	0	0	1	0	0	0	0
Parulidae	*Basileuterus lachrymosus*	0	0	0	0	0	0	0	0	0	0	0	1	0
	Cardellina pusilla	0	1	0	1	0	0	0	0	0	1	0	0	0
	Geothlypis tolmiei	0	0	1	0	0	0	0	0	0	0	1	0	0
	Icteria virens	1	1	1	1	1	1	1	1	1	0	1	1	0
	Mniotilta varia	1	0	0	0	0	0	1	0	0	0	0	0	0
	Oreothlypis luciae	0	0	0	0	0	0	0	0	0	0	1	0	0
	Oreothlypis ruficapilla	1	1	0	1	0	1	1	1	1	1	0	1	1
	Parkesia motacilla	0	0	0	0	0	1	1	0	0	0	0	0	1
	Seiurus aurocapilla	0	0	1	0	0	0	0	0	0	0	0	0	1
	Setophaga petechia	1	0	1	1	1	0	1	1	1	0	1	0	0
Polioptilidae	*Polioptila caerulea*	1	0	0	1	1	1	1	1	1	1	0	0	0
Thraupidae	*Saltator coerulescens*	1	0	0	1	1	1	1	1	1	1	1	0	1
Turdidae	*Catharus aurantiirostris*	0	1	0	0	0	0	0	0	0	0	0	0	0
	Catharus ustulatus	0	1	0	0	0	0	0	0	0	1	0	1	1
Tyrannidae	*Empidonax minimus*	1	1	1	1	1	1	0	1	1	0	1	0	1
	Myiarchus cinerascens	1	0	0	0	1	1	0	1	1	1	1	1	0
	Myiarchus tyrannulus	1	1	1	1	1	1	1	1	1	1	1	1	1
Vireonidae	*Vireo bellii*	1	0	0	0	0	0	1	1	1	0	0	0	1
	Vireo gilvus	1	0	0	0	1	0	1	1	1	0	0	1	1
	Vireo hypochryseus	0	0	0	0	1	0	0	0	0	0	0	0	0
	Species richness	14	9	8	9	15	10	15	13	16	10	12	9	10

Appendix Table A7. Incidence matrix and summary of richness for resident bird species at each study site.

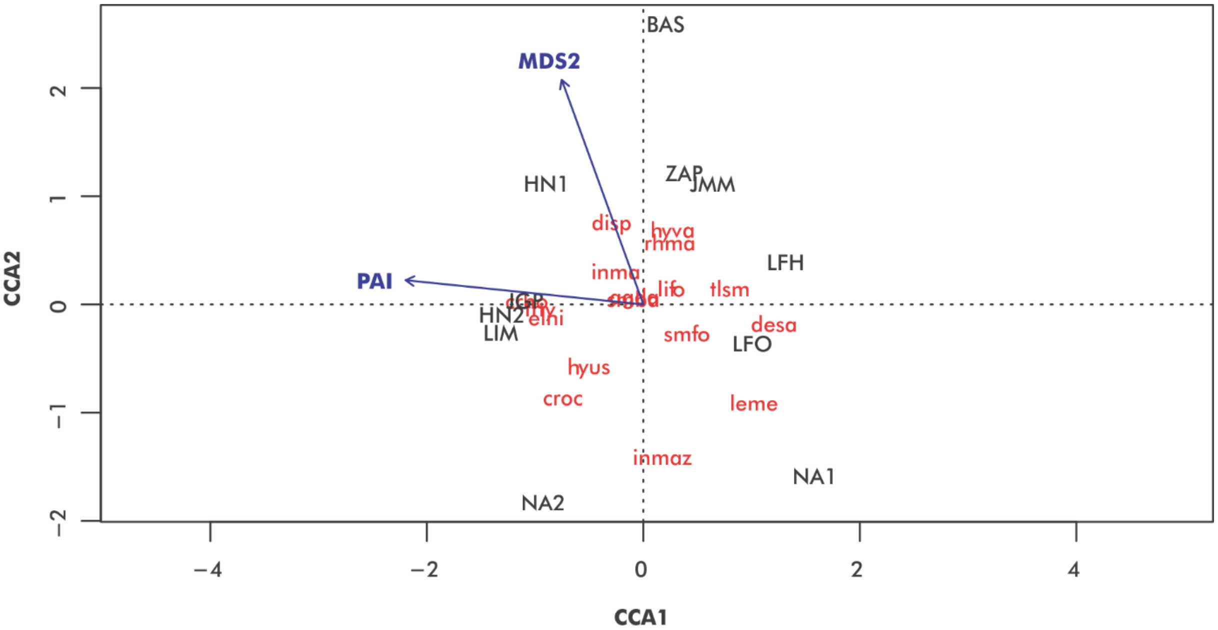
Family	Species	BAS	HN1	HN2	JGP	JMM	LFH	LFO	LIM	NA1	NA2	ZAP	UDG	UNAM
Cardinalidae	*Cyanocompsa parellina*	1	1	1	1	1	1	1	1	1	1	1	1	1
	Granatellus venustus	0	1	1	1	1	0	1	0	0	1	0	1	1
	Passerina leclancherii	1	1	1	1	1	1	1	1	1	1	1	0	1
	Pheucticus chrysopeplus	0	0	0	1	0	0	0	1	0	0	0	0	1
Corvidae	*Cyanocorax formosa*	1	1	1	1	0	1	1	0	1	1	0	1	1
	Cyanocorax sanblasianus	1	0	0	1	1	1	1	1	1	0	1	1	1
Emberizidae	*Arremonops rufivirgatus*	1	1	1	1	1	1	1	1	1	1	1	1	1
	Peucaea ruficauda	1	0	1	1	1	1	1	1	1	1	1	0	0
Furnariidae	*Xiphorhynchus flavigaster*	0	0	1	1	0	0	0	0	0	1	0	1	1
Icteridae	*Cassiculus melanicterus*	1	1	1	1	1	1	1	1	1	1	1	1	1
	Icterus pustulatus	1	1	1	1	1	1	1	1	1	1	1	1	1
	Quiscalus mexicanus	0	0	0	0	1	0	0	0	0	0	0	0	0
Mimidae	*Melanotis caerulescens*	0	0	0	0	1	1	0	0	0	0	1	0	0
Parulidae	*Setophaga pitiayumi*	1	1	1	1	1	1	0	1	0	1	1	1	1
Polioptilidae	*Polioptila nigriceps*	1	0	0	1	0	0	1	0	1	1	0	1	0
Rhodinocichlidae	*Rhodinocichla rosea*	0	0	1	0	0	0	0	1	0	1	1	1	1
Thraupidae	*Sporophila minuta*	0	0	0	0	0	0	0	0	0	0	1	0	0
	Volatinia jacarina	1	1	0	1	1	1	1	1	1	1	1	0	0
Tityridae	*Pachyramphus aglaiae*	0	0	1	0	0	0	0	1	0	1	0	0	1
	Tityra semifasciata	0	0	0	0	0	0	0	0	0	1	0	1	1
Troglodytidae	*Pheugopedius felix*	1	1	1	1	1	1	1	1	1	1	1	1	1
	Thryophilus sinaloa	1	1	1	1	1	1	1	1	1	1	1	1	1
	Uropsila leucogastra	1	1	1	1	1	1	1	1	1	0	1	1	1
Turdidae	*Turdus rufopalliatus*	1	0	1	1	1	1	1	1	1	1	1	0	1
Tyrannidae	*Attila spadiceus*	1	1	0	1	1	1	0	0	1	1	0	1	1
	Camptostoma imberbe	0	0	0	0	1	0	0	1	1	1	0	0	0
	Deltarhynchus flammulatus	1	0	0	0	1	0	0	1	0	1	0	0	1
	Empidonax difficilis	1	1	1	1	1	1	1	1	1	1	1	1	1
	Myiarchus nuttingi	1	1	1	1	1	1	1	1	1	1	1	1	1
	Myiarchus tuberculifer	1	1	1	1	1	1	1	1	1	1	1	1	1
	Myiarchus tyrannulus	0	0	1	1	1	1	1	1	1	0	1	0	1
	Myiodynastes luteiventris	0	0	0	0	0	0	0	1	0	1	0	0	0
	Pitangus sulphuratus	0	0	0	0	1	1	1	0	0	1	0	0	0
	Tyrannus crassirostris	0	0	0	0	0	0	1	0	0	0	0	0	0
	Tyrannus melancholicus	0	0	0	0	0	0	0	1	0	0	0	0	0
	Tyrannus vociferans	1	1	1	1	1	1	1	1	1	1	1	1	1
	Species richness	21	17	21	24	25	22	22	25	21	27	21	20	25

Appendix Table A8. Incidence matrix and summary of richness for rodent species at each study site.

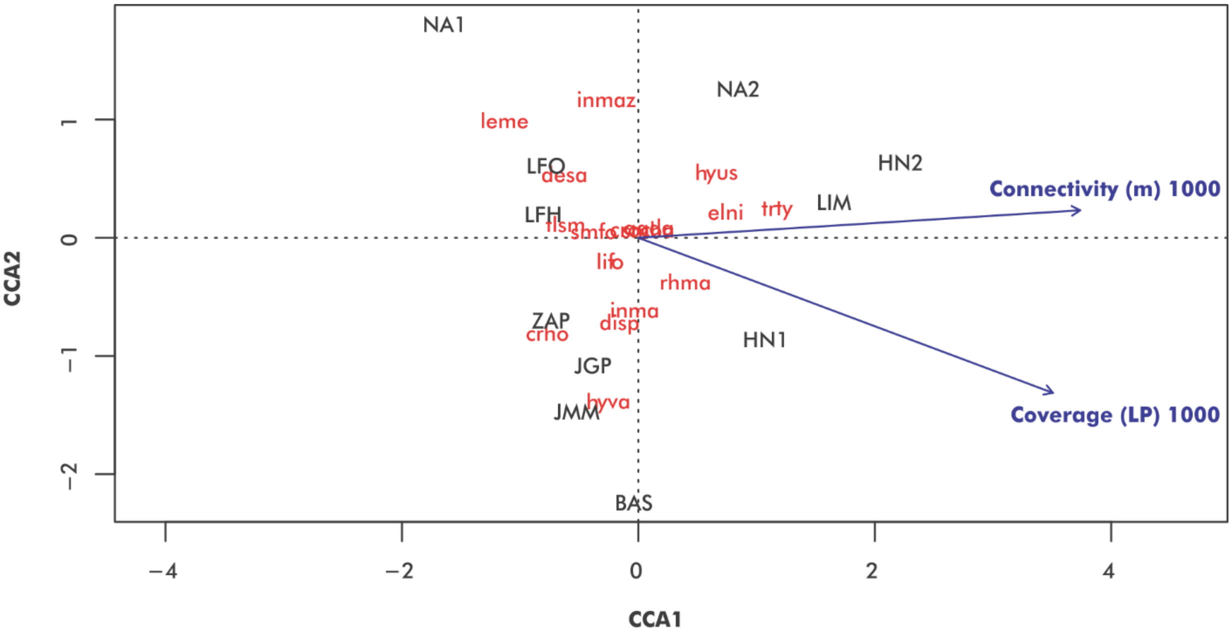
Family	Species	BAS	HN1	HN2	JGP	JMM	LFH	LFO	LIM	NA1	NA2	ZAP	UDG	UNAM
Cricetidae	*Baiomys musculus*	1	1	1	1	1	1	1	1	1	1	1	0	0
	Oryzomys couesi	1	1	1	1	1	1	1	1	1	0	1	1	1
	Osgoodomys banderanus	1	1	1	1	1	1	1	1	1	1	1	1	1
	Peromyscus perfulvus	1	1	1	1	0	1	0	0	0	0	1	1	1
	Reithrodontomys fulvescens	0	1	0	0	1	0	1	1	1	1	0	0	0
	Sigmodon alleni	1	1	0	1	1	1	1	1	1	1	1	0	1
	Sigmodon mascotensis	1	1	1	1	1	1	1	1	1	1	1	0	1
Heteromyidae	*Liomys pictus*	1	1	1	1	1	1	1	1	1	1	1	1	1
	Species richness	7	8	6	7	7	7	7	7	7	6	7	4	6

Appendix Table A9. Incidence matrix and summary of richness for bat species at each study site.

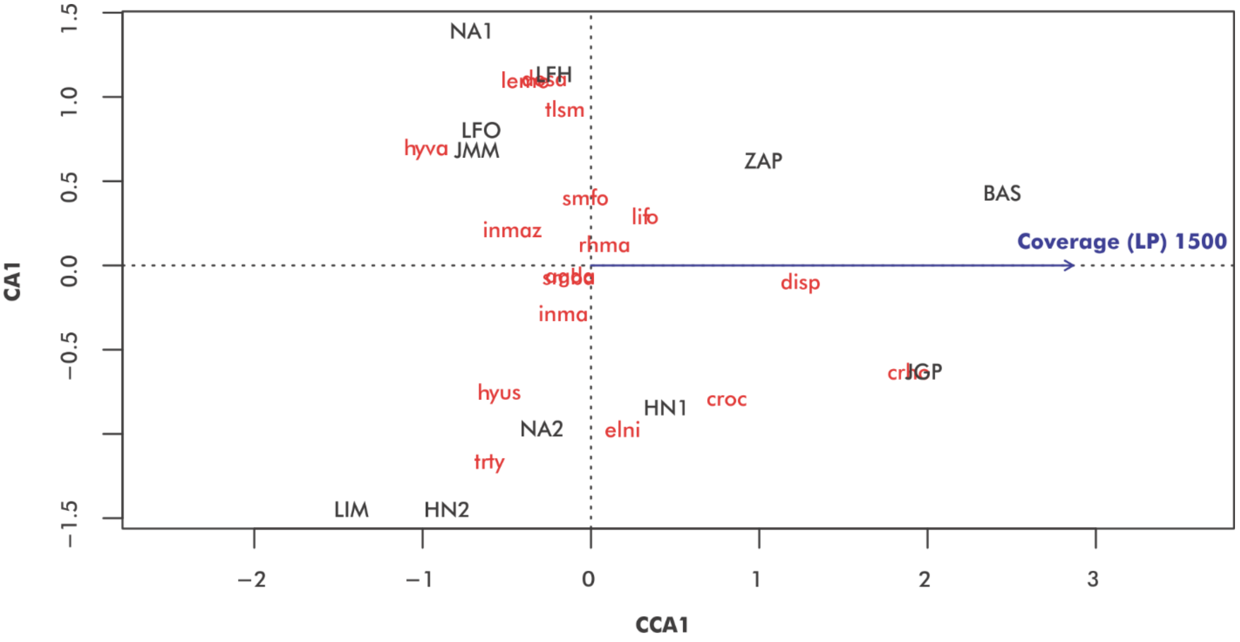
Family	Species	BAS	HN1	HN2	JGP	JMM	LFH	LFO	LIM	NA1	NA2	ZAP	UDG	UNAM
Mormoopidae	*Mormoops megalophylla*	0	0	0	0	0	0	0	0	0	0	0	0	1
	Pteronotus davyi	1	0	0	0	0	0	0	0	0	0	0	0	0
	Pteronotus parnellii	1	1	0	0	1	0	1	1	1	1	1	1	1
Phyllostomidae	*Artibeus hirsutus*	0	0	1	0	0	0	0	0	0	0	0	1	0
	Artibeus jamaicensis	1	1	1	1	1	1	1	1	1	1	1	1	1
	Artibeus lituratus	0	1	1	0	0	0	0	0	1	1	1	0	1
	Artibeus phaeotis	1	1	1	1	1	1	0	1	1	1	1	1	1
	Artibeus toltecus	1	0	0	1	0	1	0	1	1	1	0	1	0
	Centurio cenex	0	0	0	0	0	0	0	0	1	1	0	0	0
	Choeroniscus godmani	0	0	1	1	0	0	0	0	0	1	0	0	1
	Desmodus rotundus	1	1	1	1	0	1	1	0	1	1	1	1	1
	Glossophaga soricina	1	1	1	1	1	1	1	1	1	1	1	1	1
	Leptonycteris yerbabuenae	1	0	1	1	1	1	0	0	1	0	0	1	1
	Musonycteris harrisoni	0	0	0	0	0	0	0	0	1	0	0	0	0
	Sturnira parvidens	1	1	1	0	0	1	0	1	1	1	1	0	1
	Species richness	9	7	9	7	5	7	4	6	11	10	7	8	10



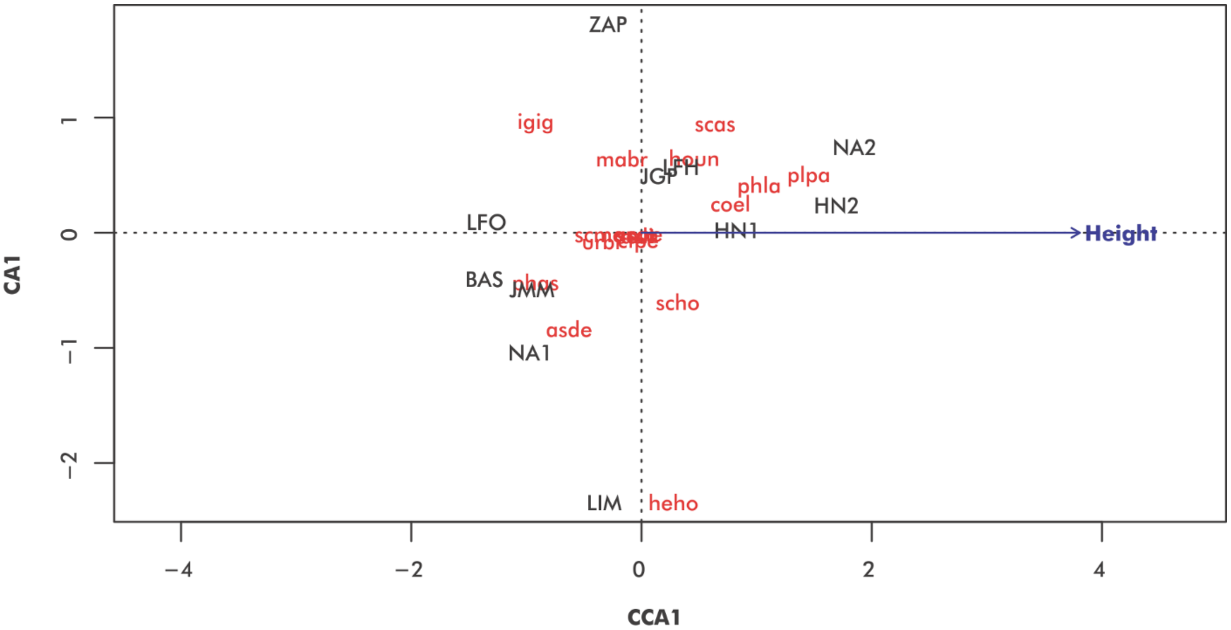
Appendix Figure A1. Canonical ordination of the anuran metacommunity in Chamela region in relation to vegetation attributes. Species are indicated with a red color. Sites are written in black. Vegetation variables are color blue and indicated as: LAI = Leaf Area Index, MDS2 = scores for the second axis of the MDS for vegetation composition. Abbreviations of anuran species are given in Appendix A.1.



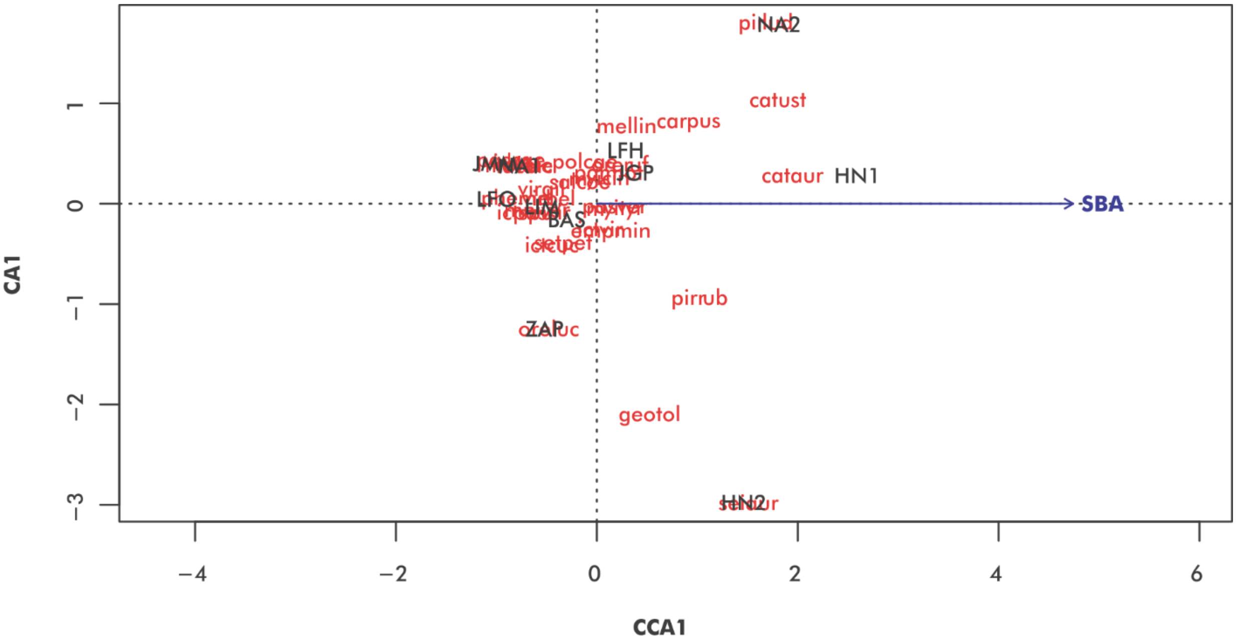
Appendix Figure A2. Canonical ordination of the anuran metacommunity in Chamela region in relation to landscape attributes of dry forest. Species are indicated with a red color. Sites are written in black. Landscape variables are color blue. Abbreviations of anuran species are given in Appendix A.1.



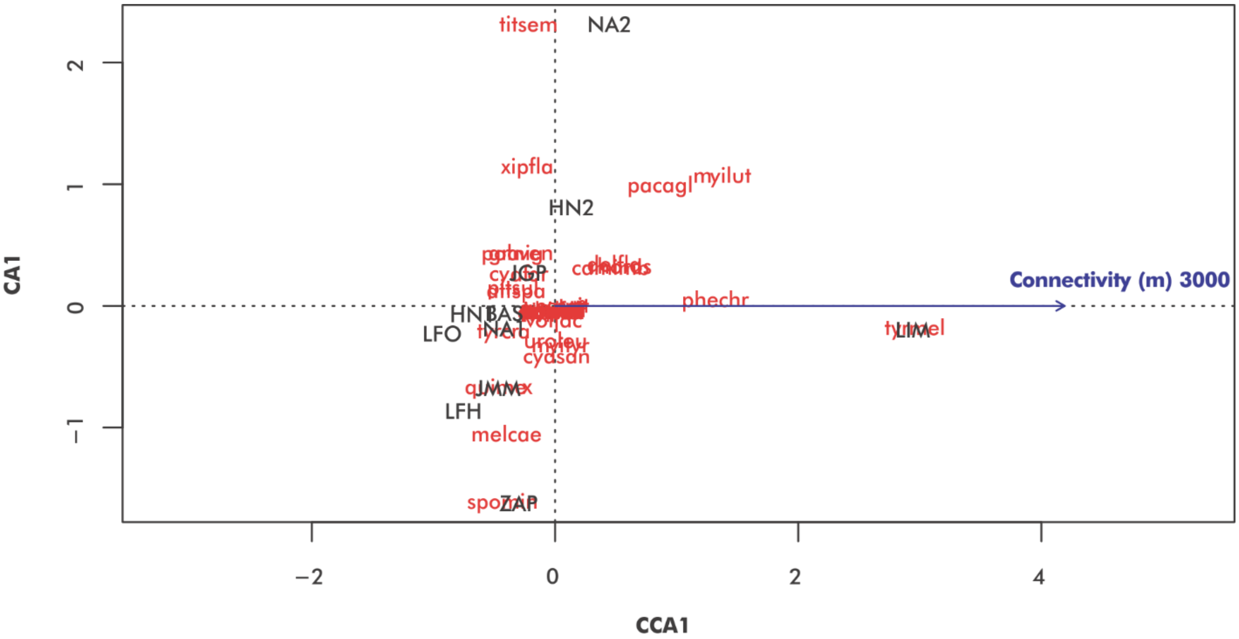
Appendix Figure A3. Canonical ordination of the anuran metacommunity in Chamela region in relation to landscape attributes of riparian forest. Species are indicated with a red color. Sites are written in black. The landscape variable is color blue. Abbreviations of anuran species are given in Appendix A.1.



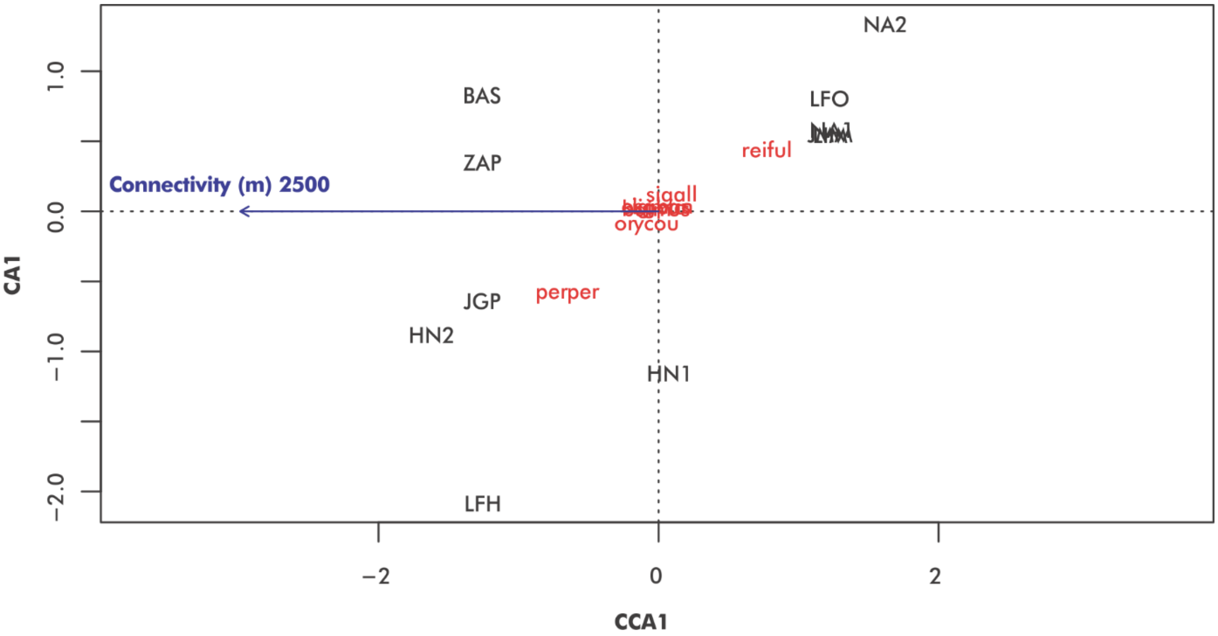
Appendix Figure A4. Canonical ordination of the lizard metacommunity in Chamela region in relation to vegetation attributes. Species are indicated with a red color. Sites are written in black. The vegetation variable is color blue. Abbreviations of lizard species are given in Appendix A.2.



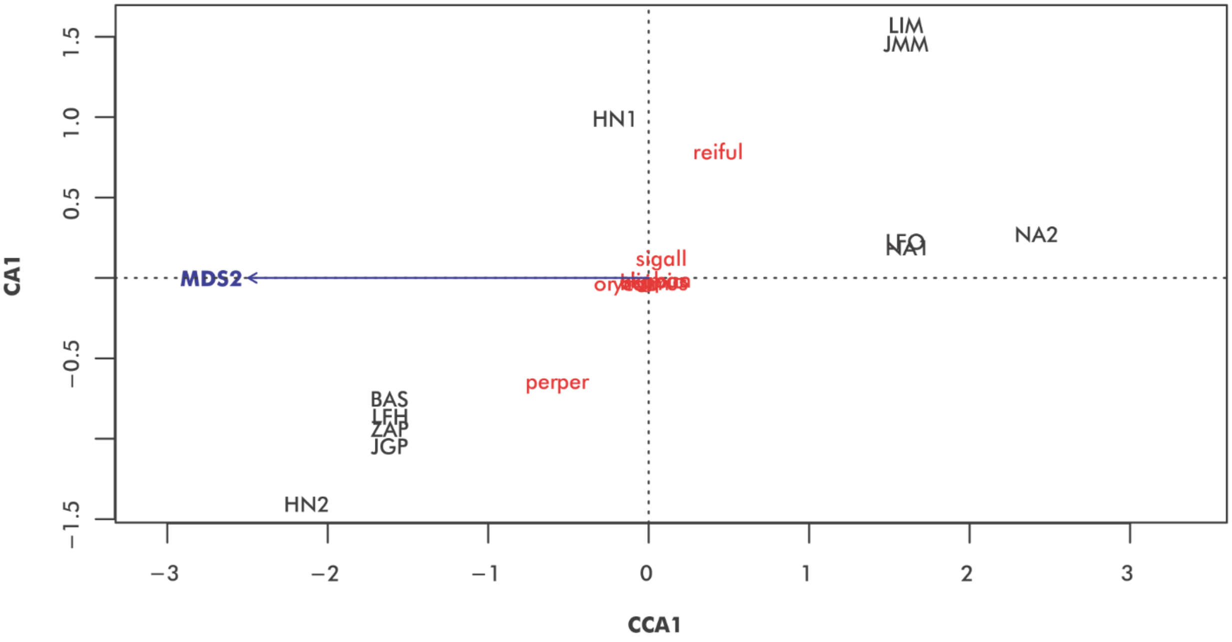
Appendix Figure A5. Canonical ordination of the metacommunity of migratory birds in Chamela region in relation to vegetation attributes. Species are indicated with a red color. Sites are written in black. The vegetation variable is color blue. Abbreviations of migratory bird species are given in Appendix A.4.



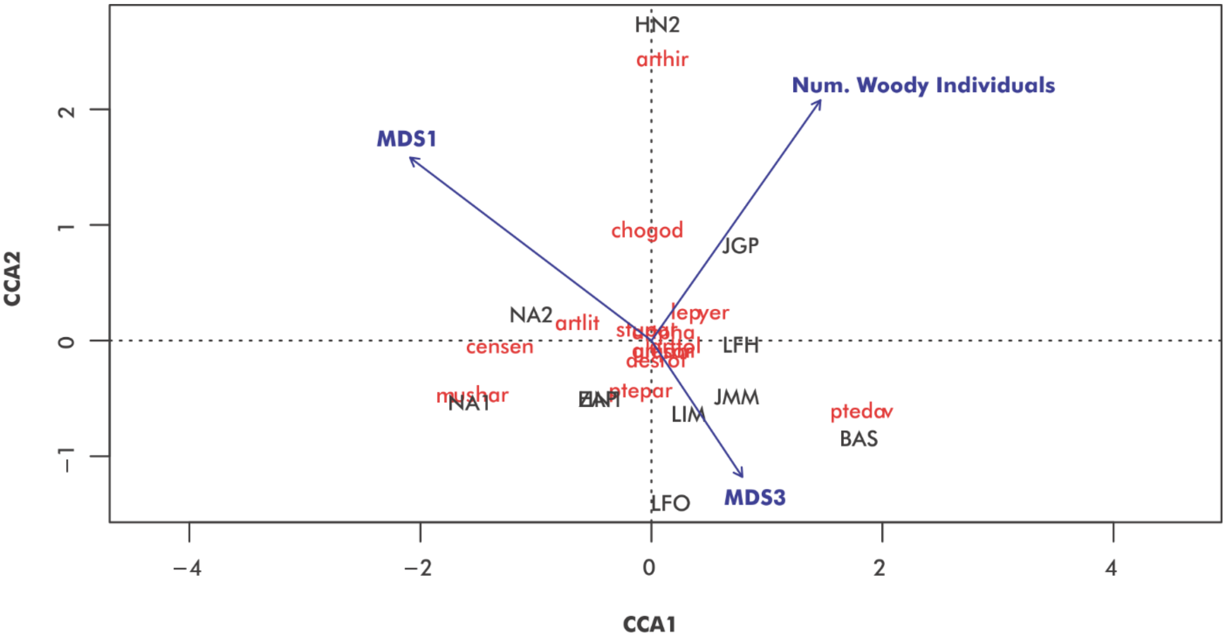
Appendix Figure A6. Canonical ordination of the metacommunity of resident birds in Chamela region in relation to landscape attributes of dry forest. Species are indicated with a red color. Sites are written in black. The landscape variable is color blue. Abbreviations of resident bird species are given in Appendix A.5.



Appendix Figure A7. Canonical ordination of the rodent metacommunity in Chamela region in relation to landscape attributes of riparian forest. Species are indicated with a red color. Sites are written in black. The landscape variable is color blue. Abbreviations of rodent species are given in Appendix A.6.



Appendix Figure A8. Canonical ordination of the rodent metacommunity in Chamela region in relation to vegetation attributes. Species are indicated with a red color. Sites are written in black. The vegetation variable is color blue and is indicated as: MDS2 = scores for the second axis of the MDS for vegetation composition. Abbreviations of rodent species are given in Appendix A.6.



Appendix Figure A9. Canonical ordination of the bat metacommunity in Chamela region in relation to vegetation attributes. Species are indicated with a red color. Sites are written in black. Vegetation variables are color blue and are indicated as: MDS1 = scores for the first axis of the MDS for vegetation composition, MDS3 = scores for the third axis of the MDS for vegetation composition, Num. Woody Individuals = number of woody individuals. Abbreviations of bat species are given in Appendix A.7.

Capítulo 3

Consideraciones finales

Esta tesis tuvo como objetivo identificar los mecanismos que estructuran a las metacomunidades de anuros, lagartijas, serpientes, aves, roedores y murciélagos en las etapas sucesionales tempranas del bosque tropical seco de Chamela. Con base en los resultados obtenidos a partir de los análisis de los elementos de la estructura de la metacomunidad, se puede concluir que las metacomunidades de vertebrados presentan en su mayoría quasi estructuras, principalmente de patrón gleasoniano, seguido por el clementsiano. Se sugiere que las especies de las metacomunidades con estructura Gleasoniana o quasi Gleasoniana en este sistema responden de manera individual a los gradientes ambientales en la región, mientras que aquellas de estructura quasi Clementsiana podrían responder de forma conjunta a este gradiente (Leibold et al., 2004; Presley et al., 2010).

Asimismo, estos resultados en conjunto con los análisis de las respuestas de los grupos vertebrados a los atributos del paisaje y la vegetación apuntan a que los principales mecanismos operando en las EST son los de “species sorting” y efecto de masa. Esto resalta la importancia conservar la conectividad y cobertura de bosque seco y ripario a diferentes escalas, así como de preservar la diversidad vegetal, ya que tanto los atributos del paisaje, así como la composición y complejidad estructural de la vegetación demostraron ser responsables de parte de la variación de las especies de vertebrados en las metacomunidades.

Por otro lado, la presencia de especies que generalmente son exclusivas de bosques maduros en los sitios en regeneración resalta la importancia de los bosques secundarios como sitios de refugio y de provisión de recursos (p. ej., alimentos) (DeWalt et al., 2003) que son utilizados por diferentes especies de vertebrados. En este sentido, aunque a simple vista los bosques en EST pudieran parecer de menor valor ecológico comparados con los bosques maduros, los altos niveles de diversidad y de recambio de especies encontrados para las comunidades locales, apoyan también la necesidad de conservar los diferentes remanentes de BTS que se encuentran en estas etapas para asegurar la protección del mayor número de especies y comunidades posibles.

Estos datos sugieren que actualmente las comunidades de vertebrados terrestres en el bosque tropical seco de Chamela son resilientes y pueden absorber en cierto grado la perturbación humana, sin embargo, esto solo es posible gracias a: 1) el papel fundamental que juega el bosque maduro de la Reserva de la Biósfera Chamela-Cuixmala, que funge como la fuente de especies que permite la dispersión, recolonización y presencia de estas en sitios que fueron perturbados y que están experimentado un proceso de sucesión secundaria; 2) la conectividad entre los fragmentos de bosque, que permiten la dispersión de las especies entre parches; 3) la capacidad de dispersión de las especies y la tolerancia a las condiciones encontradas en los bosques secundarios.

Finalmente, no hay que olvidar que el estudio de las etapas sucesionales tempranas y de los grupos que las habitan es muy importante para evaluar si el ecosistema es resiliente ante cambios ocasionados por disturbios de origen antrópico. La presencia de ciertas especies y mecanismos durante estos estadios pueden definir el camino del bosque tropical seco a lo largo de la sucesión ecológica (Swanson et al., 2011) al alterar o modificar procesos como la polinización, el reclutamiento de plantas, la dispersión de semillas, el control de herbivoría, entre otros (Cortés-Gómez et al., 2015; Dial & Roughgarden, 1995; Heithaus et al., 2012; Hilje et al., 2015; Muscarella & Fleming, 2007; Tellería et al., 2005; Velho et al., 2012). Por estos motivos, las EST deben ser tomadas en cuenta en el futuro dentro de los planes de conservación y manejo para preservar su diversidad característica y sus procesos ecológicos.

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