UNIVERSIDAD NACIONAL AUTÓNOMA DE MÉXICO

POSGRADO EN CIENCIAS BIOLÓGICAS

INSTITUTO DE INVESTIGACIONES EN ECOSISTEMAS Y SUSTENTABILIDAD

MAMÍFEROS TERRESTRES EN PAISAJES TROPICALES FRAGMENTADOS: EVIDENCIAS DE DEFAUNACIÓN, RODENTIZACIÓN, Y HOMOGENIZACIÓN Y DIFERENCIACIÓN BIÓTICA

TESIS

QUE PARA OPTAR POR EL GRADO DE:

DOCTORA EN CIENCIAS

PRESENTA:

NORMA PATRICIA ARCE PEÑA

TUTOR PRINCIPAL DE TESIS: DR. VÍCTOR ARROYO RODRÍGUEZ
INSTITUTO DE INVESTIGACIONES EN ECOSISTEMAS Y SUSTENTABILIDAD, UNAM
COMITÉ TUTOR: DRA. ELLEN ANDRESEN
INSTITUTO DE INVESTIGACIONES EN ECOSISTEMAS Y SUSTENTABILIDAD, UNAM
DR. LUIS DANIEL AVILA CABADILLA
ESCUELA NACIONAL DE ESTUDIOS SUPERIORES, UNIDAD MÉRIDA, UNAM

MORELIA, MICHOACÁN, NOVIEMBRE 2020

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COORDINACIÓN DEL POSGRADO EN CIENCIAS BIOLÓGICAS
ENTIDAD: IIES-MORELIA
OFICIO CPCB/689/2020
ASUNTO: Oficio de Jurado

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

Me permito informar a usted que en la reunión ordinaria del Subcomité de Ecología y Manejo Integral de Ecosistemas, del Posgrado en Ciencias Biológicas, celebrada el día **10 de agosto de 2020** se aprobó el siguiente jurado para el examen de grado de **DOCTORA EN CIENCIAS** de la estudiante **ARCE PEÑA NORMA PATRICIA**, con número de cuenta **405096233**, con la tesis titulada **"Mamíferos terrestres en paisajes tropicales fragmentados: evidencias de defaunación, rodentización, homogenización y diferenciación biótica"**, realizada bajo la dirección del **DR. VÍCTOR ARROYO RODRÍGUEZ**, quedando integrado de la siguiente manera:

Presidenta:	DRA. CLAUDIA ELIZABETH MORENO ORTEGA
Vocal:	DR. MIGUEL MARTÍNEZ RAMOS
Secretario:	DRA. ELLEN ANDRESEN
Suplente:	DR. EDUARDO MENDOZA RAMÍREZ
Suplente:	DR. IVÁN FRANCH PARDO

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

ATENTAMENTE
"POR MI RAZA HABLARÁ EL ESPÍRITU"
Cd. Universitaria, Cd. Mx., a 21 de octubre de 2020

COORDINADOR DEL PROGRAMA

DR. ADOLFO GERARDO NAVARRO SIGÜENZA

COORDINACIÓN DEL POSGRADO EN CIENCIAS BIOLOGICAS
UNIDAD DE POSGRADO
Edificio D, 1° Piso. Circuito de Posgrados, Ciudad Universitaria
Alcaldía Coyoacán. C. P. 04510 CDMX
Tel. (+5255)5623 7002 http://pcbiol.posgrado.unam.mx/

Agradecimientos institucionales

- Al Posgrado en Ciencias Biológicas, UNAM.
- Al Instituto de Investigaciones en Ecosistemas y Sustentabilidad.
- A CONACyT, por el apoyo económico recibido a lo largo de este doctorado.
- A la Fundación Rufford, por la beca recibida para el trabajo de campo (Rufford Small Grants No. 22049-1).
- Al Proyecto SEP-CONACyT por el apoyo económico recibido para el trabajo de campo (No. 2015-253946).
- A mi tutor, el Dr. Víctor Arroyo Rodríguez, por su apoyo y guía a través de mi formación como Doctora en Ciencias.
- A los miembros de mi Comité Tutoral, la Dra. Ellen Andresen y el Dr. Luis Daniel Ávila Cabadilla, por sus comentarios y apoyo a lo largo del doctorado, contribuyendo a mejorar significativamente esta tesis.

Agradecimientos personales

- A mis padres y hermano.
- A mis abuelos.
- A Rodrigo.
- A mi familia.
- A mis amigos.
- A mi tutor, Víctor Arroyo.
- Al Laboratorio de Ecología de Paisajes Fragmentados.
- A los miembros de mi Comité Tutoral, Ellen Andresen y Luis Daniel Avila,
- A los sinodales de esta tesis, por su revisión y comentarios.
- A Natura y Ecosistemas Mexicanos, A.C. y la Estación Biológica Chajul.
- A Loma Bonita, Audón, Adolfo, Marta, José y Jorge.
- A la selva.

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Resumen

Los mamíferos constituyen un grupo diverso en los ecosistemas tropicales y juegan papeles clave en el mantenimiento de las funciones de estos ecosistemas. Sin embargo, 25% de las especies están amenazadas de extinción y la mayoría de las especies tienen poblaciones en declive, principalmente debido a actividades humanas como la deforestación, el comercio ilegal y la cacería. Las especies tropicales están particularmente amenazadas (e.g. ~60% de los primates están amenazados) ya que los trópicos están sufriendo las mayores tasas de deforestación a nivel global. Además de reducir la cantidad de hábitat, la deforestación genera otros cambios espaciales, como la fragmentación, el incremento de bordes forestales y la expansión de diferentes tierras productivas (e.g. cultivos, pastizales, asentamientos humanos). Entender cómo responden las especies a estos cambios espaciales es fundamental para diseñar estrategias de manejo y conservación adecuadas. Sin embargo, nuestro conocimiento sobre este tema es muy limitado, ya que la mayoría de los estudios en paisajes deforestados realizan evaluaciones puntuales en el tiempo, y no consideran los cambios temporales en la estructura del paisaje.

La presente tesis tiene como objetivo conocer las respuestas de los mamíferos a los cambios temporales (2011 - 2017) en la estructura espacial del paisaje en la selva Lacandona, Chiapas. Para cumplir con este objetivo, primero se incluye una introducción general (Capítulo I) y se revisa el tema a nivel global (Capítulo II). Los capítulos III, IV y V evalúan las respuestas de las comunidades de mamíferos a los cambios temporales en el paisaje en la selva Lacandona. Primero estudiamos la comunidad de roedores terrestres para probar la hipótesis de la rodentización (Capítulo III). Segundo, estudiamos la población de monos aulladores negros – una especie amenazada de extinción – para evaluar el cambio en sus poblaciones y su relación con los cambios en la estructura del paisaje a través del tiempo (Capítulo IV). Tercero, analizamos los cambios en diversidad beta de mamíferos terrestres medianos y grandes para probar la hipótesis de la homogenización y diferenciación biótica (Capítulo V). Al final de la tesis (Capítulo VI), se discuten y analizan todos los capítulos en conjunto para evaluar cómo los cambios temporales en la estructura del paisaje afectan las comunidades de mamíferos en paisajes tropicales fragmentados.

En la revisión, encontramos 289 estudios que evalúan la respuesta de mamíferos a cambios espaciales en el hábitat, pero sólo 113 utilizan un enfoque de paisaje. Estos estudios analizaron 1367 respuestas de 304 especies a cambios espaciales en el paisaje, pero solamente el 13% de los estudios analizaron cambios temporales en el paisaje y su efecto sobre los mamíferos. La mayoría de estos estudios

utilizaron un enfoque sitio-paisaje y menos de un cuarto de los estudios analizaron la escala del efecto. De todas las respuestas analizadas más de la mitad fueron no significativas, casi tres cuartos analizaron su relación con variables de composición del paisaje, mientras que solo un cuarto evaluó su relación con variables de configuración. La cobertura forestal fue la variable más analizada y mostró una relación positiva con la mayoría de las variables de respuesta, principalmente con mamíferos amenazados, especialistas y de gran tamaño. Por otro lado, la composición de la matriz presentó mayormente respuestas negativas; sin embargo, se encontró que las respuestas de los mamíferos dependen en gran medida de la calidad de la matriz (e.g. los asentamientos humanos mostraron mayormente efectos negativos y los bosques secundarios presentaron solamente efectos positivos). La fragmentación *per se* mostró principalmente respuestas no-significativas y, cuando fueron significativas, fueron mayormente negativas, principalmente para carnívoros y mamíferos pequeños. Hacen falta estudios longitudinales que incorporen un diseño multi-escalar, que permita evaluar los efectos a largo plazo de los cambios espaciales en el paisaje en las poblaciones y comunidades de mamíferos.

Al evaluar la comunidad de roedores, nuestros hallazgos apoyan parcialmente la hipótesis de la rodentización, ya que hubo un incremento significativo en la abundancia de roedores a través del tiempo. Los cambios en la estructura del paisaje tuvieron una gran influencia sobre los cambios en abundancias. Sin embargo, concluimos que el proceso de rodentización fue moderado, ya que sólo dos especies (*Heteromys desmarestianus* y *Oryzomys* sp.) aumentaron sus abundancias, mientras que una disminuyó (*Peromyscus mexicanus*) y otra (*Sigmodon toltecus*) no modificó su abundancia a través del tiempo. Nuestros resultados sugieren que, si las tasas de deforestación se mantienen, las poblaciones de especies especialistas podrían disminuir (especies "perdedoras"), pero algunas especies generalistas podrían proliferar ("ganadoras").

Por otro lado, al evaluar a las poblaciones de monos aulladores, encontramos un aumento en el número de individos y una disminución en la relación inmaduros/hembras, ambos parámetros fuertemente relacionados con los cambios en el paisaje a través del tiempo. Ambos parámetros aumentaron en paisajes donde el número de parches aumentó, pero el porcentaje de áreas abiertas en la matriz disminuyó. La densidad de borde presentó efectos negativos sobre la relación inmaduros/hembras. Los resultados sugieren que los monos aulladores podrían no ser tan tolerantes al disturbio como generalmente se piensa, por lo que es necesario implementar estrategias efectivas que permitan su conservación en paisajes antrópicos a largo plazo.

Por último, al evaluar los cambios en la comunidad de mamíferos terrestres medianos y grandes a través del tiempo, encontramos que la diversidad beta disminuyó a través del tiempo, lo que sugiere que puede estar ocurriendo un proceso de homogenización biótica. Estos cambios se debieron principalmente a una disminución en el componente de recambio, especialmente en paisajes en los que disminuyó la cobertura forestal y aumentaron las matrices arboladas. Por otro lado, el componente de anidamiento se triplicó a través del tiempo. Se encontró el mismo número de especies en 2011 y en 2017. Los resultados sugieren que el proceso de homogenización es probablemente causado por un aumento en la dispersión de las especies a través de los sitios de bosque remanentes. Futuras modificaciones en el paisaje, principalmente la pérdida de cobertura forestal, podrían provocar la pérdida de diversidad beta, exacerbando el proceso de homogenización biótica de la comunidad de mamíferos terrestres medianos y grandes en la región.

En general, incrementar la cantidad de cobertura forestal en el paisaje parece ser la estrategia más importante para mantener y mejorar la calidad del paisaje para la biodiversidad. Para poder conservar a los mamíferos tropicales, especialmente a aquellas especies especialistas, dependientes de bosque, es necesario conservar la cobertura forestal en el paisaje, y aumentarla a través de la restauración, así como promover matrices "amigables", que presenten una composición similar a la del bosque conservado (e.g., sistemas agroforestales, bosques secundarios). Adicionalmente, es importante mantener y promover la conectividad de los parches de bosque remanentes, disminuyendo las distancias entre los parches y manteniendo un mayor número de parches en el paisaje. Para algunas especies, como los monos aulladores inmaduros, reducir la densidad de bordes permitirá reducir su vulnerabilidad ante depredadores y actividades humanas, como atropellos, cacería y extracción para el comercio ilegal. En conjunto, estas medidas permitirán disminuir los efectos negativos de las actividades humanas sobre los mamíferos tropicales, promoviendo su conservación en este importante hotspot de diversidad en Norteamérica.

Abstract

Mammals are a diversified group in tropical ecosystems and represent a key role to the maintenance of their functioning. Yet, 25% of the species are threatened with extinction and most species have declining populations, mainly due to human activities such as deforestation, illegal trade and hunting. Tropical species are particularly threatened (e.g. ~60% primate populations are threatened) due to higher deforestation rates in the tropics. Besides resulting in habitat loss, deforestation generates other spatial modifications, such as fragmentation, the increase in forest edges and the expansion of productive lands (e.g. crops, pastures, human settlements). Understanding how species respond to these spatial changes is vital to design appropriate management and conservation strategies. Yet, our understanding on this matter is limited, as most of the studies conducted in deforested landscapes are punctual evaluations in time, and do not consider temporal changes in landscape structure.

This thesis' objective is to assess mammal responses to temporal changes (2011 - 2017) in landscape spatial structure in the Lacandona rainforest, Chiapas. To achieve this objective, I first include a general introduction (Chapter I), and a revision on the subject at a global level (Chapter II). Chapter III, IV and V evaluate the responses of mammal communities to landscape temporal changes in the Lacandona rainforest. First, we studied the community of terrestrial rodents in order to test the rodentization hypothesis (Chapter III). Second, we studied the population of black howler monkeys – a species threatened with extinction – in order to evaluate changes in their populations and its relation to changes in landscape structure through time (Chapter IV). Third, we analyze changes in beta diversity of the community of medium and large terrestrial mammals, in order to test the biotic homogenization and differentiation hypotheses (Chapter V). At the end (Chapter VI), we discuss and analyze all chapters in order to evaluate how temporal changes in landscape structure affect mammal communities in tropical fragmented rainforests.

In the global revision, we found 289 studies that assess the response of tropical mammals to spatial changes in their habitat, but only 113 used a landscape approach. These studies assessed 1367 responses of 304 species to landscape spatial changes, but only 13% assessed temporal changes in the landscape and their effect on mammals. Most of these studies used a site-landscape approach, and less than a quarter evaluated the scale of effect. Of all assessed responses, more than half were non-significant, almost three quarters analyzed their relation to landscape composition variables, and only a quarter analyzed their relation to landscape configuration variables. Forest cover was the most assessed variable, showing a positive relation to most response variables, mostly with endangered, forest specialist and large-sized

mammals. On the other hand, matrix composition mostly presented negative responses; yet, we found that mammal responses depend greatly on matrix quality (e.g. human settlements presented mostly negative effects, whereas secondary forests presented only positive effects). Fragmentation *per se* showed mainly non-significant responses and, when significant, they were mostly negative, mainly for carnivores and small mammals. Longitudinal studies are lacking, incorporating a multiscale approach, which allows to evaluate the long-term effects of landscape spatial changes on mammal populations and communities.

When evaluating rodent community, our findings partially support the rodentization hypothesis, as we found a significant increase in rodent abundance through time. Changes in landscape structure had a great influence on changes in rodent abundances. Yet we concluded that the rodentization process was moderate, as only two species (*Heteromys desmarestianus* and *Oryzoys* sp.) increased in abundance, one decreased (*Peromyscus mexicanus*) and another (*Sigmodon toltecus*) did not change through time. Our results suggest that, if current deforestation rates are maintained, specialist species populations could decrease ("loser" species), but generalist species could proliferate ("winner" species).

On the other hand, while evaluating howler monkey populations, we found an increase in the number of individuals and a decrease in the immature/female ratio, both parameters strongly related to landscape changes through time. Both parameters increased in landscapes where the number of patches increased, but the percentage of open areas in the matrix decreased. Edge density showed negative effects on the immature/female ratio. Results suggest that howler monkeys could not be as tolerant to disturbance as generally thought, making it is necessary to implement effective strategies that allow their conservation in anthropic landscapes at the long term.

Finally, when evaluating changes in the community of medium and large terrestrial mammals through time, we found that beta diversity decreased, which suggests a possible ongoing biotic homogenization process. These changes were mostly driven by a decrease in species turnover, especially in landscapes with decreasing forest cover and increasing treed matrices. The nestedness component showed a 3-fold increase through time. We found the same number of species on 2011 and 2017. Results suggest that the homogenization process is probably being caused by an increase in species dispersal through the remaining forest sites. Future landscape modifications, mainly forest loss, could result in the loss of beta diversity, exacerbating the biotic homogenization process of the mammal community of the region.

In general, increasing the amount of forest cover in the landscape appears to be the most important strategy to maintain and improve the quality of the landscape for biodiversity. In order to conserve tropical mammals, specially specialist, forest dependent species, it is necessary to conserve and increase the amount of forest cover in the landscape, though forest restoration, as well as to promote friendly matrices, similar to the preserved forest (e.g. corridors, tree plantations, forest management areas and secondary forests). In addition, it is important to maintain and promote the connectivity between remaining forest patches, decreasing the distances between patches and maintaining a higher number of patches in the landscape. For some species, such as immature howler monkeys, reducing the amount of forest edges will allow to reduce their vulnerability to predators and human-related activities, such as road-kills, hunting and extraction for illegal trade. Jointly, all these measures will allow to decrease the negative effects of human activities on tropical mammals, promoting their conservation in this important diversity North American hotspot.

Capítulo 1.

Introducción general

Norma P. Arce-Peña

Introducción

Las actividades humanas, como la ganadería, la agricultura, la minería y las actividades relacionadas con la generación de energía están ocasionando una rápida pérdida de bosques, afectando fuertemente a la biodiversidad. Las especies tropicales están particularmente amenazadas, ya que los trópicos están sufriendo las mayores tasas de deforestación a nivel global. En este contexto, es fundamental entender cómo la biodiversidad responde a estos cambios para diseñar estrategias de manejo o conservación, o paisajes amigables, apropiados para su protección.

Cambio de uso de suelo en el mundo

La pérdida y degradación de los bosques es uno de los mayores problemas ambientales a nivel mundial. De 1990 a 2015 se perdieron alrededor de 129 Mha de bosques (3.1%), reduciendo su extensión a menos de 4 mil Mha (FAO 2016; Fig. 1). Los bosques tropicales son los más afectados (Hansen et al. 2013, Song et al. 2008). Mientras que en los ecosistemas templados existe una ganancia neta anual de bosques de 2.7 Mha, en los trópicos existe una tasa de deforestación neta anual de 5.5 Mha (Keenan et al. 2015). Esta pérdida se debe principalmente a causas antropogénicas, derivadas de un acelerado crecimiento poblacional y una mayor demanda de recursos (Aide et al. 2013, FAO 2016). La gran mayoría de los ecosistemas tropicales han sido o están siendo afectados por el cambio de uso de suelo a gran escala (e.g. monocultivos, ganadería, minería) así como por otras perturbaciones (e.g. cacería, contaminación, cambio climático; Laurance et al. 2014), que han promovido la conversión de ecosistemas naturales a sistemas agropecuarios (Sachs et al. 2010, Malhi et al. 2014). Esta situación constituye la mayor amenaza para la biodiversidad terrestre mundial (Fahrig 2003, Malhi et al. 2014, Newbold et al. 2016, Watling et al. 2020), ya que se estima que los bosques tropicales son el principal hábitat de la biodiversidad terrestre mundial (Dirzo y Raven 2003, Wright 2005).

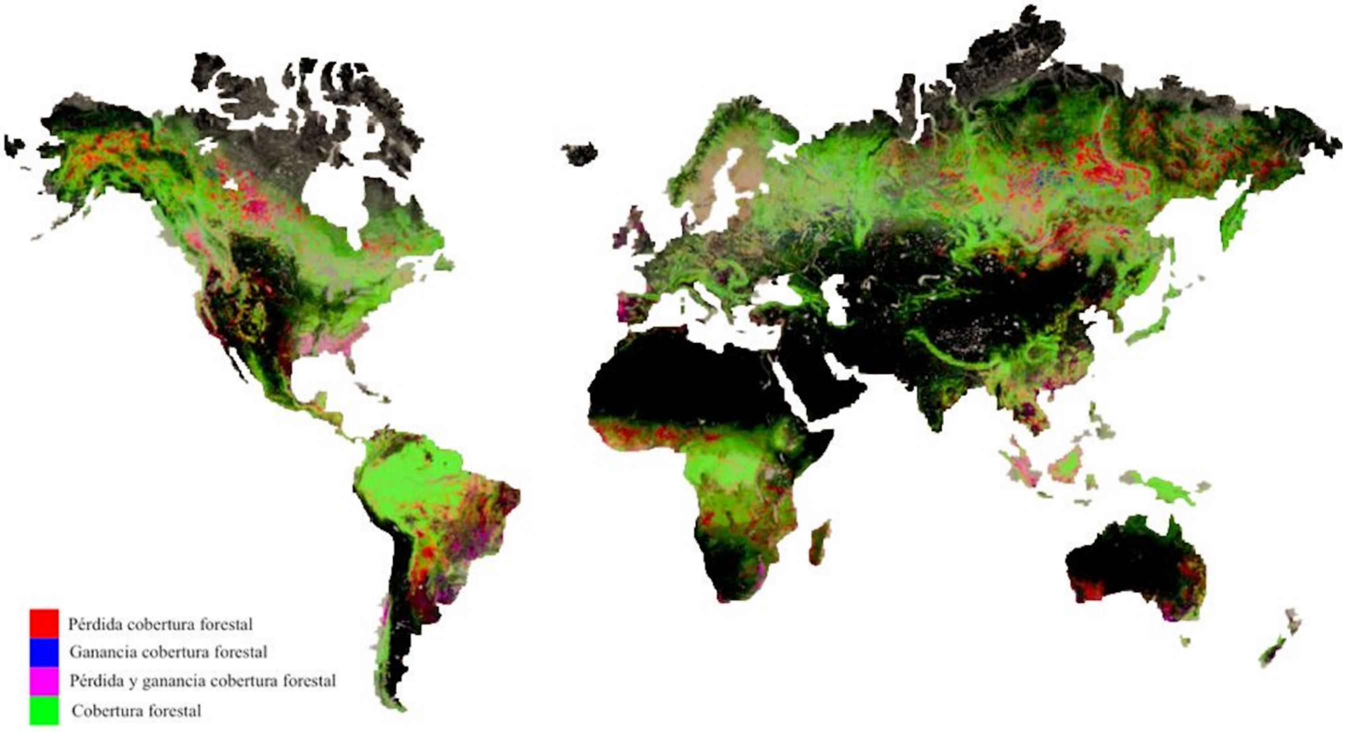


Figura 1. Mapa global de pérdida y ganancia de cobertura forestal durante el periodo 2000-2019 (tomado de Hansen et al. 2013). Los colores indican el cambio y la densidad de cambio de cobertura forestal.

En México existe un acelerado proceso de cambio de uso de suelo. Se estima que al menos 50% de la superficie forestal original del país ha desaparecido o se ha deteriorado (Velázquez et al. 2002). Del 2002 al 2019, México perdió un total de 602,000 ha de cobertura de bosque tropical primario, equivalente a una disminución del 6.5% (Global Forest Watch 2019). Los procesos de cambio de cobertura y uso de suelo, así como sus causas, son muy complejos y variados dentro de las distintas ecorregiones y estados (Ellis et al. 2017). En el país, cuatro estados representaron más de la mitad de la pérdida total de bosques en 2018: Chiapas, Oaxaca, Campeche y Veracruz. De 2002 a 2019, Chiapas perdió 164,000 ha de cobertura de bosque tropical primario (Global Forest Watch 2019).

Las causas principales de la pérdida de bosques en el país incluyen la sobreexplotación de recursos (incluyendo la tala ilegal), incendios forestales y la expansión de la agricultura y ganadería (Hansen et al. 2013, Global Forest Watch 2019). Al igual que los patrones de deforestación a nivel mundial, los bosques tropicales del país han sido más afectados que los bosques templados. Esta situación es altamente preocupante, ya que los bosques tropicales tienen los más elevados niveles de riqueza de especies que cualquier otro ecosistema terrestre (Challenger y Soberón 2008).

Paisajes antrópicos y su estructura espacial

Los bosques tropicales están siendo rápidamente convertidos en paisajes antrópicos heterogéneos compuestos de parches de bosque rodeados de una matriz conformada por diferentes tipos de coberturas (Melo et al. 2013). Así, una proporción cada vez mayor de la biodiversidad global se encuentra en paisajes antrópicos fragmentados con diferente composición y configuración espacial (Fahrig et al. 2011).

Existen diferentes definiciones de paisaje. Para propósitos de esta tesis, un paisaje se define como un área espacialmente heterogénea, compuesta por una mezcla de diferentes coberturas vegetales y tipos de uso de suelo (Foreman 1995, Turner y Gardner 2015). La estructura de un paisaje se define por su composición y su configuración espacial (Fig. 2). La composición se refiere a la cantidad y tipos de coberturas existentes dentro del paisaje (e.g., cantidad o porcentaje de cobertura forestal, cantidad o porcentaje de áreas abiertas en la matriz). Por otro lado, la configuración se refiere al arreglo espacial de cada cobertura dentro del paisaje (e.g., número de fragmentos de bosque, densidad de borde, aislamiento entre fragmentos; Dunning et al. 1992, Fahrig 2013).

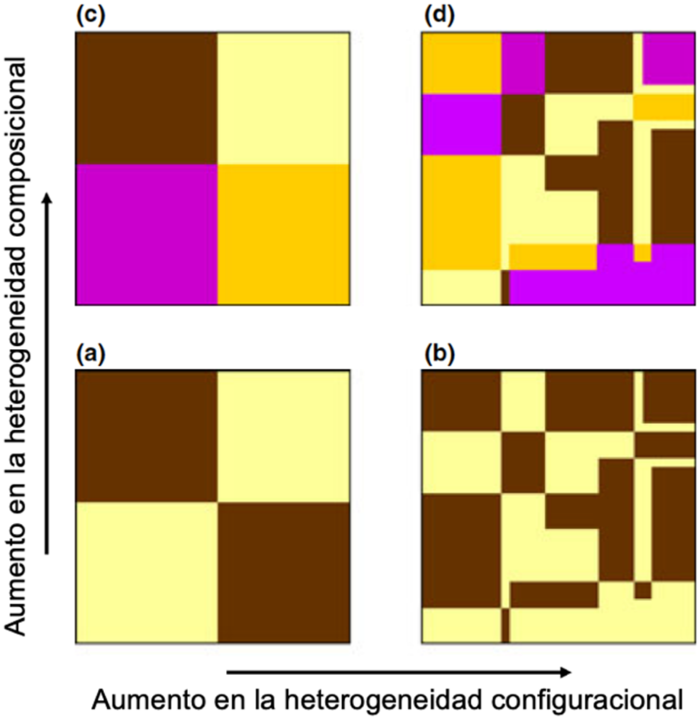


Figura 2. Ilustración de los dos tipos de componentes de la estructura del paisaje y la heterogeneidad espacial: la heterogeneidad composicional y la configuracional. Cada cuadro representa un paisaje y cada color dentro del cuadro representa diferentes coberturas forestales. La heterogeneidad composicional aumenta con el aumento en el número y/o equidad de las coberturas. Por otro lado, la heterogeneidad configuracional aumenta con el incremento en la complejidad del patrón espacial (modificado de Fahrig et al. 2011).

Tanto la composición como la configuración son aspectos importantes que definen la estructura del paisaje y pueden influenciar una variedad de respuestas ecológicas como el movimiento de individuos, la persistencia de poblaciones, la ocurrencia de interacciones bióticas y el funcionamiento de los ecosistemas, entre otros (Fahrig et al. 2011). Por lo tanto, los cambios en la estructura del paisaje pueden afectar la distribución y la abundancia de las poblaciones locales, así como los patrones de diversidad de las comunidades biológicas (Gascon et al. 1999). Por esto, entender el papel relativo de la composición y configuración del paisaje sobre la biodiversidad es fundamental para elaborar estrategias de conservación más efectivas (Fahrig et al. 2011, Arroyo-Rodríguez et al. 2020).

Respuesta de la biodiversidad a los cambios en el paisaje

La estructura del paisaje puede tener diversos y contrastantes efectos sobre la biodiversidad (Fahrig 2011; Arroyo-Rodríguez et al. 2019). El atributo más estudiado de la composición del paisaje es la cantidad de cobertura forestal (Fahrig 2003, 2013). Esta variable está positivamente relacionada con la conectividad del paisaje y la disponibilidad de alimentos, lo que aumenta el movimiento de los individuos, el tamaño de las poblaciones, la persistencia de las especies dependientes de bosque y la diversidad de especies (Fahrig 2003, 2013, Newbold et al. 2016). La pérdida de cobertura forestal en el paisaje tiene, generalmente, mayores efectos negativos sobre la biodiversidad que los atributos de configuración del paisaje, como la fragmentación *per se* (Fahrig 2003, 2017, Jackson y Fahrig 2016, Watling et al. 2020). De hecho, la "hipótesis de la candidad de hábitat" (i.e. "habitat amount hypothesis"; Fahrig 2013) propone que la densidad de especies dentro de un parche de hábitat depende en mayor medida de la cantidad de hábitat en el paisaje que rodea a dicho parche, que del tamaño o aislamiento del parche (Fahrig 2013, Arroyo-Rodríguez et al. 2019). Una revisión global reciente encontró fuerte evidencia a favor de esta hipótesis (Watling et al. 2020).

Otro atributo de la composición del paisaje, de gran importancia para procesos que determinan los patrones de biodiversidad, es la composición de la matriz antrópica (Arroyo-Rodríguez et al. 2020). Esta se refiere a los diferentes tipos de cobertura de suelo, que no son el hábitat principal de la especie de estudio. La naturaleza de la matriz tiene un gran impacto sobre la dinámica de poblaciones dentro de los paisajes antrópicos (Tscharntke et al. 2012) y puede influenciar la persistencia de una población a través de efectos asociados al movimiento y dispersión, disponibilidad de recursos y el ambiente abiótico (Driscoll et al. 2013). Por ejemplo, las matrices con baja permeabilidad o un alto contraste pueden prevenir o impedir el movimiento de los individuos entre los parches de hábitat, lo que causa baja conectividad y promueve el aislamiento poblacional y un intercambio de genes limitado (Bennet y Saunders 2010). Sin embargo, otras especies pueden tolerar y hasta beneficiarse de la matriz, que puede ofrecer recursos complementarios y/o suplementarios (Dunning et al. 1992; Galán-Acedo et al. 2019). De hecho, se ha reportado que las especies dependientes de bosque que evitan utilizar la matriz tienen una mayor probabilidad de extinción en paisajes fragmentados (Laurance et al. 1991; Vetter et al. 2011; Carrara et al. 2015).

Por otro lado, la configuración del paisaje ha sido menos estudiada. A pesar de que se asume que la fragmentación es una de las principales causas de la extinción global, pocos estudios han estudiado sus efectos en las poblaciones de manera independiente a la pérdida de hábitat (Crooks et al. 2017). Los efectos de la fragmentación son muy variables (Vetter et al. 2011, Fahrig 2003) y han generado un gran debate a lo largo de los años (Fahrig 2003, 2017, 2019, Fahrig et al. 2019, Fletcher et al. 2018, Miller et al. 2019). Fahrig (2017) reporta efectos mayormente positivos de la fragmentación *per se* (i.e., es decir la fragmentación independientemente de la pérdida de hábitat), incluyendo el aumento en la conectividad del paisaje. Se ha reportado que pequeños parches de vegetación dispersos en la matriz pueden servir como peldaños (i.e. "stepping stones") para la dispersión o recolonización de las especies, pueden proteger a especies raras o con ámbitos hogareños pequeños y proveer heterogeneidad en la configuración de la matriz (Forman 1995). Por otro lado, algunos autores reportan efectos negativos de la fragmentación *per se*. Por ejemplo, Crooks et al. (2017) establecen que al aumentar el grado de fragmentación aumenta el riesgo de extinción, aún después de tomar en cuenta otros predictores de riesgo, como el tamaño corporal y el ámbito hogareño de la especie.

La pérdida de hábitat y la reducción en el tamaño de los parches aumentan la proporción de bordes en el paisaje y disminuyen la conectividad en el paisaje. El aumento en la proporción de bordes expone a los interiores de los fragmentos a la influencia de factores externos. Por ejemplo, los bordes son más secos y calientes, con mayor influencia del viento y una mayor intensidad de luz, lo que modifica la composición de plantas y la estructura del hábitat (Asquith et al. 2005, Didham 2010, Arroyo-Rodríguez et al. 2017), con efectos positivos o negativos para las especies (Ewers y Didham 2006, Pfeifer et al. 2017). Por otro lado, la conectividad tanto dentro del paisaje, como entre paisajes permite a las especies moverse y dispersarse entre parches de hábitat y diferentes tipos de uso de suelo. Esto puede disminuir el impacto de la pérdida de hábitat (Thompson et al. 2017) y es esencial para prevenir extinciones y mantener un pool de variación que permita lidiar con el cambio climático (Tscharntke et al. 2012).

Importancia de los estudios multi-escalares

Los patrones de biodiversidad reflejan la combinación de diversos factores y procesos ecológicos que actúan a diferentes escalas espaciales y temporales (Tscharntke et al. 2012). Las escalas en las que los organismos utilizan y responden al ambiente varía significativamente entre especies debido a sus atributos ecológicos y a la heterogeneidad del hábitat (Turner y Gardner 2015). Espacialmente, las comunidades y poblaciones se rigen por procesos que suceden a escala de parches, paisajes y regiones (Lawton 1999). Por otro lado, generalmente la respuesta de las especies ante disturbios y cambios ambientales no es instantánea, por lo que el estudio de la biodiversidad requiere de análisis a diversas escalas temporales. Los datos de estudios ecológicos a largo plazo permiten evaluar el efecto de factores y mecanismos a través del tiempo (Hanski 2013, Beaudrot et al. 2016) e identificar respuestas lentas a dichos cambios (Metzger et al. 2009, Hanski 2013).

La magnitud y dirección de las respuestas de la biodiversidad a factores externos, depende de la escala en que se midan (Socolar et al. 2016). La escala es tan importante que puede influenciar en gran medida los resultados y conclusiones obtenidos (McGill et al. 2015). Sin embargo, muy pocos estudios analizan la respuesta de la biodiversidad a diferentes escalas espaciotemporales (Jackson y Fahrig 2015, McGill et al. 2015, Chase et al. 2018). A pesar de que los estudios de los efectos de la estructura del paisaje sobre la biodiversidad deberían conducirse a un nivel de paisaje (Fahrig 2003), la mayoría de los estudios se han realizado a niveles locales o de parche y tienden a ignorar el contexto del paisaje (Watling y Donnelly 2006). Por otro lado, la mayoría de los estudios se llevan a cabo con una aproximación temporal estática, y son pocos los estudios longitudinales y a largo plazo que permitan determinar la respuesta dinámica de la biodiversidad ante factores y mecanismos que actúan a lo largo del tiempo.

Efectos de los cambios en el paisaje sobre los mamíferos tropicales

Los mamíferos que habitan en los bosques tropicales son un grupo muy diverso (Rovero et al. 2017) y son un componente crítico para el funcionamiento de los ecosistemas (e.g. herbivoría, dispersión y depredación de semillas, control biológico de las comunidades; Terborgh et al. 2001, Dirzo et al. 2014, Palmeirim et al. 2018, Schipper et al. 2008). Sin embargo, sus poblaciones están disminuyendo a tasas muy rápidas – de 5487 especies existentes, 25% están amenazadas de extinción y alrededor del 52% tienen poblaciones en declive (Schipper et al. 2008; Fig. 3). Esta situación es causada principalmente por actividades humanas como la deforestación y la degradación del hábitat, la cacería y el comercio ilegal de especies (Schipper et al. 2008, Ceballos et al. 2015, Beaudrot et al. 2016).

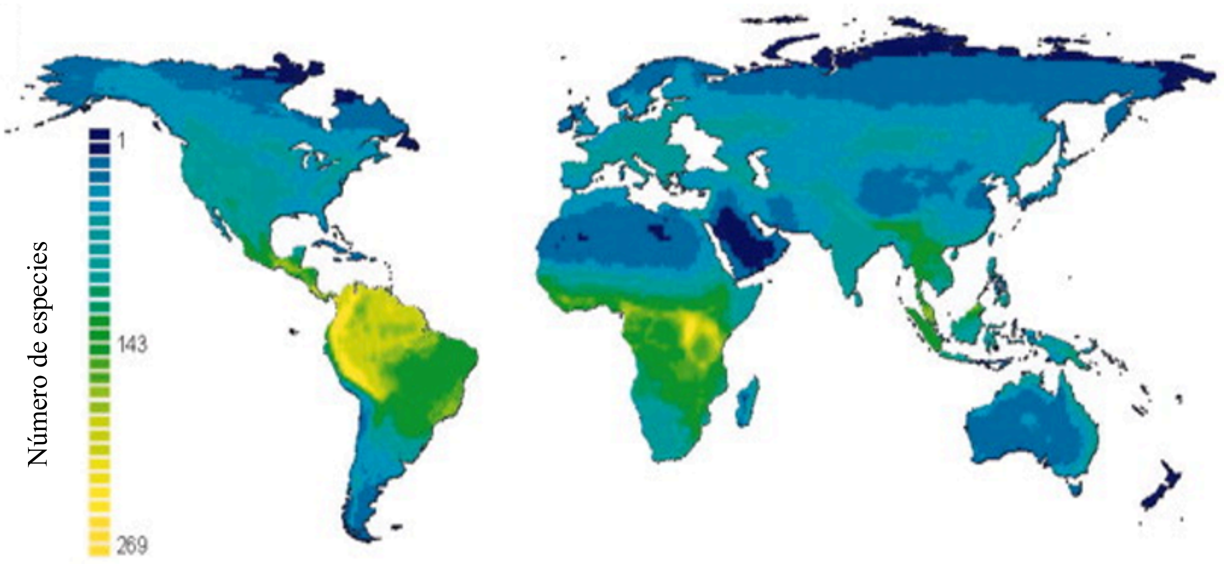


Figura 3. Patrones de distribución de especies de mamíferos amenazadas en el mundo (modificado de Ceballos y Ehrlich 2006).

México es uno de los países con mayor diversidad de mamíferos a nivel mundial, con 462 especies de mamíferos terrestres, de los cuales 32% son especies endémicas al país (Ceballos 2007). Sin embargo, las especies están siendo afectadas por las actividades humanas, principalmente la expansión de la frontera agropecuaria. Actualmente, el 18% está en peligro de extinción o amenazadas (Ceballos 2007).

No todas las especies son afectadas de la misma manera por las perturbaciones de su hábitat, sino que algunas especies pueden ser beneficiadas por procesos de cambio de uso de suelo y disturbios, aumentando en abundancia, rango de distribución y/u ocupación a través del tiempo (McGill et al. 2015). Estas especies tienden a proliferar en paisajes antrópicos, por lo que se les conoce como especies 'ganadoras' (Tabarelli et al. 2012). Por otro lado, otras especies, conocidas como 'perdedoras', son afectadas negativamente, disminuyendo en abundancia y rango de distribución, por lo que pueden llegar a desaparecer (Tabarelli et al. 2012). Este recambio de especies 'ganadoras' por especies 'perdedoras' puede desencadenar diferentes alteraciones o procesos ecológicos en paisajes antrópicos como la defaunación, la rodentización, la homogenización y la diferenciación biótica (Arroyo-Rodríguez et al. 2013a, Dirzo et al. 2014, Solar et al. 2015).

Algunas especies 'ganadoras', son animales generalistas, de rápido desarrollo y reproducción, con áreas de actividad pequeñas, como es el caso de algunas especies de roedores pequeños. La rodentización (o ratización) se refiere a un aumento en la densidad de roedores en paisajes degradados, debido a la ausencia de competidores o depredadores, y/o a un aumento en la disponibilidad de ciertos recursos (Mendes 2014). Los roedores son especies muy importantes para el funcionamiento de los bosques tropicales: están involucrados en procesos ecológicos como la dispersión y depredación de semillas y la herbivoría, y son una fuente importante de alimento para numerosas especies de animales. Sin embargo, el aumento de sus poblaciones puede tener implicaciones muy importantes, desde la alteración de las dinámicas de regeneración del bosque, el daño a cultivos, hasta el incremento del riesgo de transmisión de enfermedades a humanos (Sánchez-Cordero y Martínez-Meyer 2000, Lidicker 2007). Desafortunadamente, no existen pruebas empíricas sobre este proceso en ecosistemas tropicales.

Por otro lado, la defaunación es la reducción o pérdida de poblaciones animales (Dirzo et al. 2014). Este proceso es particularmente palpable en mamíferos de gran tamaño, con dietas especializadas y/o que requieren grandes áreas para sobrevivir (e.g., Ewers y Didham 2006, Dirzo et al. 2014). La defaunación tiene un impacto directo sobre la estructura y composición de la comunidad biótica y el funcionamiento del ecosistema (Young et al. 2015). Por ejemplo, la pérdida de mamíferos de talla grande puede tener como consecuencia un aumento en la abundancia y masa corporal de especies más pequeñas como algunas especies de roedores (Keesing y Young 2014, Young et al. 2015, 2016). Sin embargo, el proceso de defaunación en comunidades de mamíferos tropicales ha sido raramente estudiado debido a las complicaciones metodológicas que conlleva.

Por último, el reemplazo de especies "perdedoras" por especies "ganadoras" puede incrementar la similitud composicional (pérdida de diversidad beta) entre fragmentos de bosque – un proceso conocido como homogenización biótica (Olden et al. 2004, Solar et al. 2015). Este proceso puede limitar la cantidad de especies en un paisaje o región (diversidad gamma; Socolar et al. 2016). Sin embargo, un proceso opuesto, conocido como diferenciación biótica, también puede ocurrir en paisajes fragmentados. Esto ocurre cuando el incremento en la distancia entre fragmentos limita la dispersión de individuos y especies entre fragmentos. Esto, aunado a las diferencias ambientales entre fragmentos promovidas por trayectorias sucesionales contrastantes (ver Arroyo-Rodríguez et al. 2017), puede incrementar la disimilitud composicional entre fragmentos (Arroyo-Rodríguez et al. 2013a, Solar et al. 2015). Este aumento de diversidad beta puede contribuir al mantenimiento de la diversidad gamma a pesar de que a nivel local (diversidad alfa) se pierdan algunas especies (ver "hipótesis de la dominancia de beta"; Tscharntke et al.

2012). Sin embargo, este tema no es bien conocido ya que los estudios se han enfocado en bosques templados, y muy pocos estudian bosques tropicales.

Para tener un mayor entendimiento de la ecología y conservación de los mamíferos tropicales en paisajes antrópicos, es muy importante evaluar y determinar los factores que afectan a sus poblaciones y comunidades, incluyendo los efectos de los cambios en la estructura del paisaje a través del tiempo (Rovero et al. 2017). Una de las mejores maneras para poder estudiar estos cambios y los efectos en los mamíferos (incluyendo los procesos de defaunación, rodentización, homogenización biótica y diferenciación biótica) es el realizar estudios longitudinales. Este tipo de estudios son de gran importancia debido a que proveen información sobre la variación en la presencia y abundancia de las especies a lo largo del tiempo, información clave para diseñar e implementar estrategias adecuadas de manejo y conservación. Sin embargo, muy pocos estudios han analizado la respuesta de los mamíferos terrestres a lo largo del tiempo (Chase et al. 2018, McGill et al. 2015, Jackson y Fahrig 2015), ya que los análisis a largo plazo y a escalas espaciales grandes suelen ser complicados y requerir muchos recursos (Andrén 1994, Ewers et al. 2013, Laurance et al. 2008). Esto limita la capacidad de comprender las dinámicas poblacionales y de la comunidad en paisajes tropicales modificados (Andrén 1994).

En la selva Lacandona se han realizado diversos estudios con mamíferos terrestres para conocer, por ejemplo, el efecto de la estructura del paisaje sobre la riqueza de especies (Garmendia et al. 2013), la estructura poblacional de primates (Arroyo-Rodríguez et al. 2013b), la abundancia y diversidad de roedores pequeños (San José et al. 2014). Sin embargo, antes de la presente tesis, no se habían realizado estudios longitudinales que permitieran determinar cómo varían las poblaciones y comunidades a través del tiempo y que permitieran evaluar si los mamíferos en la región están experimentando un proceso de defaunación y/o rodentización, ni si los cambios que están ocurriendo provocan la homogenización o la diferenciación biótica en el paisaje fragmentado.

Objetivos

El objetivo general de esta tesis fue conocer la respuesta de la comunidad de mamíferos a los cambios en la estructura espacial del paisaje en la selva Lacandona (Chiapas) entre el año 2011 y el 2017. Para ello, se plantearon los siguientes objetivos específicos:

1. Revisar los estudios disponibles sobre las respuestas de los mamíferos tropicales a los cambios en la estructura espacial del paisaje (Capítulo 2).

2. Evaluar los cambios temporales en la comunidad de roedores pequeños para conocer los atributos del paisaje que pueden explicar estos cambios, así como para identificar a las especies "perdedoras" y "ganadoras" (Capítulo 3).

3. Identificar cambios temporales en la población de monos aulladores negros (*Alouatta pigra*) y determinar el efecto de la estructura del paisaje sobre estos cambios (Capítulo 4).

4. Comparar la diversidad beta de la comunidad de mamíferos terrestres medianos y grandes entre fragmentos en 2011 y 2017, así como la diversidad beta temporal dentro de cada fragmento, para identificar si está ocurriendo un proceso de homogenización o de diferenciación biótica, e identificar los atributos del paisaje responsables de estos cambios (Capítulo 5).

Descripción del área y sitios de estudio

El área de estudio se encuentra en la Selva Lacandona, Chiapas (16º 05´ N, 90º 52´ W), situada en el noreste del estado de Chiapas y delimitada al sur y al este por la frontera con Guatemala y al norte y oeste por la zona conocida como los Altos de Chiapas. El clima de la región es cálido-húmedo, con temperaturas mensuales promedio de 24-26 ºC, y una precipitación anual de 2500-3500 mm (Instituto Nacional de Ecología 2000). La Selva Lacandona solía comprender una extensión amplia de bosque tropical húmedo de alrededor de 1.4 millones de hectáreas (Dirzo y Miranda 1991). Actualmente, es un área prioritaria para la conservación de la biodiversidad en México y Mesoamérica. Representa el área con mayor extensión de bosque tropical húmedo continuo (Dirzo y Miranda 1991), así como la región con la mayor riqueza de mastofauna en México (Medellín 1994).

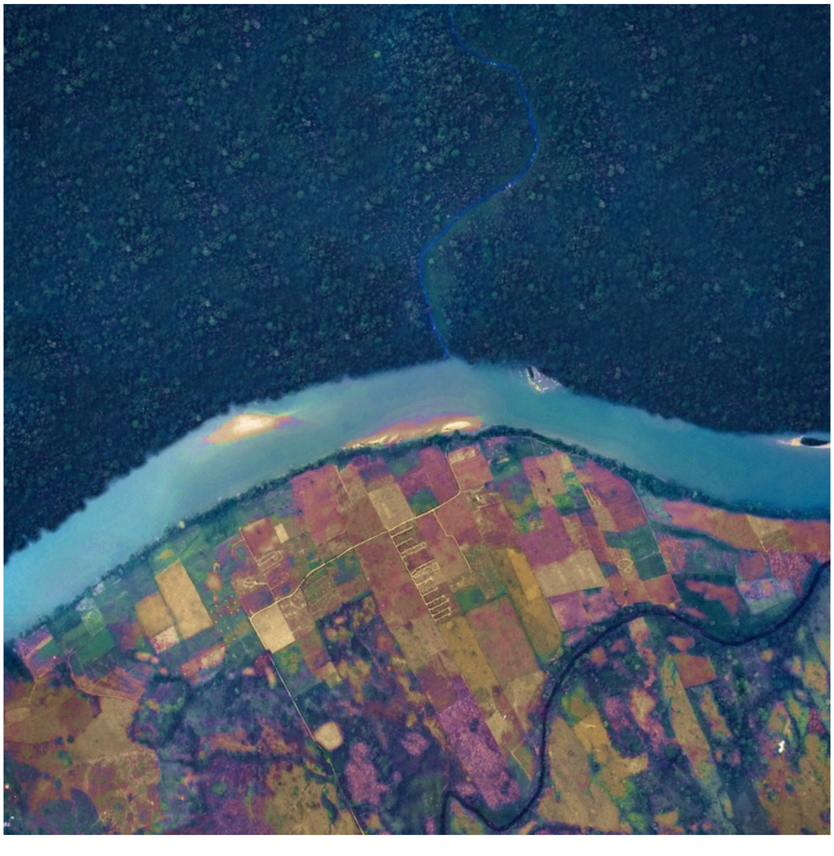


Figura 4. Imagen de una parte de la zona de estudio. En la parte inferior se observa la zona de Marqués de Comillas, altamente deforestada, mientras que en la parte superior se observa la Reserva de la Biósfera Montes Azules. Foto: Santiago Arau.

Dentro de la región, la Reserva de la Biósfera de Montes Azules (RBMA) fue creada en 1978 para proteger la biodiversidad y comprende un área de 331,200 hectáreas (Martínez-Ramos 2006). Sin embargo, el área está altamente amenazada por la cacería y el cambio de uso de suelo en los límites de la Reserva (Medellín 1994). Al sur de la RBMA, se encuentra la zona conocida como Marqués de Comillas, colonizada hace alrededor de 50 años. La falta de organización territorial ha ocasionado la rápida pérdida y fragmentación del ecosistema original (Fig. 4). A pesar de su gran importancia ecológica, la región ha sido rápidamente alterada debido a un aumento en la población humana, el avance de la frontera agrícola y ganadera, y la caza ilegal. Alrededor del 60-70% de los bosques maduros primarios de la región han sido convertidos a paisajes heterogéneos compuestos por parches de selva de diferentes tamaños, rodeados por una matriz de pastizales, tierras agrícolas y asentamientos humanos (Carabias et al. 2015; Fig. 5). La Selva Lacandona en general, es un área altamente heterogénea en términos de composición y configuración del paisaje.

Figura 5. Ejemplos de cambio de uso de suelo en la zona de Marqués de Comillas en la Selva Lacandona, Chiapas. A) Deforestación de un sitio de bosque tropical para el establecimiento de plantaciones o pastizales de pastoreo; B) matriz antrópica, con un cultivo de palma de un lado y un terreno listo para la agricultura (probablemente maíz o chile). Fotos: Norma Arce.

Los sitios de estudio estuvieron dentro de la Reserva de la Biósfera Montes Azules y en fragmentos de bosque fuera de la reserva, en la región de Marqués de Comillas. Los roedores fueron muestreados en 12 sitios (9 fragmentos y 3 sitios dentro de la reserva; San-José et al. 2014), los monos aulladores en 22 sitios (19 fragmentos y 3 sitios en la reserva; Arroyo-Rodríguez et al. 2013b) y los mamíferos terrestres medianos y grandes en 26 sitios (22 fragmentos y 4 sitios en la reserva; Garmendia et al. 2013). Todos los sitios están a la misma altitud y están separados entre sí por al menos 3 km; los sitios dentro de la reserva se encuentran separados por más de 1 km del borde del Río Lacantún (Fig. 6).

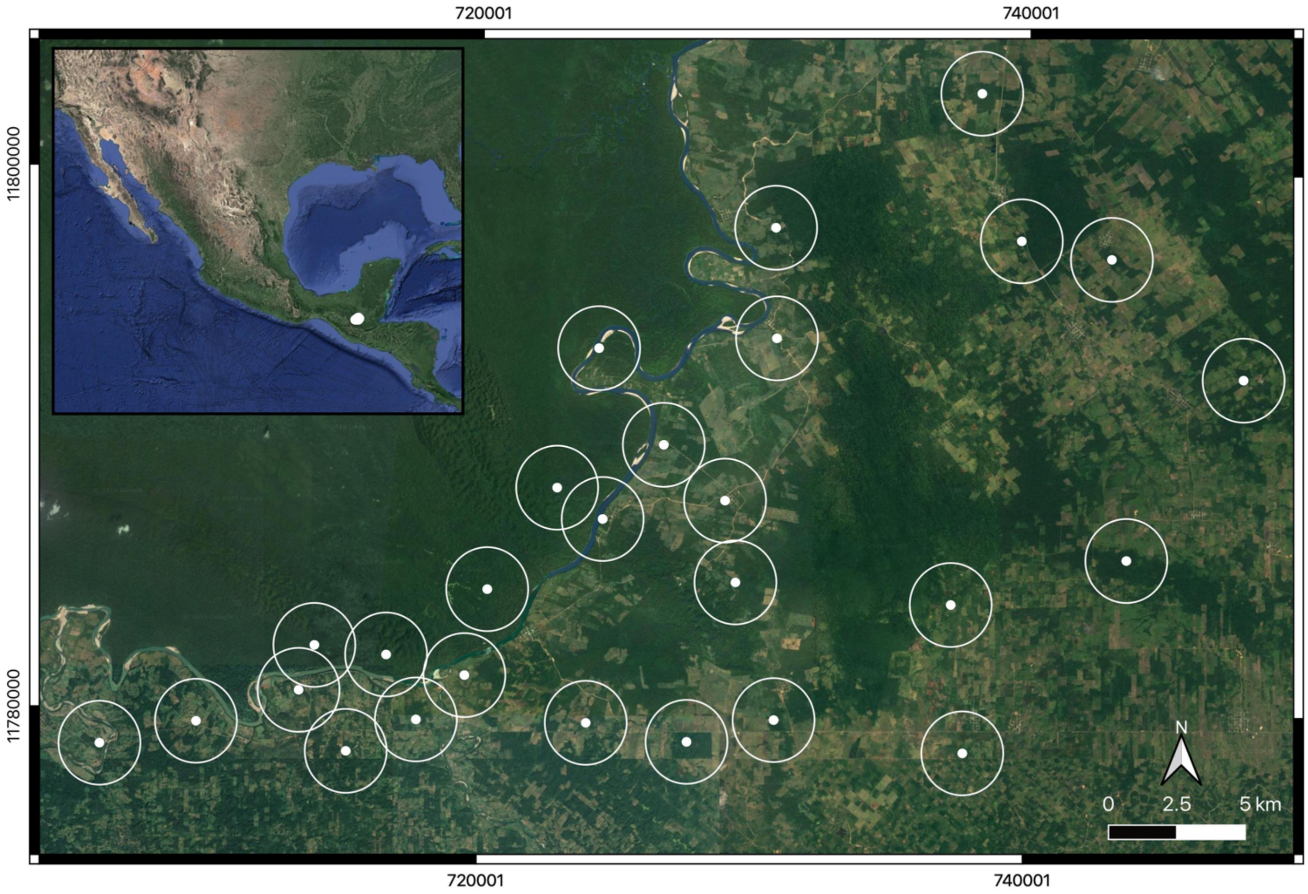


Figura 6. Ubicación geográfica del área de estudio y de los sitios incluidos en el estudio, 4 sitios de bosque continuo y 23 fragmentos de bosque. En la parte izquierda de la imagen se encuentra la Reserva de la Biósfera de Montes Azules, mientras que en la derecha se encuentra la región del Marqués de Comillas; están separadas por el Río Lacantún.

Esquema de la tesis

Esta tesis está conformada por 6 capítulos: la introducción general (Capítulo 1), un artículo de revisión (Capítulo 2), tres artículos basados en datos de campo (Capítulos 3-5) y la discusión general y conclusiones (Capítulo 6).

Recientemente ha aumentado la cantidad de estudios que evalúan los efectos de la estructura del paisaje sobre las especies de mamíferos. Sin embargo, estos estudios muestran resultados variados, por lo que surge la necesidad de revisar la literatura existente sobre el tema para poder identificar patrones generales de respuesta. En el Capítulo 2 se hace esta revisión y se identifican las principales respuestas de los mamíferos tropicales ante los cambios en la estructura del paisaje a través del tiempo.

Son pocos los estudios longitudinales que analizan los efectos de los cambios en la estructura del paisaje sobre la biodiversidad considerando diferentes escalas espaciales. Dichos estudios son necesarios para poder detectar procesos dinámicos como la rodentización, la defaunación, la homogenización y la diferenciación biótica. Por lo anterior, en los Capítulos 3-5 se analizan las respuestas de diferentes grupos de mamíferos a través del tiempo, así como el efecto de los cambios en la estructura del paisaje a diferentes escalas espaciales. En el Capítulo 3 se analizan los cambios en las poblaciones de pequeños roedores terrestres, evaluando la hipótesis de la rodentización e identificando a las especies 'ganadoras' y 'perdedoras'. En el Capítulo 4 se evalúan cambios demográficos en las poblaciones de monos aulladores negros (*Alouatta pigra*). Por último, en el Capítulo 5 se analizan los cambios en la diversidad beta de los mamíferos terrestres medianos y grandes, para determinar si está sucediendo un proceso de homogenización o de diferenciación biótica en la región. Finalmente, en el Capítulo 6 se evalúan los resultados e implicaciones de los capítulos anteriores.

Referencias

Aide, T.M., Clark, M.K., Grau, H.R., López-Carr, D., Levy, M.A., Redo, D., Bonilla-Moheno, M., Riner, G., Andrade-Núñez, M.J., Muñiz, M. 2013. Deforestation and reforestation of Latin America and the Caribbean (2001–2010). Biotropica 45: 262–271.

Andrén, H. 1994. Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. Oikos 71: 355–366.

Arroyo-Rodríguez, V., Arasa-Gisbert, R., Arce-Peña, N., Cervantes-López, M.J., Cudney-Valenzuela, S.J., Galán-Acedo, C., Hernández-Ruedas, M.A., Rito, K. F., San-José, M. 2019. Determinantes de la biodiversidad en paisajes antrópicos: Una revisión teórica. En: Moreno, C.E. (Ed.) La biodiversidad en un mundo cambiante: Fundamentos teóricos y metodológicos para su estudio. Universidad Autónoma del Estado de Hidalgo y Libermex. Ciudad de México, pp 65–112. ISBN: 978-607-98479-3-7.

Arroyo-Rodríguez, V., Fahrig, L., Tabarelli, M., Watling, J.I., Tischendorf, L., Benchimol, M., Cazetta, E., Faria, D., Leal, I.R., Melo, F.P.L, Morante-Filho, J.C., Santos, B.A., Arasa-Gisbert, R., Arce-Peña, N., Cervantes-López, M.J., Cudney-Valenzuela, S., Galán-Acedo, C., San-José, M., Vieira, I.C.G., Slik, J.W.F., Nowakowski, J., Tscharntke, T. 2020. Designing optimal human-modified landscapes for forest biodiversity conservation. Ecology Letters 23: 1404–1420.

Arroyo-Rodríguez, V., González-Perez, I.M., Garmendia, A., Solà, M., Estrada, A. 2013a. The relative impact of forest patch and landscape attributes on black howler monkey populations in the fragmented Lacandona rainforest, Mexico. Landscape Ecology 8: 1717–1727.

Arroyo-Rodríguez, V., Melo, F.P.L., Martínez-Ramos, M., Bongers, F., Chazdon, R., Meave, J.A., Norden, N., Santos, B.A., Leal, I.R., Tabarelli, M. 2017a. Multiple successional pathways in human-modified tropical landscapes: New insights from forest succession, forest fragmentation and landscape ecology research. Biological Reviews 92: 326–340.

Arroyo-Rodríguez, V., Rös, M., Escobar, F., Melo, F.P.L., Santos, B.A., Tabarelli, M., et al. 2013b. Plant β-diversity in fragmented rain forests: testing floristic homogenization and differentiation hypotheses. Journal of Ecology 101: 1449–1458.

Arroyo-Rodríguez, V., Saldaña-Vázquez, R.A., Fahrig, L., Santos, B.A. 2017. Does forest fragmentation cause an increase in forest temperature? Ecological Research 32: 81–88.

Asquith, N.M., Mejía-Chang, M. 2005. Mammals, edge effects, and the loss of tropical forest diversity. Ecology 86: 379–390.

Beaudrot L., Ahumada, J.A., O´Brien, T., Alvarez-Loayza, P., Boekee, K., Campos-Arceiz, A., Eichberg, D., Espinosa, S., Fegraus, E., Fletcher, C., Gajapersad, K., Hallan, C., et al. 2016. Standarized assessment of biodiversity trends in tropical forest protected areas: the end is not in sight. PLoS Biol 14: e1002357.

Bennett, A.F., Saunders, D.A. 2010. Habitat fragmentation and landscape change. En: Sodhi N.S., Ehrlich P.R. (Eds.) Conservation Biology for All. Oxford University Press, Oxford, pp 88–106.

Brodie, J.F., Giordano, A.J., Dickson, B., Hebblewhite, M., Bernanrd, H., Mohd-Azlan, J., Anderson, J., Ambu, L. 2015. Evaluating multispecies landscape connectivity in a threatened tropical mammal community. Conservation Biology 29: 122–132.

Carabias, J., de la Maza, J., Cadena, R. 2015. Conservación y desarrollo sustentable en la Selva Lacandona. 25 años de actividades y experiencias. Natura y Ecosistemas Mexicanos, Mexico City.

Carrara, E., Arroyo-Rodríguez, A., Veha-Rivera, J.H., Schondube, J.E., de Freitas, S.M., Fahrig, L. 2015. Impact of landscape composition and configuration on forest specialist and generalist bird species in the fragmented Lacandona rainforest, Mexico. Biological Conservation 184: 117–126.

Ceballos, G. 2007. Conservation priorities for mammals in megadiverse Mexico: the efficiency of reserve networks. Ecological Applications 17: 569–578.

Ceballos, G., Ehrlich, P.R. 2006. Global mammal distributions, biodiversity hotspots, and conservation. PNAS: 19374-19379.

Ceballos, G., Ehrlich, P.R., Barnosky, A.D., García, A., Pringle, R.M., Palmer, T.M. 2015. Accelerated modern human-induced species losses: entering the sixth mass extinction. Science Advances 1: e1400253.

Challenger, A., Soberón, J. 2008. Los ecosistemas terrestres. En: Capital Natural de México, Vol. I: Conocimiento actual de la biodiversidad. CONABIO, México: 87–108.

Chase, J.M., McGill, B.J., McGlinn, D.J., May, F., Blowes, S.A., Xiao, X., Knight, T.M., Purschke, O., Gotelli, N.J. 2018. Embracing scale-dependence to achieve a deeper understanding of biodiversity and its change across communities. Ecology Letters 21: 1737–1751.

Crooks, K.R., Burdett, C.L., Theobald, D.M., King, S.R.B., Di Marco, M., Rondinini, C., Boitani, L. 2017. Quantification of habitat fragmentation reveals extinction risk in terrestrial mammals. Proceedings of the National Academy of Sciences 114: 7635–7640.

Didham, R.K. 2010. Ecological consequences of habitat fragmentation. En: Encyclopedia of Life Sciences. John Wiley & Sons, LTD, Chichester.

Dirzo, R., Miranda, A. 1991. Altered patterns of herbivory and diversity in the forest understory: a case study of the possible consequences of contemporary defaunation. En: Plant-animal interactions: evolutionary ecology in tropical and temperate regions. Prince, P.W., Lewinsohn, T.M., Fernandes, G.W., Benson W.W. (Eds.) John Wiley & Sons, Inc.: 273–288.

Dirzo, R., Raven, P.H. 2003. Global state of biodiversity and loss. Annual Review of Environment and Resources 28: 137–167.

Dirzo, R., Young, H.S., Galetti, M., Ceballos, G., Isaac, N.J.B., Collen, B. 2014. Defaunation in the Anthropocene. Science 345: 401–406.

Driscoll, D.A., Banks, S.C., Barton P.S., Lindenmayer D.B., Smith A.L. 2013. Conceptual domain of the matrix in fragmented landscapes. Trends in Ecology and Evolution 28: 605–613.

Dunning, J.B., Danielson, B.J., Pulliam, H.R. 1992. Ecological processes that affect populations in complex landscapes. Oikos 65: 169–175.

Ellis, E.A., Hernández-Gómez, I.U., Romero-Montero J.A. 2017. Los procesos y causas del cambio en la cobertura forestal de la Península Yucatán, México. Ecosistemas 26: 101–111.

Ewers, R.M., Didham, R.K. 2006. Confounding factors in the detection of species responses to habitat fragmentation. Biological Reviews 81: 117–142.

Ewers, R.M., Didham, R.K., Pearse, W.D., Lefebvre, V., Rosa, I.M.D., Carreiras, J.M.B., Lucas, R.M., Reuman, D.C. 2013. Using landscape history to predict biodiversity patterns in fragmented landscapes. Ecology Letters 16: 1221–1233.

FAO. 2016. State of the World´s Forests 2016. Forests and agriculture: land-use challenges and opportunities. Roma.

Fahrig, L. 2003. Effects of habitat fragmentation on biodiversity. Annual Review of Ecology, Evolution, and Systematics 34: 487–515.

Fahrig, L. 2013. Rethinking patch size and isolation effects: the habitat amount hypothesis. Journal of Biogeography 40: 1649–1663.

Fahrig, L. 2017. Ecological responses to habitat fragmentation per se. Annual Review of Ecology, Evolution, and Systematics 48: 1–23.

Fahrig, L. 2019. Habitat fragmentation: a long and tangled tale. Global Ecology and Biogeography 28: 33–41.

Fahrig, L., Baudry, J., Brotons, L., Burel, F.G., Crist, T.O., Fuller, R.J., Sirami, C., Siriwardena, G.M., Martin, J.L. 2011. Functional landscape heterogeneity and animal biodiversity in agricultural landscapes. Ecology Letters 14*:* 101–12.

Fahrig, L., Arroyo-Rodríguez, V., Bennet, J.R., Boucher-Lalonde, V., Cazetta, E., Currie, D.J. et al. 2019. Is habitat fragmentation bad for biodiversity? Biological Conservation 230: 179–186. doi:10.1111/geb.12839

FitzGibbon, S.I., Putland, D.A., Goldizen, A.W. 2007. The importance of functional connectivity in the conservation of a ground-dwelling mammal in an urban Australian landscape. Landscape Ecology 22: 1513–1525.

Fletcher, R.J., Didham, R.K., Banks-Leite, C., Barlow, J., Ewers, R.M., Rosindell, J., et al. 2018. Is habitat fragmentation good for biodiversity? Biological Conservation 226: 9–15.

Foreman, R.T.T. 1995. Some general principles of landscape and regional ecology. Landscape Ecology 10: 133–142.

Galán-Acedo, C., Arroyo-Rodríguez, V., Andresen, E., Arregoitia, L.V., Vega, E., Peres, C.A., Ewers, R.M. 2019. The conservation value of human-modified landscapes for the world's primates. Nature Communications 10: 152.

Garmendia, A., Arroyo-Rodríguez, V., Estrada, A., Naranjo, E., Stoner, K.E. 2013. Landscape and patch attributes impacting medium- and large-sized terrestrial mammals in a fragmented rain forest. Journal of Tropical Ecology 29: 331–344.

Gascon, C., Lovejoy, T.E., Bierregaard, R.O.Jr., Malcolm, J.R., Stouffer, P.C., Vasconcelos, H.L., Laurance, W.F., Zimmerman, B., Tocher, M., Borges, S. 1999. Matrix habitat and species richness in tropical forest remnants. Biological Conservation 91: 223–229.

Global Forest Watch. 2019. GEW Technology offers options to combat Mexico's high rate of tree cover loss. World Resources Institute. https://blog.globalforestwatch.org/data-and-research/gfw-technology-offers-options-to-combat-mexicos-high-rate-of-tree-cover-loss. Accessed on January 19th, 2020.

Haddad, N.M., Brudvig, L.A., Clobert, J., Davies, K.F., Gonzalez, A., Holt, R.D., Lovejoy, T.E., Sexton, J.O., Austin, M.P., Collins, C.D., Cook, W.M., Damschen, E.I., Ewers, R.M., Foster, B.L., Jenkins, C.N., et al. 2015. Habitat fragmentation and its lasting impact on Earth's ecosystems. Science Advances 1: e1500052.

Hansen, M.C., Potapov, P.V., Moore, R., Hancher, M., Turubanova, S.A., Tyukavina, A., Thau, D., Stehman, S.V., Goetz, S.J., Loveland, T.R., Kommareddy, A., Egorov, A., Chini, L., Justice, C.O., Townshend, J.R. 2013. High-resolution global maps of 21st-century forest cover change. Science 34: 850–853. https://earthenginepartners.appspot.com/science-2013-global-forest

Hanski, I. 2013. Extinction debt at different spatial scales. Animal Conservation 16: 12–13.

Instituto Nacional de Ecología. 2000. Programa de Manejo Reserva de la Biósfera Montes Azules. Secretaría de Medio Ambiente y Recursos Naturales.

Jackson, H.B., Fahrig, L. 2015. Are ecologists conducting research at the optimal scale? Global Ecology and Biogeography 24: 52–63.

Keenan, R.J., Reams, G.A., Achard, F., de Freitas, J.V., Grainger, A., Lindquist, E. 2015. Dynamics of global forest area: Results from the FAO Global Forest Resources Assessment 2015. Forest Ecology and Management 352: 9–20.

Keesing, F., Young, T.P. 2014. Cascading consequences of the loss of large mammals in an African Savanna. BioScience 64: 487–495.

Laurance, WF. 1991. Ecological correlates of extinction proneness in Australian tropical rain forest mammals. Conservation Biology 5: 79–89.

Laurance, W.F., Nascimento, H.E.M., Laurance, S.G., Andrade, A., Ewers, R.M., Harms, K.E., *et al.* 2007. Habitat fragmentation, variable edge effects, and the landscape divergence hypothesis. PLoS ONE 2: e1017.

Laurance W.F., Sayer J., Cassman K.G. 2014. Agricultural expansion and its impacts on tropical nature. Trends in Ecology & Evolution 29: 107–116.

Lawton, J.H. 1999. Are there general laws in ecology? Oikos 84: 177–192.

Lidicker, W.Z.J. 2007. Issues in Rodent Conservation. En: Wolff, J.O., Sherman, P.W. (Eds.), Rodent Societies: An Ecological and Evolutionary Perspective. University of Chicago Press; Chicago: pp. 453–462.

Magioli, M., de Barros, K.M.P.M., Setz, E.Z.F., Percequillo, A.R., Santos, M.V.S., Kuhnen, V.V., da Silva, M.C., Almeida, K.E., Zukeran, C., de Lima, G., Alves, H., Ferreira, M.K., Ribeiro, M.C., Schmidt, P.M., Lehmann, L., Gonçalves, M. 2016. Connectivity maintains mammal assemblage's functional diversity within agricultural and fragmented landscapes. European Journal of Wildlife Research 62: 431–446.

Malhi, Y., Gardner, T.A., Goldsmith, G.R., Silman, M.R., Przemyslaw, Z. 2014. Tropical forests in the Anthropocene. Annual Review of Environment and Resources 39: 125–159.

McGill, B.J., Dornelas, M., Gotelli, N.J., Magurran, A.E. 2015. Fifteen forms of biodiversity trend in the Anthropocene. Trends in Ecology & Evolution 30: 104–113.

Medellín, R. 1994. Mammal diversity and conservation in the Selva Lacandona, Chiapas, Mexico. Conserv Biol 8: 780–799.

Melo, F., Arroyo-Rodríguez, V., Fahrig, L., Martínez-Ramos, M., Tabarelli, M. 2013. On the hope for biodiversity-friendly tropical landscapes. Trends in Ecology and Evolution 28: 462–468.

Mendes, C., Ribeiro, M.C., Galetti, M. 2015. Patch size, shape and edge distance influence seed predation on a palm species in the Atlantic forest. Ecography 38: 1–11.

Metzger, J.P., Camargo, A.M., Dixo, M., Bernacci, L.C., Ribeiro, M.C., Godoy, A.M.T., Pardini, R. 2009. Time-lag in biological responses to landscape changes in a highly dynamic Atlantic forest region. Biological Conservation 142: 1166–1177.

Miller-Rushing, A. J., Primack, R. B., Devictor, V., Corlett, R. T., Cumming, G. S., Loyola, R., et al. 2019. How does habitat fragmentation affect biodiversity? A controversial question at the core of conservation biology. Biological Conservation 232: 271–273.

Newbold, T., Hudson, L.N., Arnell, A.P., Contu, S., de Palma, A., Ferrier, S., Hill, S.L.L., Hoskins, A.J., Lysenko, I., Phillips, H.R.P., Burton, V.J., Chng, C.W.T., Emerson, S., Gao, D., Pask-Hale, G., Hutton, J., Jung, M., Sanchez-Ortiz, K., Simmons, B.I., Whitmee, S., Zhang, H., Scharlemann, J.P.W., Purvis, A. 2016. Has land use pushed terrestrial biodiversity beyond the planetary boundary? A global assessment. Science 353: 288–291.

Olden, J.D., Poff, N.L., Douglas, M.R., Douglas, M.E., Fausch, K.D. 2004. Ecological and evolutionary consequences of biotic homogenization. Trends in Ecology and Evolution 19: 18–24.

Palmeirim, A.F., Benchimol, M., Vieira, M.V., Peres, C.A. 2018. Small mammal responses to Amazonian forest islands are modulated by their forest dependence. Oecologia 187: 191–204.

Pfeifer, M., Lefebvre, V., Peres, C.A., Banks-Leite, C., Wearn, O.R., Marsh, C.J., Butchart, S.H.M., Arroyo-Rodríguez, V., Barlow, J., Cerezo, A., Cisneros, L., et al. 2017. Creation of forest edges has a global impact on forest vertebrates. Nature 551: 187–195.

Rovero, F., Owen, N., Jones, T., Canteri, E., Iemma, A., Tattoni, C. 2017. Camera trapping surveys of forest mammal communities in the Eastern Arc Mountains reveal generalized habitat and human disturbance responses. Biodiversity and Conservation 26: 1103–1119.

Sachs, J., Remans, R., Smukler, S., Winowiecki, L., Andelman, S.J., Cassman, K.G., Castle, D., DeFries, R., Denning, G., Fanzo, J., Jackson, L.E., Leemans, R., Lehmann, J., Milder, J.C., Naeem, S., Nziguheba, G., Palm, C.A., Pingali, P.L., Reganold, J.P., Richter, D.D., Scherr, S.J., Sircely, J., Sullivan, C., Tomich, T.P., Sanchez, P.A. 2010. Monitoring the world's agriculture. Nature 466: 558–560.

Sánchez-Cordero, V., Martínez-Meyer, E. 2000. Museum specimen data predict crop damage by tropical rodents. Proceedings of the National Academy of Sciences 97: 7074–7077.

San-José, M., Arroyo-Rodríguez, V., Sánchez-Cordero, V. 2014. Association between small rodents and forest patch and landscape structure in the fragmented Lacandona rainforest, Mexico. Tropical Conservation Science 7: 403–422.

Schipper, J., Chanson, J.S., Chiozza, F., Cox, N.A., Hoffmann, M., Katariya, V., Lamoreux, J., Rodrigues, A.S.J., Stuart, S.N., Temple, H.J., et al. 2008. The status of the world's land and marine mammals: diversity, threat, and knowledge. Science 322: 225–230.

Socolar, J.B., Gilroy, J.J., Kunin, W.E., Edwards, D.P. 2016. How should beta-diversity inform biodiversity conservation? Trends in Ecology and Evolution 31: 67–80.

Solar, R.R.D., Barlow, J., Ferreira, J., Berenguer, E., Lees, A.C., Thomson, J.R., Louzada, J., Maués, M., Moura, N.G., Oliveira, V.H.F., Chaul, J.C.M., Schoereder, J.H., Vieria, I.C.G., Mas Nally, R., Gardner, T.A. Ecology Letters 18: 1108–1118.

Song, X.P., Hansen, M.C., Stehman, S.V., Potapov, P.V., Tyukavina, A., Vermote, E.F., Townshend, J.R. 2018. Global land change from 1982 to 2016. Nature 560: 639–643.

Tabarelli, M., Peres, C.A., Melo, F.P. 2012. The 'few winners and many losers' paradigm revisited: emerging prospects for tropical forest biodiversity. Biological Conservation 155: 136–140.

Terborgh, J., López, L., Nuñez, P.V., Rao, M., Shahabuddin, G., Orihuela, G., Riveros, M., Ascanio, R., Adler, G.H., Lambert, T.D., Balbas, L. 2001. Ecological meltdown in predator-free forest fragments. Science 294: 1923–1926.

Thompson, P.L., Rayfield, B., Gonzalez, A. 2017. Loss of habitat and connectivity erodes species diversity, ecosystem functioning, and stability in metacommunity networks. Ecography 40: 98–108.

Tscharntke, T., Tylianakis, J.M., Rand, T.A., Didhma, R.K., Fahrig, L., Batáry, P., Bengtsson, J., et al. 2012. Landscape moderation of biodiversity patterns and processes – eight hypotheses. Biological Reviews 87: 661–685.

Turner, M.G., Gardner, R.H. 2015. Landscape ecology in theory and practice. Pattern and process. Springer-Verlag, New York.

Velázquez, A., Mas, J.F., Mayorga-Saucedo, R., Díaz, J.R., Alcántara, C., Castro, R., Fernández, T., Palcio, J.L., Bocco, G., Gómez-Rodríguez, G., Luna-González, L., Trejo, I., López-García, J., Palma, M., Peralta, A., Prado-Molina, J., González-Medrano, F. 2002. Estado actual y dinámica de los recursos forestales de México. CONABIO. Biodiversitas 41:8–15.

Vetter, D., Hansbauer, M.M., Végvári, Z., Storch, I. 2011. Predictors of forest fragmentation sensitivity in Neotropical vertebrates: a quantitative review. Ecography 34: 1–8.

Watling, J.I., Arroyo-Rodríguez, V., Pfeifer, M., Baetenm L., Banks-Leite, C., Cisneros, L.M., Fang, R., Hamel-Leigue, A.C., Lanchat, T., Leal, I.R., Lens, L., Possingham, H.P., Raheem, D.C., Ribeiro, D.B., Slade, E.M., Urbina-Cardona, J.N., Wood, E., Fahrig, L. 2020. Support for the habitat amount hypothesis from a global synthesis of species density studies. Ecology Letters 23 :674–681.

Watling, J.I., Donnelly, M.A. 2006. Fragments as islands: a synthesis of faunal responses to habitat patchiness. Conservation Biology 20: 1016–1025.

Wright, S.J., Stoner, K.E., Beckman, N., Corlett, R.T., Dirzo, R., Muller-Landau, H., Nuñez-Iturri, G., Peres, C.A., Wang, B.C. 2005. The plight of large animals in tropical forests and the consequences for plant regeneration. Biotropica 39: 289–291.

Young, H.S., McCauley, D.J., Dirzo, R., Goheen, J.R., Agwanda, B., Brook, C., Otárola-Castillo, E., Ferguson, A.W., Kinyua, S.N., McDonough, M.M., Palmer, T.M., Pringle, R.M., Young, T.P., Helgen, K.M. 2015. Context-dependent effects of large-wildlife declines on small-mammal communities in central Kenya. Ecological Applications 25: 348–360.

Young, H.S., McCauley, D.J., Galetti, M., Dirzo, R. 2016. Patterns, causes, and consequences of Anthropocene defaunation. Annual Review of Ecology, Evolution, and Systematics 47: 333–358.

Capítulo 2.

The global impact of landscape structure on tropical terrestrial mammals

Norma P. Arce-Peña, Víctor Arroyo Rodríguez, Ellen Andresen, Claudia Moreno

Introduction

The ongoing global extinction crisis of animals is being caused by habitat loss, habitat disturbance, climate change, invasive species, emergent diseases, and hunting (Barnosky et al. 2011, Symes et al. 2018, Scheffers et al. 2019). Tropical species are particularly threatened by habitat loss because, while in temperate regions there is actually an annual forest gain of 2.7 Mha, the annual deforestation rate in the tropics is of 5.5. Mha per year (Keenan et al. 2015). The remaining forest patches are exposed to increasing levels of hunting, logging, and other post-deforestation threats (Laurance and Bierregaard 1997, Barlow et al. 2016). Deforestation results in heterogeneous human-modified landscapes, which are composed of forest patches surrounded by a matrix of agricultural lands, cattle pastures, secondary forests, and human settlements (Melo et al. 2013, Arroyo-Rodríguez et al. 2017). These emerging landscapes differ in spatial composition, which refers to the different types of land covers and their proportions in the landscape, and spatial configuration, which refers to the spatial arrangement of each land cover (Dunning et al. 1992). Assessing the relative effect of each of these two components of landscape structure on species is urgently needed to inform conservation plans (Fahrig 2003, Fahrig et al. 2011).

Tropical forest mammals constitute a charismatic and diverse group, which account for a large proportion of animal biomass in these ecosystems (Rovero et al. 2017). They play critical roles in ecosystem functioning (e.g. grazing, seed dispersal and seed predation, biological control of populations, structural habitat modifiers, etc.; Dirzo et al. 2014, Palmeirim et al. 2018, Schipper et al. 2008) and provide important ecosystem services (Schipper et al. 2008). However, their populations are declining at a very rapid rate – from 5487 recognized extant mammal species, 25% are threatened with extinction, and ~ 52% have declining populations (Schipper et al. 2008), mainly due to human activities, such as deforestation, habitat degradation, and illegal hunting and trade (Schipper et al. 2008, Ceballos et al. 2015, Beaudrot et al. 2016). In order to gain a better understanding of their ecology in human-modified landscapes, it is very important to assess and unveil the factors affecting their populations and communities, including the effects of landscape changes (Rovero et al. 2017). However, most studies focus on assessing the effects of habitat loss and hunting on mammal species and there is relatively less information on the landscape variables that help us predict their abundance and diversity.

Even when the analysis of the effects of landscape structure should be conducted at a landscape level (Fahrig 2003), most studies are conducted at local and patch scales and tend to ignore the landscape context (Watling and Donnelly 2006, Fahrig 2019). Studies on mammals generally evaluate the effects of patch attributes (e.g. patch size and shape, distance from the patch to continuous forest and human settlements) on response variables, or only qualitatively compare sites with different land covers (e.g. Karanth et al. 2010); few studies have assessed the landscape context (e.g. Arroyo-Rodríguez et al. 2013, Garmendia et al. 2013, San José et al. 2014). Fortunately, there has been a recent increase in the number of studies evaluating the effect of landscape structure on species. However, these studies show contrasting results, making it necessary to review existing literature on the subject in order to identify general patterns, as well as species-specific attributes that may predict their responses.

There are important study design considerations when conducting research with a landscape approach (Fahrig 2005, Galán-Acedo et al. 2019). One of the most important considerations is to measure the ecological response and predictor variables in several landscapes, i.e. that the landscape be the sample unit. For this purpose, there are three possible study designs, which vary according to how the response variables are measured: i) site-landscape; ii) patch-landscape; and iii) landscape-scale designs (McGarigal and Cushman 2002, Arroyo-Rodríguez and Fahrig 2014, Galán-Acedo et al. 2019). The first two measure response variables in sample sites of a given size, or in habitat patches, respectively, and predictor variables are measured within a specified radius from each focal site or patch (McGarigal and Cushman 2002). In the landscape-scale design, response variables are measured in several sites in each landscape, and the data are combined into a single data point, with the corresponding landscape predictor variable (Brennan et al. 2002).Another important methodological consideration is analyzing landscape structure at several spatial scales and assessing the scale of effect, which allows the detection of the spatial extent within which a species' response to a landscape variable is strongest (Arroyo-Rodríguez and Fahrig 2014, Jackson and Fahrig 2015, Ordóñez-Gómez et al. 2015). Finally, to prevent potential confounding effects of overlapping landscapes on study findings, it is of utmost importance to use spatially independent, non-overlapping landscapes (i.e. thus avoiding pseudo-replication issues; Eigenbrod et al. 2011).

As far as we know, no study to date has reviewed the responses of tropical terrestrial mammals to landscape structure. Thus, here we aim to conduct the first global assessment of the influence of landscape spatial structure on tropical and subtropical terrestrial mammals. We analyze how many studies have been conducted and present a detailed and updated summary of the available literature on the subject. We evaluate the time and geographic distributions of the studies, and the methodology and study design most commonly used. We then identify which tropical and subtropical mammal groups have been more frequently studied, and their responses to landscape structure, identifying possible trends in the response of tropical terrestrial mammal to landscape structure.

Methods

Literature search

We searched the literature using the Scopus and Google Scholar databases on January 28th, 2019 using the following terms: [(mammal*) AND (“radius” AND/OR “radii” AND/OR “forest cover” AND/OR “buffer” AND/OR “windows” AND/OR “circle” AND/OR “multiscale” AND/OR “landscape” AND/OR “multi-scale” AND/OR “landscape metric*” AND/OR “landscape variable*” AND/OR “landscape approach” AND/OR “landscape scale” AND/OR “percentage” AND/OR “forest” AND/OR “landscape structure” AND/OR “landscape heterogeneity” AND/OR “landscape predictor” AND/OR “percentage of forest” AND/OR “matrix” AND/OR “matrices” AND/OR “isolation” AND/OR “fragment*” AND/OR “connectivity”)].

We looked for studies published in English and Spanish, in international peer-reviewed journals, excluding “grey literature”. These criteria probably lead to a publication bias, with a higher chance of significant results being published compared to results in which no significant effects of landscape structure were found, but they also guarantee a certain level of quality (Gray et al. 2007). We limited our review to studies that explicitly assessed the response of tropical and subtropical terrestrial mammals to landscape composition and/or configuration variables. We did not set any limit with respect to the year of publication. We also excluded studies on biophysical landscape variables, such as elevation, terrain aspect, and soil properties. Furthermore, we did not include studies that did not measure the landscape predictors on a quantitative scale.

An initial search resulted in more than 5000 articles; after filtering the results according to the above criteria, we obtained 289 articles. We read them in full and further filtered them using a second set of criteria, excluding articles that included arboreal mammals, those that were outside the tropics or sub-tropics, those that were not performed at the landscape level, and those that were meta-analyses that conducted analysis in sites other than the tropics and pooled all responses together. Finally, we only included studies in which the ecological response was directly measured, not inferred (e.g. from a model). The assessment of studies was performed by one person to avoid bias. As a result of this second and final screening process we excluded 176 articles; the remaining 113 articles were included in our analyses.

Data extraction

We created two different datasets to analyze the information found in the studies. The first database included the following: year, country, region (Africa, Asia, North and Central America, South America and Oceania), whether the study was conducted at least partially inside a natural protected area, the methodology used (e.g. camera traps, interviews, live traps), and the main study purpose (e.g. extinction risk, landscape change, habitat use and occupancy). In the second database, we registered the study design (patch-landscape, site-landscape or landscape-scale designs; Arroyo-Rodríguez and Fahrig 2014), the number of scales (buffers) included in the study and the scale ratio (i.e. the largest scale divided by the smallest scale, both measured as the radius of each buffer in meters), whether the used scales were ecologically justified, and whether they analyzed the scale of effect. Also, we registered the average distance between study sites and determined the existence of spatial overlap between sites (i.e. pseudoreplication problems; Eigenbrod et al. 2011). We obtained the response variables used in each study, classifying them in the following categories: 1) abundance-related variables (i.e. relative abundance, encounter/capture frequency or rate, density of individuals, density of signs); 2) diversity (i.e. species richness, local/landscape taxonomic species diversity, functional diversity, eveness, compositional disimilarity, beta diversity); 3) occurrence (i.e. presence/absence data, occupancy, probability of detection, available vs. occupied landscapes); 4) health index (i.e. body condition index, red blood cell count, neutrophil to lymphocite ratio); 5) post-deforestation human impacts (i.e. road-kills, number of conflicts, hunting pressure); and 6) others (i.e. capture-recapture information, survival rates, behavior, activity rates). We did not include assessements of community composition, as it is a non-directional response variable. We also recorded all landscape predictor variables, and classified them into compositional and configurational variables (sensu McGarigal and Cushman 2002). Finally, the effect (i.e. positive, negative or non-significant) of each landscape variable on each response was recorded. We did not carry out a formal meta-analysis because we are not attempting to estimate the overall effect size of each landscape variable on each response, but only summarize the number (and direction) of significant effects documented so far.

To explore possible causes of the responses we registered, we also recorded the species' conservation status according to the IUCN (i.e. Least Concern, Vulnerable, Near Threatened, Endangered, Critically Endangered), and some ecological traits: feeding guild (i.e. carnivore, herbivore, omnivore), body size [grouped into small (<1 kg), medium (1 – 29.99 kg) and large (30 kg or more)], IUCN activity period (diurnal, nocturnal, cathemeral), maximum lifespan (months), maximum territory size (hectares), and forest specialization (specialist, non-specialist). All ecological information was obtained from the PanTHERIA Database (Jones et al. 2009), the IUCN Red List webpage (IUCN 2018) and the University of Michigan's Animal Diversity Web (University of Michigan 2014).

Results and discussion

As has been previously reported in other reviews and meta-analyses (e.g. Chalfoun et al. 2002), we found that the number of publications that cited hypotheses about mammal responses to landscape structure greatly exceeded the number that actually tested them. From the 113 studies focused on tropical and subtropical terrestrial mammals, that used a landscape approach, we were able to extract 1367 responses of 304 tropical terrestrial mammal species to landscape structure. The majority of studies assessed mammal defaunation and extinction risk (32%), the effect of different landscape features (26%) and landscape change (19%), and distribution, habitat use and occupancy (19%). Studies were conducted worldwide, but the majority was from the New World (56% in South America and 17% in North and Central America), followed by Asia (19%), Oceania (4%) and finally Africa (3%). Almost half of the studies were conducted outside natural protected areas (43%), 48% both inside and outside, and only 7% completely inside protected areas. All studies were published since 2004, increasing steadily through time (Fig. 1).

Figure 1. Increase of published studies on tropical and subtropical terrestrial mammals, using a landscape approach, through time. The earliest articles including these criteria were published in 2004.

Study design

Reported studies collected data between 1990 and 2016, with only 13% of them being longitudinal studies. Research methods for obtaining the mammal response variables involved the use of camera traps (n= 49), track surveys (n= 32), live traps (n= 31), interviews (n= 21), radio-tracking (n= 6), literature review (n= 5), and hair and DNA (n= 1). False absences are a major source of bias in wildlife studies (MacKenzie 2005, MacKenzie et al. 2006), however, an evaluation of sampling e methodologies used, is beyond the scope of this review.

Most the studies were conducted using a site-landscape design (71.7%), followed by patch-landscape (17.7%), landscape scale (8.0%), and finally a combination of patch/site-landscape and landscape scales (2.7%). The number of landscapes studied varied from 1-10 (12%), 11-30 (28%), 31-100 (31%), 101-1000 (26%) and more than 1000 (4%). More than half of the studies (56%) measured spatial predictors in only one spatial scale (buffer), 12% in 2 scales, 32% in 3 to 12, and only 1% in more than 12 spatial scales. However, only 24% assessed the scale of effect, considering all studies, and 54%, considering those that measured 2 or more spatial scales. Only 43% of the studies gave an ecological justification for the size of the buffers used in analyses. In the studies using a site- or patch-landscape design, 81% measured landscape variables from the center of the site/patch where response variables were measured, as it is recommended (Arroyo-Rodríguez and Fahrig 2014), while the rest measured them from the edge of the site/patch. In other words, the first ones included the focal site/patch as part of the landscape. Furthermore, 18% presented overlapping buffers, which might imply pseudo-replication problems (Eigenbrod et al. 2011). Another 17% did not mention anything about spatial overlap. Scale ratios (largest scale / smallest scale) were divided into 0.1-3 (6%), 3.1-6 (14%), 6.1-9 (4%), 9.1-12 (7%), 12.1-30 (3%), 30.1-50 (4%) and more than 50 (2%).

Landscape structure effects on mammal species

Different response variables were used in the studies, which were grouped into seven categories, as previously mentioned (Table 1). According to Gibson et al. (2011), much of the previous research on the biodiversity impacts of land-use change has focused on community-level parameters, specially species richness. However, in our analysis, most response records included variables related to occurrence, habitat use and distribution (711 records), followed by diversity (314 records) and abundance-related variables (295 records).

From 1367 response records analyzed, 805 were non-significant, 353 showed a positive statistical relationship to landscape predictors, and 209 a negative one (Table 2). Furthermore, 1001 response records correspond to landscape composition attributes (73%), 352 to landscape configuration attributes (26%), and 14 to both kinds (1%).

Landscape composition attributes

Mammal responses to landscape composition attributes were in its majority statistically non-significant (54%), and the percentage of positive responses was higher than the percentage of negative ones (30 to 16% respectively). Among all the landscape composition attributes assessed, habitat amount (generally percentage of forest cover) corresponded to 71% of all records, followed by matrix composition (15%), habitat heterogeneity (7%), landscape quality index (4%), and matrix contrast (3%).

The importance of the remaining habitat in the landscape for species diversity and species density is widely accepted (Fahrig 2013, Arroyo-Rodríguez et al. 2020, Watling et al., 2020). In this study, as expected, positive responses of mammals to native habitat amount were almost three times more frequent than negative responses (32 *vs.* 11%); however, most records were for non-significant effects of habitat amount (56%; Figure 2). There results confirm that habitat amount is vital for the conservation of tropical biodiversity (Benchimol and Peres 2013, Arce-Peña et al. 2019a, Arce-Peña et al. 2019b), probably due to its positive association with landscape connectedness and resource availability (Fahrig 2003, 2013).

The effects of matrix composition on biodiversity have been less studied, compared to assessments of habitat amount or configuration (Fahrig et al. 2011, Klingbeil and Willig 2016). Here, we found that mammals' response to matrix composition was mostly non-significant (46% of records), but the percentage of negative effects (34%) was higher than that of positive effects (20%). Yet, there is a gradient from low-quality matrices, were negative impacts to forest species are very high, to high-quality matrices, where survival of forest species is high (Arroyo-Rodríguez et al. 2020). The percentage of human settlements in the matrix had the highest negative effects on mammal populations (65% of the records), followed by palm plantations (25%), forestry (22%), sugarcane (20%), pastures (20%) and agriculture (19%). On the other hand, secondary forest had the highest positive effects on mammals (50%), with no negative responses reported, followed by forestry (39%), water bodies (33%), agriculture (31%), and palm plantations (25%). Matrices with low permeability, or high contrast, can prevent or impede movement among habitat patches, causing lower connectivity, which may promote population isolation and a limited gene flow (Bennett and Saunders 2010, Mech and Hallett 2001). However, some species can benefit from the matrix, which may offer complementary and/or supplementary resources (Dunning et al. 1992), with consequences for species persistence, dispersal and colonization (Tscharntke et al. 2012). We did not analyze the different responses of mammals depending on their ability to use and benefit from the matrix.

Table 1. Response variables used in the studies analyzed. We show a classification of the response variables, the number of records for each response category, their response to landscape structure attributes (i.e. percentage of positive and negative responses), and the different response variables included in each category.

Category	Records (composition/configuration) (No.)	Positive (%)	Negative (%)	Response variables included
Abundance-related variables	295 (227-75)	25.1	19.3	Relative abundance, encounter/capture frequency or rate, total/mean density, density of signs
Diversity	314 (220-94)	28.0	10.8	Local/landscape functional and taxonomic diversity, species richness and evenness, composition dissimilarity, beta diversity
Health index	18 (10-8)	27.8	16.7	Body condition index, body mass, red blood cell count, neutrophil to lymphocyte ratio
Occurrence	711 (537-180)	66.7	0.0	Presence/absence, occupancy, probability of detection, available vs. occupied landscape, movement probability, habitat use
Post-deforestation human-impacts	15 (10-5)	24.2	15.3	Number of road kills registered, number of conflicts, hunting pressure
Other	14 (14-0)	28.6	42.9	Capture-recapture data, activity rates, population rate of change

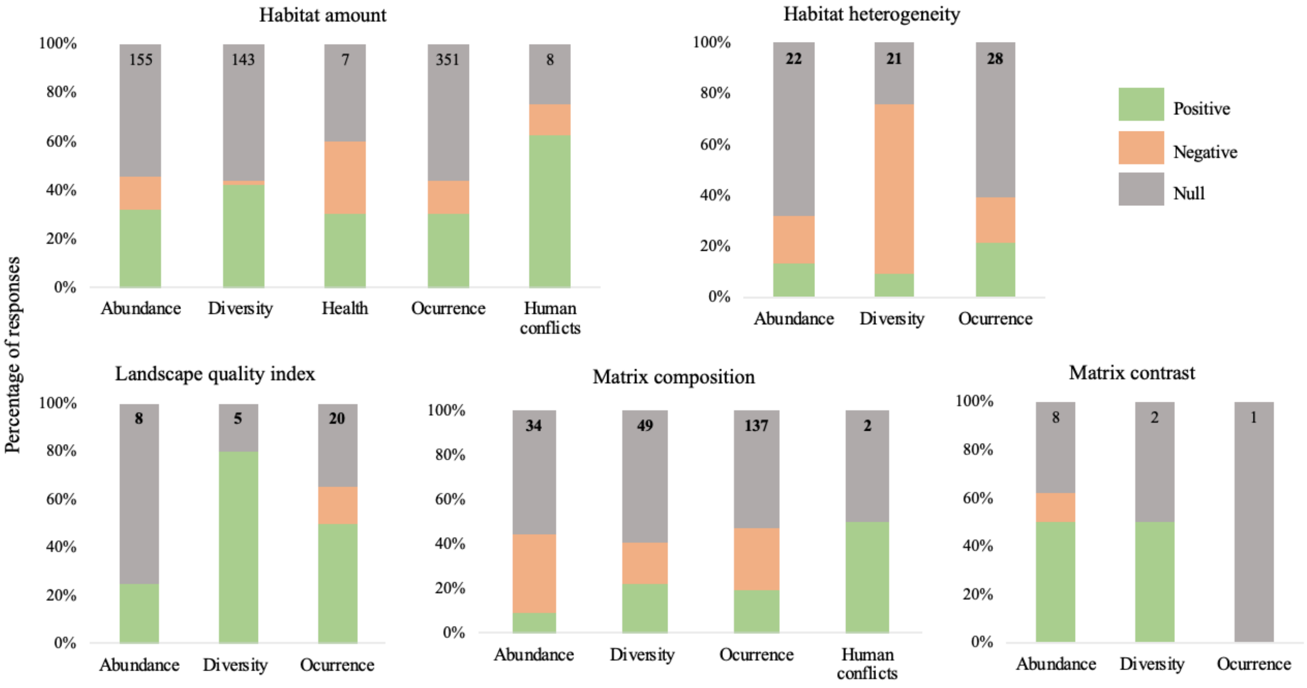


Figure 2. Percentages (and numbers inside bars) of positive, negative and null effects of each landscape composition variable (habitat amount, habitat heterogeneity, landscape quality index, matrix composition and matrix contrast) on all recorded responses (abundance, diversity, health, occurrence and human conflicts).

Table 2. Landscape composition and configuration variables analyzed in the tropical terrestrial mammal studies analyzed.

Landscape variable categories	Records (No.)	Negative (%)	Positive (%)	Landscape variables
Landscape composition				
Native habitat amount	707	11.3	32.2	Percentage/sum/proportion of the original habitat cover (e.g., forest cover, savanna) in the landscape
Habitat heterogeneity	69	36.2	13.0	Index of different land-covers in the landscape
Landscape quality	42	4.8	42.9	Measure of the suitability of differing land-cover classes in the landscape for biodiversity
Matrix composition	153	34.0	19.6	Proportion/percentage/area of different land covers (e.g. water, secondary vegetation, forestry, crops) in the anthropogenic matrix
Land-cover proportion	1	0.0	100.0	Number/proportion of land covers in the landscape
Matrix contrast	27	18.5	29.6	Measure of open areas in the matrix (e.g., agriculture, human settlements)
Landscape permeability	1	0.0	100.0	Percentage of each land-cover type within the landscape weighted by their suitability for mammal dispersion and averaged over the landscape
Landscape configuration				
Aggregation metrics	46	4.3	28.3	Aggregation, cohesion, contiguity, juxtaposition, interspersion, proximity, similarity indexes, referring to the tendency of patches to be spatially aggregated
Connectivity	88	5.7	29.5	Degree in which a landscape facilitates or impedes movement of organisms among land covers
Edge metrics	66	18.2	10.6	Sum of forest-matrix edge divided by landscape area, proportion/sum of edges
Fragmentation	118	12.7	6.8	Number/density of forest patches, including the splitting index
Shape metrics	18	0.0	5.6	Landscape/mean- patch shape, referring to the geometric complexity of patch shapes, mean shape index
Matrix configuration	23	21.7	21.7	Number or density of different land covers (i.e. road abundance, drainage density, herbaceous density), matrix resistance
Isolation metrics	28	10.7	0.0	Mean isolation distance (mean inter-patch isolation distances between patches in the landscape), mean nearest-neighbors
Area	15	0.0	20.0	Arithmetic mean of patch sizes, largest patch index

Landscape configuration attributes

Mammal responses to landscape configuration variables were less often assessed than responses to composition variables. As with composition attributes, most records showed no significant response of mammals to landscape configuration attributes (74%); only 15% of the records corresponded to positive responses and 11% to negative responses. The most evaluated attributes were fragmentation-related (33%), followed by edge metrics (18%), aggregation metrics (13%), and connectivity metrics (8%). All the other variables were assessed in less than 7% each (Table 2, Figure 3).

Although the effect of habitat fragmentation has been a subject of high debate (Fahrig 2003, Fahrig 2017, Haddad et al. 2015), and fragmentation is commonly assumed to be a driver of global extinction, few studies have assessed the effects of fragmentation per se on mammal populations and extinction risk (Crooks et al. 2017). We found only 18 studies that evaluated mammals' responses to habitat fragmentation *per se*, mostly non-significant responses (81%). However, contrary to Fahrig (2017) – who, among significant responses, found a higher percentage of positive responses to habitat fragmentation – we found a higher percentage of negative ones (13 *vs.* 7%). Finally, only a few studies assessed connectivity at the landscape level and its effects on mammal species (16 studies with 88 records), which reported 6% negative responses, compared to 30% of positive responses. Connectivity can facilitate species' dispersal among habitat patches, potentially lessening the impact of habitat loss on biodiversity (Thompson et al. 2017) and is essential to prevent extinctions and maintain a pool of genetic variation to cope with environmental change (Tscharntke et al. 2012).

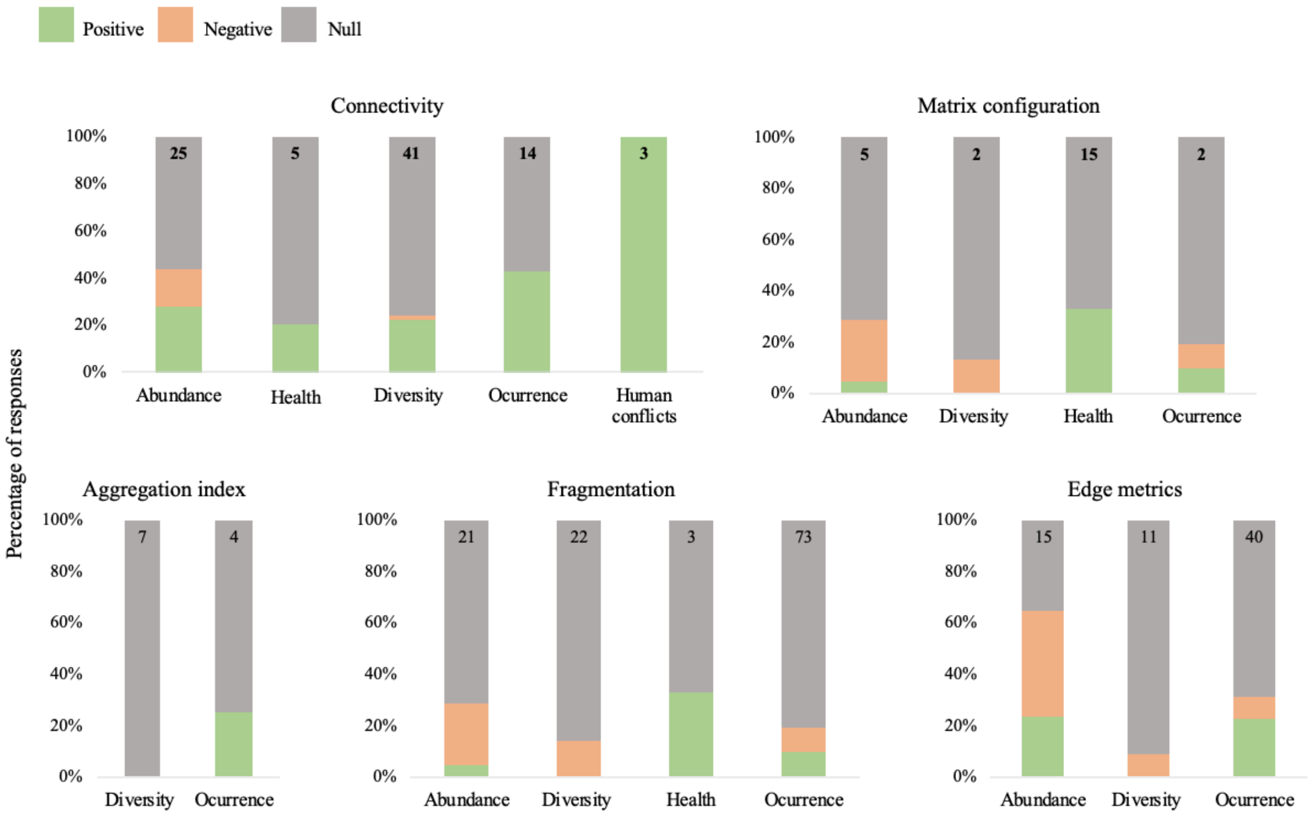


Figure 3. Percentages (and numbers in bars) of positive, negative and null responses of landscape configuration variables (connectivity, matrix configuration, aggregation index, fragmentation and edge metrics) for all of the response variables (abundance, diversity, health, occurrence and human conflicts) registered.

Trends in mammal responses to landscape structure

Although the effects of landscape disturbance on individual species are complex, certain species traits such as small population size, small geographic range, low growth rates, high trophic level, large body size and matrix intolerance have been shown to predict species' sensitivity (Laurance 1991, Terborgh et al. 2001, Vetter et al. 2011, Newmark et al. 2014, Keinath et al. 2017). Terrestrial mammals are no exception, with the most affected and threatened being specialist, medium and large species (Ceballos et al. 2015, Karanth et al. 2010).The extinction and population decrease due to human activities (i.e. defaunation; Dirzo et al. 2014, Galleti and Dirzo 2013), is becoming evident and occurring at an alarming rate. On the other hand, some mammal species benefit from anthropic activities and are positively impacted in human-modified landscapes. These species can be categorized as human adapters or even human exploiter species (Riggio et al. 2018). These differential responses by particular groups of mammals could disrupt many interactions and impact community structure and diversity, with important implications for ecosystem functions and services (Galetti and Dirzo 2013, Johnson et al. 2017).

The analyzed studies comprised a total of 304 tropical and subtropical mammal species, corresponding to 18 orders and 50 families. Studies analyzed species-specific responses to landscape structure for 163 out of the 304 mammal species. According to their order, carnivores were the most studied (34% of all the studies at the species level), with 80 species included; among them, the ones most often studied were *Eira barbara* (22 studies), *Leopardus pardalis* (19), *Puma concolor* (18), *P. yagouaroundi* (16), *Panthera onca* (14), *Cerdocyon thous* (14), *Nasua nasua* (13), *Procyon crancrivorou*s (12) and *Leopardus wieddii* (12), with all the other species assessed in six or fewer studies each. Rodents were the second most studied order (27%), with 113 different species represented, including *Cuniculus paca* (21 studies), *Hydrochaeris hydrochaeris* (13), *Dasyprocta leporina* (5), *D. punctata* (5), *Cavia aperea* (5) and *Hystrix brachyura* (5), with all other species with one to three studies. Among Cetartiodactyla (15% of the studies, 34 species), *Pecari tajacu* (23), *Tayassu pecari* (16), *Mazama americana* (14), and *Sus scro*fa (10) were the most studied species. Finally, *Didelphis aurita* (9), *D. marsupialis* (8) and *D. albiventris* (7) were the most studied Didelphimorphia species (9% of studies, 29 species). All other mammalian orders were each assessed in less than 3% of studies (Figure 4, Table A1). According to their size, we found that 142 species were classified as small, 124 as medium and only 38 were considered large. In addition, 72 species were classified as habitat specialists. Finally, according to their IUCN status (IUCN 2018), 74% were classified as Least Concern, 12% as Vulnerable, 4% as Near Threatened, 4% as Endangered, less than 1% as Critically Endangered, and 5% are Data Deficient.

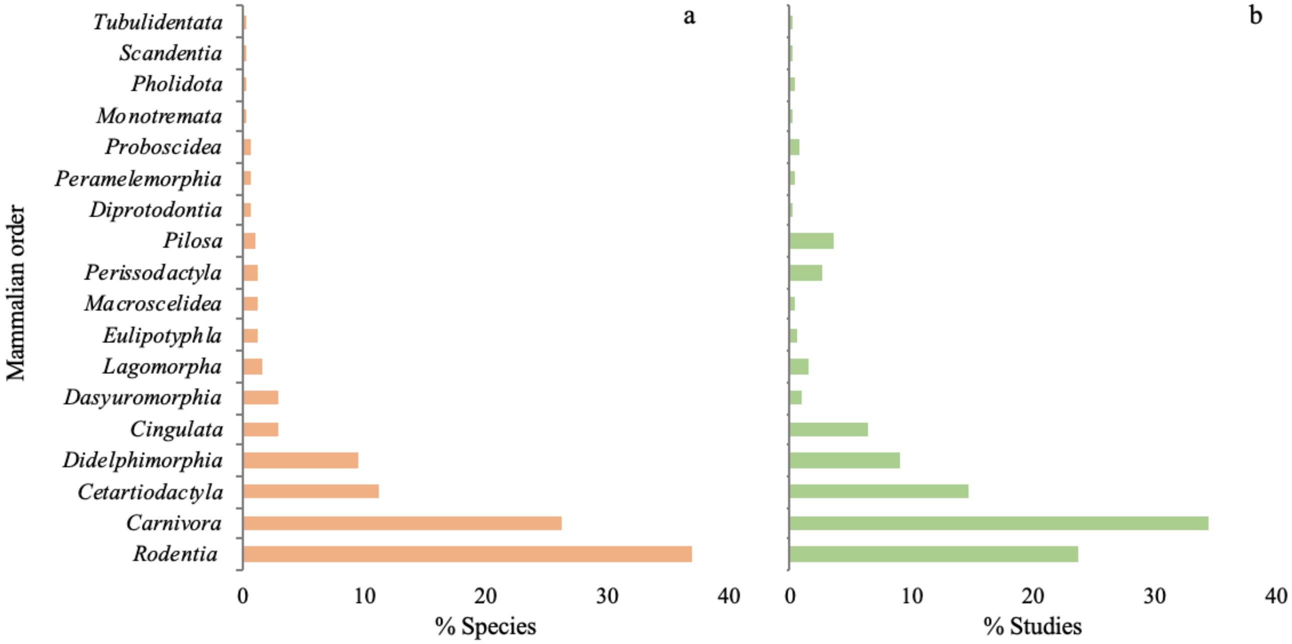


Figure 4. Percentage of species (a) and studies (b) registered for each of the 18 mammal orders recorded in existing landscape scale studies assessing tropical and subtropical terrestrial mammals.

The number of different responses assessed of each mammal to landscape attributes varied from 1 to 25. The species with the highest number of responses analyzed were *P. tajacu* (25)*, L. pardalis* (24)*, P. onca* (24)*, C. thous* (21)*, E. barbara* (21)*, Tapirus bairdii* (20), *Dasypus novemcinctus* (19), *Nasua narica* (19), *C. paca* (17), *Elephas maximus* (16), *Leopardus guigna* (16), *D. aurita* (15), *Procyon lotor* (15), *P. concolor* (15) and *T. pecari* (15).

We then analyzed trends in mammal responses to landscape structure based on their ecological traits. A positive association has been reported between mammal body size and threat, with large species dominating the most threatened families worldwide (Schipper et al. 2008, Ripple et al. 2017). Here, we found that large terrestrial mammals presented a higher percentage of significant, positive responses to habitat amount than medium and small mammals, although positive responses were more frequent than negative responses in all groups (Figure 5). The landscape configuration attributes most frequently assessed were fragmentation, edge metrics, aggregation and connectivity metrics. Connectivity did not have any negative effects, showing mostly non-significant responses in all size categories, while positive responses were more frequent in large mammals. Similarly, the effects of landscape fragmentation were mostly null for all three categories. However, small mammals more frequently had negative responses to fragmentation than large and medium mammals (Figure 5, Table S2).

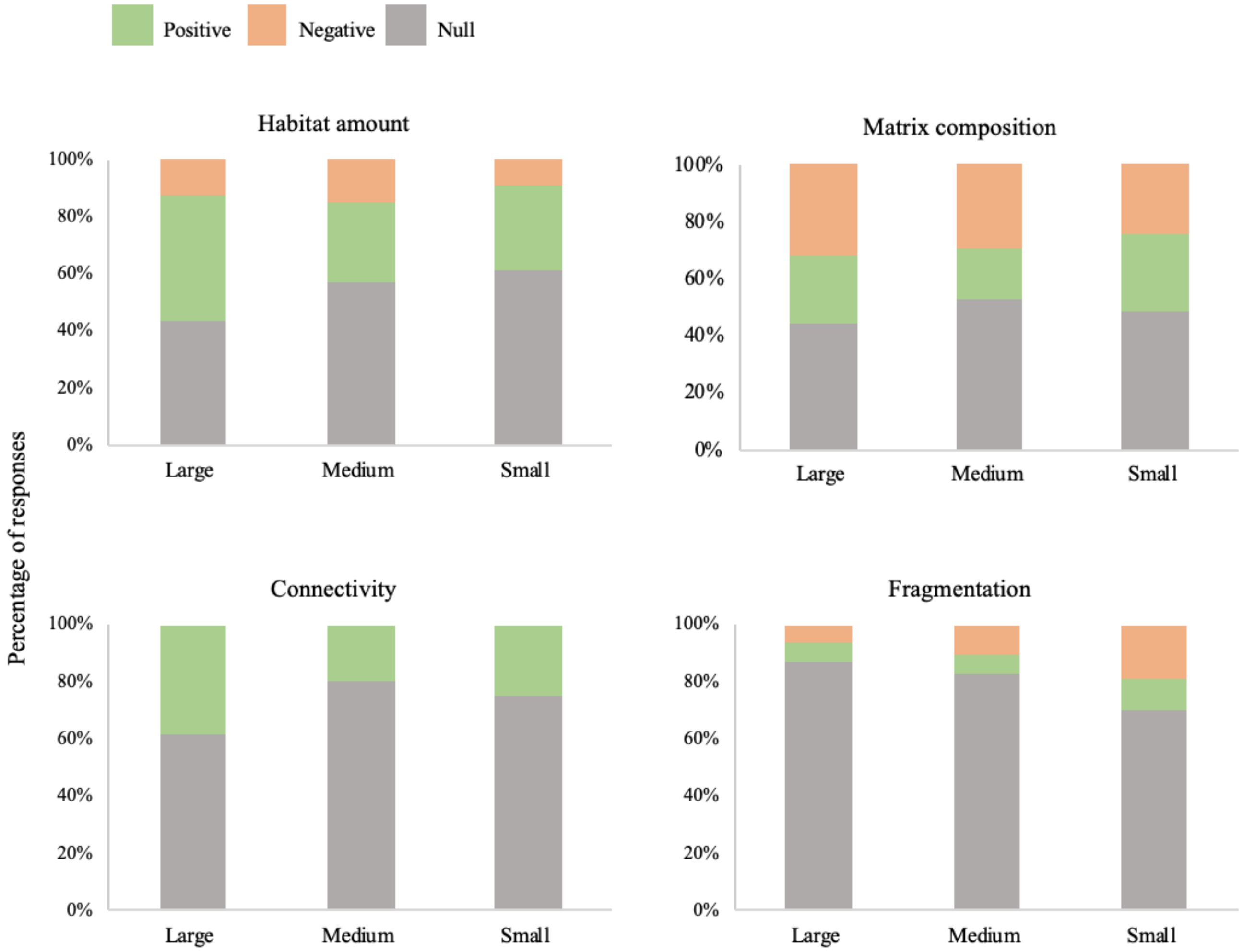


Figure 5. Mammal responses (positive, negative, non-significant) to habitat amount, matrix composition, connectivity and fragmentation metrics, classified according to their size (large, medium and small).

We classified mammals according to their feeding guild into carnivores, herbivores and omnivores and analyzed their responses to landscape attributes, as trophic level has been shown to be correlated to extinction risk and influence responses to habitat disturbances (Terborgh et al. 2001, Vetter et al. 2011). Again, most landscape composition and configuration attributes presented a higher percentage of non-significant effects (Figure 6, Table S2). For habitat amount, positive responses were higher than negative responses for all groups. On the other hand, responses to matrix composition were different for carnivores (equal negative and positive responses) than herbivores and omnivores, which presented more negative than positive responses. Herbivores had few negative responses to landscape configuration variables and most of their responses were not significant, specially to edge metrics and fragmentation. Carnivores had a high percentage of positive responses related to connectivity metrics, but a low percentage of positive responses related to edge and fragmentation metrics. Finally, omnivores had mostly null responses, with more positive responses to connectivity and to edge metrics than to fragmentation. None of the groups presented negative responses to connectivity metrics (Figure 6, Table S2).

Regarding the species' conservation status, IUCN Red List endangered mammals had a higher percentage of positive responses to original habitat amount, whereas vulnerable and least concern species presented a higher percentage of non-significant responses. On the other hand, endangered mammals presented more negative responses to fragmentation than the other categories. These findings agree with a study that stated that degree of fragmentation was related to higher extinction risk, even after accounting for the effect of other extinction-risk drivers, such as body size and home-range size (Crooks et al. 2017).

The previous results are somehow corroborated with the results obtained when analyzing forest specialist vs. non-specialist species, since IUCN endangered species tend to be forest specialists. Forest specialists did not have any positive response to either fragmentation or edge metrics, meaning that they were more negatively affected by these landscape attributes than non-specialists, which did show some positive responses to them. In fact, the positive responses of non-specialists to edge metrics were more frequent than the negative responses. As expected, the positive responses of habitat specialists to habitat amount were more frequent compared to those of non-specialist species. This is not surprising, as habitat specialists are more sensitive than non-specialists regarding anthropic disturbance and changes in the amount of available habitat (Keinath et al. 2017, Galán-Acedo et al. 2019). Only 87 studies assessed the response of forest specialists to landscape spatial change, 71% assessed landscape composition attributes, mostly the effect of habitat amount (with 40% of positive and 9% of negative responses), and 29% assessed landscape configuration attributes, mainly connectivity and fragmentation responses. Finally, range size has been found to be a very important predictor of extinction risk (Crooks et al. 2017, Ripple et al. 2017), however we could not analyze this ecological trait, as data was unavailable for a high number of species.

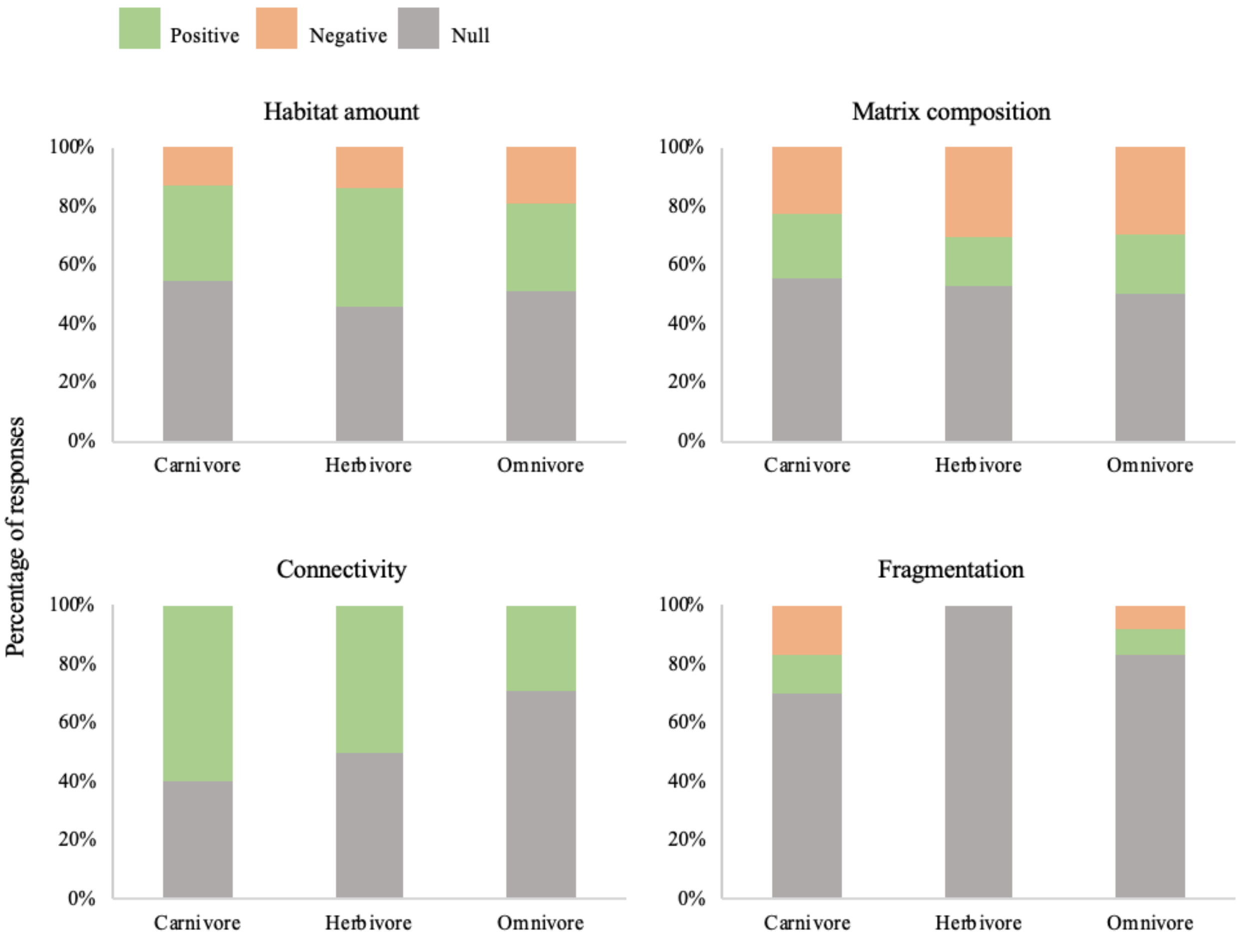


Figure 6. Mammal responses (positive, negative, non-significant) to habitat amount, matrix composition, connectivity and fragmentation metrics, classified according to their diet (carnivores, herbivores and omnivores).

Conclusions

Although many more studies stated to be landscape-scale studies than those that actually assessed the effect of landscape attributes at a landscape-scale, it is clear that the importance of landscape scale studies is being recognized and applied, which is reflected in the growing number of studies that use a landscape context. However, there is still a strong gap of information for large part of the tropical forest regions, as most studies have been conducted in the Neotropics. Furthermore, there are still common design flaws in landscape-scale studies, which often do not follow the methodological recommendations established for this kind of studies. Some still use limited number of landscapes or sites and apply only one scale of analysis, while others which do use several scales do not account for their spatial overlapping, or do not analyze the scale of effect (Fahrig 2003, Jackson and Fahrig 2015).

In addition, there is a significant difference in the number of existing studies involving tropical mammals' responses to landscape composition vs. configuration attributes, with composition attributes being the most frequently assessed. In terms of landscape composition, habitat amount was the most studied landscape composition attribute, and was mostly associated with positive responses, as expected. Habitat loss is very important for biodiversity conservation (Fahrig 2003, 2017, Watling et al. 2020), which has several conservation implications, stressing the importance of maintaining primary habitats (e.g. creation of natural protected areas), and increasing habitat amount (i.e. through restoration). Matrix composition was the second most researched landscape attribute. It is well-known that forest dependent species that avoid using the matrix are more prone to extinction in fragmented rainforests (Laurance 1991, Vetter et al. 2011, Carrara et al. 2015). Yet, matrix composition is comprised by different land covers and presents different quality and permeability. Here, human settlements had the greatest negative effects, whereas secondary forests and forestry had positive effects on mammal populations. Yet, our findings would have to be further analyzed, dividing results according to mammal tolerance or use of the matrix. Potential conservation actions include the maintenance of permeable matrices, with quality land-covers such as managed forests and tree plantations.

As mentioned above, landscape configuration attributes were less often assessed and had fewer significant effects on mammals. Recent studies have stated that the effect of landscape configuration on biodiversity is stronger in landscapes with an intermediate habitat amount (30-50% remaining habitat; Pardini et al. 2010, Villard and Metzger 2014). Mammals responded mostly in a positive way to connectivity metrics, particularly species with large home ranges, such as carnivores and large mammals. While, species' responses to fragmentation *per se* were non-significant most of the times, they were mostly negative for small species and carnivores, contrary to previous findings (Fahrig 2017).

Our results suggest that community variables, such as diversity metrics, might not be the best response variables to assess the effects of landscape composition and configuration, due to different species-specific responses. We found that > 60% of the recorded diversity responses were non-significant. The coexistence of species that are negatively impacted and species that are positively impacted by human alterations requires attention, in order to inform management practices for mammal conservation in modified landscapes.

Despite the fact that the number of mammal species studies is relatively high, as with the geographic distribution of studies, there is also a strong taxonomic bias. Most studies focused on a few species and orders, mainly carnivores and rodents, with a strong bias toward "charismatic" species, such as jaguars, pumas, tapirs, ocelots and elephants. On the one hand, this bias limits our understanding about the responses of other species. On the other hand, however, it can help conservation initiatives focused on umbrella species (e.g. jaguars), which may help maintain high-quality core habitat for sympatric mammals (Crooks et al. 2017).

Finally, we strongly encourage the development of longitudinal studies, to be able to better assess the dynamic and long-term effects of landscape change on mammal populations and communities, as well as multi-scale designs. These approaches will unveil important factors related to biodiversity in changing environments and will allow us to reach clear insights into the ecology and conservation of tropical terrestrial mammals in human-modified landscapes.

References

Arce-Peña, N.P., Arroyo-Rodríguez, V., Dias, P.A.D., Franch-Pardo, I., Andresen, E. 2019a. Linking changes in landscape structure to population changes of an endangered primate. Landscape Ecology 34: 2687–2701.

Arce-Peña, N.P., Arroyo-Rodríguez, V., San-José, M., Jiménez-González, D., Franch-Pardo, I., Andresen, E., Ávila-Cabadilla, L.D. 2019b. Landscape predictors of rodent dynamics in fragmented rainforests. Biodiversity and Conservation 28: 655–669.

Arroyo-Rodríguez, V., Fahrig, L. 2014. Why is a landscape perspective important in studies of primates? American Journal of Primatology 76: 901–909.

Arroyo-Rodíguez, V., Fahrig, L., Tabarelli, M., Watling, J.I., Tischendorf, L., Benchimol, M., Cazetta, E., Faria, D., Leal, I.R., Melo, F.P.L., Morante-Filho, J.C., Santos, B.A., Arasa-Gisbert, R., Arce-Peña, N., Cervantes-López, M.J., Cudney-Valenzuela, S., Galán-Acedo, C., San-José, M., Vieira, I.C.G., Slik, J.W.F., Nowakowski, A.J., Tscharntke, T. 2020. Designing optimal human-modified landscapes for forest biodiversity conservation. Ecology Letters: https://doi.org/10.1111/ele.13535

Arroyo-Rodríguez, V., González-Perez, I.M., Garmendia, A., Solà, M., Estrada, A. 2013. The relative impact of forest patch and landscape attributes on black howler monkey populations in the fragmented Lacandona rainforest, Mexico. Landscape Ecology 8: 1717–1727.

Arroyo-Rodríguez, V., Saldaña-Vázquez, R.A., Fahrig, L., Santos, B.A. 2017. Does forest fragmentation cause an increase in forest temperature? Ecological Research 32: 81–88.

Barlow, J., França, F., Gardner, T.A., Hicks, C.C., Lennox, G.D., Berenguer, E., Castello, L., Economo, E.P., Ferreira, J., Guénard, B., Leal, C.G., Isaac, V., Lees, C.A., Parr, C.L., Wilson, S.K., Young, P.J., Graham, N.A.J. 2018. The future of hyperdiverse tropical ecosystems. Nature 559: 517–526.

Barnosky, A.D., Matzke, N., Tomiya, S., Wogan, G.O.U., Swartz, B., Quental, T.B., Marshall, C., McGuire, J.L., Lindsey, E.L., Maguire, K.C., Mersey, B., Ferrer, E.A. 2011. Has the Earth's sixth mass extinction already arrived? Nature 471: 51–57.

Beaudrot L., Ahumada, J.A., O´Brien, T., Alvarez-Loayza, P., Boekee, K., Campos-Arceiz, A., et al. 2016. Standarized assessment of biodiversity trends in tropical forest protected areas: the end is not in sight. PLoS Biol 14(1): e1002357.

Benchimol, M., Peres, C.A. 2013. Anthropogenic modulators of species-area relationships in Neotropical primates: a continental-scale analysis of fragmented forest landscapes. Diversity and Distributions 19: 1339–1352.

Bennett, A.F., Saunders, D.A. 2010. Habitat fragmentation and landscape change. In: Sodhi, N.S., Ehrlich, P.R. (Eds.) Conservation Biology for All. Oxford University Press, Oxford, pp 88–106.

Brennan, J.M., Bender, D.J., Contreras, T.A., Fahrig, L. 2002. Focal patch landscape studies for landscape wildlife management: optimizing sampling effort across scales. In: Liu, J., Taylor, W.W. (Eds.) Integrating: landscape ecology into natural resource management. Cambridge University Press, pp 68–91.

Carrara, E., Arroyo-Rodríguez, A., Veha-Rivera, J.H., Schondube, J.E., de Freitas, S.M., Fahrig, L. 2015. Impact of landscape composition and configuration on forest specialist and generalist bird species in the fragmented Lacandona rainforest, Mexico. Biological Conservation 184: 117–126.

Ceballos, G., Ehrlich, P.R., Barnosky, A.D., García, A., Pringle, R.M., Palmer, T.M. 2015. Accelerated modern human-induced species losses: entering the sixth mass extinction. Science Advances 1: e1400253.

Chalfoun, A.D., Thompson III, F.R., Ratnaswamy, M.J. 2002. Nest predators and fragmentation: A review and meta-analysis. Conservation Biology 16: 306–318.

Crooks, K.R., Burdett, C.L., Theobald, D.M., King, S.R.B., Di Marco, M., Rondinini, C., Boitani, L. 2017. Quantification of habitat fragmentation reveals extinction risk in terrestrial mammals. Proceedings of the National Academy of Sciences 114: 7635–7640.

Dirzo, R., Young, H.S., Galetti, M., Ceballos, G., Isaac, N.J.B., Collen, B. 2014. Defaunation in the Anthropocene. Science 345: 401–406.

Dunning, J.B., Danielson, B.J., Pulliam, H.R. 1992. Ecological processes that affect populations in complex landscapes. Oikos 65: 169–175.

Eigenbrod, F., Hecnar, S.J., Fahrig. L. 2011. Sub-optimal study design has major impacts on landscape-scale inference. Biological Conservation 144: 298–305.

Fahrig, L. 2003. Effects of habitat fragmentation on biodiversity. Annual Review of Ecology, Evolution, and Systematics 34: 487–515.

Fahrig, L. 2005. When is a landscape perspective important? Issues and perspectives in landscape ecology: 3–10.

Fahrig, L. 2013. Rethinking patch size and isolation effects: the habitat amount hypothesis. Journal of Biogeography 40: 1649–1663.

Fahrig, L. 2017. Ecological responses to habitat fragmentation *per se*. Annual Review of Ecology, Evolution, and Systematics 48: 1–23.

Fahrig, L. 2019. Habitat fragmentation: A long and tangled tale. Global Ecology and Biogeography 28: 33–41.

Fahrig, L., Baudry, J., Brotons, L., Burel, F.G., Crist, T.O., Fuller, R.J., Sirami, C., Siriwardena, G.M., Martin, J.L. 2011. Functional landscape heterogeneity and animal biodiversity in agricultural landscapes. Ecology Letters 14: 101–112.

Galán-Acedo, C., Arroyo-Rodríguez, V., Cudney-Valenzuela, S., Fahrig, L. 2019. A global assessment of primate responses to landscape structure. Biological Review 94: 1605–1618.

Galetti, M., Dirzo, R. 2013. Ecological and evolutionary consequences of living in a defaunated world. Biological Conservation 163: 1–6.

Garmendia, A., Arroyo-Rodríguez, V., Estrada, A., Naranjo, E., Stoner, K.E. 2013. Landscape and patch attributes impacting medium- and large-sized terrestrial mammals in a fragmented rain forest. Journal of Tropical Ecology 29: 331–344.

Gibson, L., Lee, T.M., Koh, L.P., Brook, B.W., Gardner, T.A., Barlow, J., Peres, C.A., Bradshaw, C.J.A., Laurance, W.F., Lovejoy, T.E., Sodhi, N.S. 2011. Primary forests are irreplaceable for sustaining tropical biodiversity. Nature 478: 378–381.

Gray, M.A., Baldauf, S.L., Mayhew, P.J., Hill, J.K. 2007. The response of avian feeding guilds to tropical forest disturbance. Conservation Biology 21: 133–141.

Haddad, N.M., Brudvig, L.A., Clobert, J., Davies, K.F., Gonzalez, A., Holt, R.D., Lovejoy, T.E., Sexton, J.O., Austin, M.P., Collins, C.D., Cook, W.M., Damschen, E.I., Ewers, R.M., Foster, B.L., Jenkins, C.N., et al. 2015. Habitat fragmentation and its lasting impact on Earth's ecosystems. Science Advances 1: e1500052.

IUCN. 2018. The IUCN Red List of Threatened Species. Version 2018-1. International Union for Conservation of Nature and Natural Resources. http://www.iucnredlist.org.

Jackson, H.B., Fahrig, L. 2015. Are ecologists conducting research at the optimal scale? Global Ecology and Biogeography 24: 52–63.

Johnson, C.N., Balmford, A., Brook, B.W., Buettel, J.C., Galetti, M., Guangchun, L., Wilmshurst, J.M. 2017. Biodiversity losses and conservation responses in the Anthropocene. Science 356: 270–275.

Jones, K.E., Bielby, J., Cardillo, M., Fritz, S.A., O´Dell, J., Orme, C.D.L., Safi, K., Sechrest, W., Boakes, E.H., Carbone, C., Connolly, C., et al. 2009. PanTHERIA: a species-level database of life history, ecology, and geography of extant and recently extinct mammals. Ecology 90: 2648–2648.

Karanth, K.K., Nichols, J.D., Ullas Karanth, K., Hines, J.E., Christensen Jr., N.L. 2010. The shrinking ark: patterns of large mammal extinctions in India. Proceedings of the Royal Society B 277: 1971–1979.

Keenan, R.J., Reams, G.A., Achard, F., de Freitas, J.V., Grainger, A., Lindquist, E. 2015. Dynamics of global forest area: Results from the FAO Global Forest Resources Assessment 2015. Forest Ecology and Management 352: 9–20.

Keinath, D.A., Doak, D.F., Hodges, K.E., Prugh, L.R., Fagan, W., Sekercioglu, C.H., Buchart, S.H.M., Kauffman, M. 2017. A global analysis of traits predicting species sensitivity to habitat fragmentation. Global Ecology and Biogeography 26: 115–127.

Klingbeil, B.T., Willig, M.R. 2016. Matrix composition and landscape heterogeneity structure multiple dimensions of biodiversity in temperate forest birds. Biodiversity and Conservation 25: 2687–2708.

Laurance, WF. 1991. Ecological correlates of extinction proneness in Australian tropical rain forest mammals. Conservation Biology 5: 79–89.

Laurance, W.F., Bierregaard, R.O. 1997. Tropical forest remnants: ecology, management, and conservation of fragmented communities. The University of Chicago Press, Chicago, Illinois, 616 pp.

MacKenzie, D. 2005. What are the issues with presence-absence data for wildlife managers? Journal of Wildlife Management 69: 849–860.

MacKenzie, D.I., Nichols, J.D., Royle, J.A., Pollock, K.H., Bailey, L.L., Hines, J.E. 2006. Occupancy estimation and modeling. Inferring patterns and dynamics of species occurrence. Academic Press, San Diego, California, 324 pp.

McGarigal, K., Cushman, S.A. 2002. Comparative evaluation of experimental approaches to the study of habitat fragmentation effects. Ecological Applications 12: 335–345.

Mech, S.G., Hallett, J.G. 2001. Evaluating the effectiveness of corridors: a genetic approach. Conservation Biology 15: 467–474.

Melo, F., Arroyo-Rodríguez, V., Fahrig, L., Martínez-Ramos, M., Tabarelli, M. 2013. On the hope for biodiversity-friendly tropical landscapes. Trends in Ecology and Evolution 28: 462–468.

Newmark, W.D., Stanley, W.T., Goodman, S.M. 2014. Ecological correlates of vulnerability to fragmentation among Afrotropical terrestrial small mammals in northeast Tanzania. Journal of Mammalogy 95: 269–275.

Ordóñez-Gómez J.D., Arroyo-Rodríguez, V., Nicasio-Arzeta, S., Cristóbal-Azkarate, J. 2015. Which is the appropriate scale to assess the impact of landscape spatial configuration on the diet and behavior of spider monkeys? American Journal of Primatology 77: 56–65.

Palmeirim, A.F., Benchimol, M., Vieira, M.V., Peres, C.A. 2018. Small mammal responses to Amazonian forest islands are modulated by their forest dependence. Oecologia 187: 191–204.

Pardini, R., Bueno, A.D.A., Gardner, T.A., Prado, P.I., Metzger, J.P. 2010. Beyond the fragmentation threshold hypothesis: regime shifts in biodiversity across fragmented landscapes. PLoS ONE 5: e13666.

Riggio, J., Kija, H., Masenga, E., Mbwilo, F. Van de Perre, F., Caro, T. 2018. Sensitivity of Africa's larger mammals to humans. Journal for Nature Conservation 43: 136–145.

Ripple, W.J., Wolf, C., Newsome, T.M., Hoffmann, M., Wirsing, A.J., McCauley, D.J. 2017. Extinction risk is most acute for the world's largest and smallest vertebrates. Proceedings of the National Academy of Sciences 114: 10678–10683.

Rovero, F., Owen, N., Jones, T., Canteri, E., Iemma, A., Tattoni, C. 2017. Camera trapping surveys of forest mammal communities in the Eastern Arc Mountains reveal generalized habitat and human disturbance responses. Biodiversity Conservation 26: 1103–1119.

San-José, M., Arroyo-Rodríguez, V., Sánchez-Cordero, V. 2014. Association between small rodents and forest patch and landscape structure in the fragmented Lacandona rainforest, Mexico. Tropical Conservation Science 7: 403–422.

Scheffers, B.R., Oliveira, B.F., Lamb, I., Edwards, D.P. 2019. Global wildlife trade across the tree of life. Science, 366: 71–76.

Schipper, J., Chanson, J.S., Chiozza, F., Cox, N.A., Hoffmann, M., Katariya, V., Lamoreux, J., Rodrigues, A.S.J., Stuart, S.N., Temple, H.J., et al. 2008. The status of the world's land and marine mammals: diversity, threat, and knowledge. Science 322: 225–230.

Symes, W.S., Edwards, D.P., Miettinen, J., Rheindt, F.E., Carrasco, L.R. 2018. Combined impacts of deforestation and wildlife trade on tropical biodiversity are severely underestimated. Nature Communications 9: 4052.

Terborgh, J., López, L., Nuñez, P., Rao, M., Shahabuddin, G., Orihuela, G., Riveros, M., Ascanio, R., Adler, G.H., Lambert, T.D., Balbas, L. 2001. Ecological meltdown in predator-free forest fragments. Science 294: 1923–1926.

Thompson, P.L., Rayfield, B., Gonzalez, A. 2017. Loss of habitat and connectivity erodes species diversity, ecosystem functioning, and stability in metacommunity networks. Ecography 40: 98–108.

Tscharntke, T., Tylianakis, J.M., Rand, T.A., Didhma, R.K., Fahrig, L., Batáry, P., Bengtsson, J., et al. 2012. Landscape moderation of biodiversity patterns and processes – eight hypotheses. Biological Reviews 87: 661–685.

University of Michigan. 2014. Animal Diversity Web. University of Michigan, Museum of Zoology. http://animaldiversity.org.

Vetter, D., Hansbauer, M.M., Végvári, Z., Storch, I. 2011. Predictors of forest fragmentation sensitivity in Neotropical vertebrates: a quantitative review. Ecography 34: 1–8.

Villard, M.A., Metzger, J.P. 2014. Beyond the fragmentation debate: a conceptual model to predict when habitat configuration really matters. Journal of Applied Ecology 51: 309–318.

Watling, J.I., Donnelly, M.A. 2006. Fragments as islands: a synthesis of faunal responses to habitat patchiness. Conservation Biology 20: 1016–1025.

Watling, J.I., Arroyo-Rodríguez, V., Pfeifer, M., Baeten, L., Banks-Leite, C., Cisneros, L.M., Fang, R., Hamel-Leigue, A.C., Lachat, T., Leal, I.R., Lens, L., Possingham, H.P., Raheem, D.C., Ribeiro, D.B., Slade, E.M., Urbina-Cardona, J.N., Wood, E.M., Fahrig, L. 2020. Support for the habitat amount hypothesis from a global synthesis of species density studies. Ecology Letters 23: 674–681.

Supplementary material

Table A1. Frequency of mammals' positive, negative, and non-significant (NS) responses to landscape composition and configuration attributes, separated according to the different mammalian orders studied. Hab.am = native habitat amount; Hab-het = habitat heterogeneity; Land.qua = landscape quality; Mat.comp = matrix composition; Aggr. = aggregation metrics; Conne. = connectivity; Edg. = edge metrics; Shap. = shape metrics; Mat.conf. = matrix configuration; Isol. = isolation.

	Landscape composition attributes				***Landscape configuration attributes***						
	Hab.am	**Hab.het**	**Land.qua**	**Mat.comp**	**Aggr.**	**Conne.**	**Edg.**	**Frag.**	**Shap.**	**Mat.conf.**	**Isol.**
Carnivora											
Positive	44	4	4	12	1	3	4	4	1	3	0
Negative	27	8	13	16	0	0	6	3	0	3	0
NS	94	15	1	39	3	1	19	25	11	8	4
Cetartiodactyla											
Positive	43	0	3	0	0	1	0	0	0	1	0
Negative	11	5	0	6	0	0	0	0	0	0	0
NS	40	3	0	8	0	0	3	5	0	0	2
Cingulata											
Positive	8	1	0	3	0	0	1	0	0	0	0
Negative	5	1	0	1	0	0	0	1	0	0	0
NS	19	0	0	4	0	0	2	11	0	0	1
Dasyuromorphia											
Positive	2	0	0	0	0	0	0	1	0	0	0
Negative	2	0	0	0	0	0	0	3	0	0	0
NS	4	0	0	0	0	0	0	4	0	0	0
Didelphimorphia											
Positive	7	1	0	1	0	0	1	1	0	0	0
Negative	3	0	0	4	0	0	0	0	0	0	0
NS	16	2	4	2	0	6	3	5	2	0	0

Diprotodontia											
Positive	0	0	0	0	1	0	0	0	0	0	0
Negative	1	0	0	1	0	0	0	0	0	0	0
NS	1	0	0	0	0	0	0	1	0	0	0
Eulipotyphla											
Positive	0	0	1	0	0	0	0	0	0	0	0
Negative	0	1	0	0	0	0	0	0	0	0	0
NS	0	0	0	0	0	0	0	0	0	0	0
Lagomorpha											
Positive	1	0	0	1	0	0	0	0	0	0	0
Negative	0	0	0	2	0	0	0	0	0	0	0
NS	4	0	0	7	0	0	1	0	0	0	0
Macroscelidea											
Positive	0	0	0	0	0	0	0	0	0	0	0
Negative	0	0	0	0	0	0	0	0	0	0	0
NS	0	0	0	0	0	0	0	0	0	0	0
Monotremata											
Positive	0	0	0	0	1	0	0	0	0	0	0
Negative	1	0	0	1	0	0	0	0	0	0	0
NS	0	0	0	0	0	0	0	0	0	0	0
Peramelemorphia											
Positive	0	0	0	0	0	1	0	0	0	0	0
Negative	1	0	0	0	0	0	0	0	0	0	0
NS	1	0	0	0	0	1	0	1	0	0	0
Perissodactyla											
Positive	9	0	0	1	0	0	0	0	0	0	0
Negative	2	1	0	1	0	0	0	0	0	0	0
NS	9	0	0	2	0	0	2	4	0	2	2
Pholidota											
Positive	0	0	0	0	0	0	0	0	0	0	0

Negative	0	0	0	0	0	0	0	0	0	0	0
NS	1	0	0	0	0	0	0	0	0	0	0
Pilosa											
Positive	1	0	0	0	0	0	0	0	0	0	0
Negative	1	1	0	0	0	0	0	0	0	0	0
NS	2	0	0	1	0	0	1	2	0	0	0
Proboscidea											
Positive	6	2	0	1	0	0	0	0	0	0	0
Negative	2	0	0	1	0	0	0	0	0	1	0
NS	0	3	0	0	0	0	0	0	0	0	0
Rodentia											
Positive	25	1	3	11	1	5	0	3	0	1	0
Negative	10	4	0	9	0	0	0	4	0	0	0
NS	48	5	8	24	0	12	4	22	0	0	0
Scandentia											
Positive	0	0	0	0	0	0	0	0	0	0	0
Negative	0	0	0	0	0	0	0	0	0	0	0
NS	0	0	0	0	0	0	0	0	0	0	0
Tubulidentata											
Positive	0	0	0	0	0	0	0	0	0	0	0
Negative	0	0	0	0	0	0	0	0	0	0	0
NS	0	0	0	0	0	0	0	0	0	0	0

Table A2. Frequency of mammals' positive, negative, and non-significant (NS) responses to landscape composition and configuration attributes, classified into different ecological traits (body size [grouped into small (<1 kg), medium (1 – 29.99 kg) and large (30 kg or more)], feeding guild, IUCN conservation status, habitat-dependence. Hab.am = native habitat amount; Hab-het = habitat heterogeneity; Land.qua = landscape quality; Mat.comp = matrix composition; Aggr. = aggregation metrics; Conne. = connectivity; Edg. = edge metrics; Shap. = shape metrics; Mat.conf. = matrix configuration; Isol. = isolation; LC=Least Concern; VU=Vulnerable; NT=Near Threatened; EN=Endangered; CR=Critically Endangered.

	Landscape composition attributes				***Landscape configuration attributes***						
	Hab.am	**Hab.het**	**Land.qua**	**Mat.comp**	**Aggr.**	**Conne.**	**Edg.**	**Frag.**	**Shap.**	**Mat.conf.**	**Isol.**
Body size											
Large											
Positive	56	3	2	6	1	5	0	1	0	4	0
Negative	16	7	0	8	0	0	2	1	0	4	0
NS	56	9	0	11	1	8	6	13	2	5	3
Medium											
Positive	74	6	5	17	2	4	6	4	1	1	0
Negative	42	12	2	29	0	0	3	6	0	0	0
NS	156	17	4	51	2	16	24	47	8	6	6
Small											
Positive	26	0	6	10	2	7	0	4	0	0	0
Negative	8	2	0	9	0	0	1	7	0	0	0
NS	54	1	10	18	0	21	3	26	3	0	0
Feeding guild											
Carnivore											
Positive	44	4	4	10	2	3	2	4	1	3	0
Negative	17	7	0	10	0	0	4	5	0	3	0
NS	74	10	1	25	3	2	13	21	8	6	2
Herbivore											
Positive	57	2	3	7	1	1	0	0	0	2	0
Negative	19	8	0	12	0	0	0	0	0	1	0

NS	64	8	0	21	0	1	8	14	0	3	4
Omnivore											
Positive	49	2	4	11	1	5	4	3	0	0	0
Negative	32	9	2	16	0	0	2	3	0	0	0
NS	84	7	8	27	0	12	12	30	5	1	3
Conservation status											
LC											
Positive	87	5	8	22	3	5	4	6	0	1	0
Negative	47	15	1	30	0	0	3	8	0	0	0
NS	159	15	13	62	0	18	21	51	5	0	6
VU											
Positive	26	0	0	1	1	1	0	3	1	3	0
Negative	10	5	0	6	0	0	1	1	0	2	0
NS	39	1	0	6	2	1	7	13	6	6	0
EN, CR											
Positive	16	2	0	3	0	0	0	0	0	0	0
Negative	3	1	0	1	0	0	0	1	0	1	0
NS	7	3	0	2	0	0	2	4	0	2	2
Habitat dependence											
Specialist											
Positive	43	0	3	4	1	4	0	0	0	2	0
Negative	7	2	0	6	0	0	2	2	0	2	0
NS	51	4	6	11	1	9	6	11	6	0	0
Non-specialist											
Positive	102	7	9	25	2	7	6	9	1	3	0
Negative	57	19	2	35	1	1	4	10	0	2	0
NS	180	19	7	67	2	11	26	61	6	9	9

Capítulo 3.

Landscape predictors of rodent dynamics in fragmented rainforests

Norma P. Arce-Peña, Víctor Arroyo Rodríguez, Miriam San-José, Iván Franch Pardo, Ellen Andresen, Luis Daniel Ávila Cabadilla

Arce-Peña, N., Arroyo-Rodríguez, V., San-José, M., Franch-Pado, I., Andresen, E., Ávila-Cabadilla, L.D. 2019. Landscape predictors of rodent dynamics in fragmented rainforests. Biodiversity and Conservation 28:655-669.

Abstract

Land-use change threatens a large number of tropical species (so-called 'loser' species), but a small subset of disturbance-adapted species may proliferate in human-modified landscapes ('winner' species). Identifying such loser and winner species is critically needed to improve conservation plans, but this task requires longitudinal studies that are extremely rare. We assessed this topic with small rodent assemblages in the Lacandona rainforest, a relatively new and highly dynamic agricultural frontier from southeastern Mexico. In particular, we measured the abundance of four rodent species in 12 forest sites during a six-year period. We related changes in abundance to differences across time in landscape structure (i.e., percentage of forest cover, matrix contrast, number of forest patches, and forest edge density) surrounding each site. Total rodent abundance was almost two times higher in 2016 than in 2011, although abundances were generally low in all years. The abundance of *Heteromys desmarestianus* increased through time, mainly in forest sites with increasing matrix contrast. *Oryzomys* sp. also tended to increase in abundance, especially in sites with decreasing edge density. *Sigmodon toltecus* remained stable through time, but *Peromyscus mexicanus* tended to decrease in abundance, particularly in sites with decreasing edge density and increasing matrix contrast across time. Therefore, spatial variations in landscape structure lead to species-specific responses. If current deforestation rates persist, we predict a population decline of forest-specialist species (*P. mexicanus*), and an increase in generalist species (*S. toltecus* and *Oryzomys* sp.). Improving matrix quality is crucial for preventing the extinction of forest-specialist rodent species.

Keywords Habitat fragmentation · Human-modified landscape · Lacandona rainforest · Landscape structure · Multi-scale approach · Winner species

Introduction

Tropical forests are being rapidly deforested and fragmented worldwide, mainly because of human activities such as agriculture, cattle ranching and selective logging (FAO 2016). As a consequence, the tropics are increasingly dominated by human-modified landscapes composed of patches of natural ecosystems embedded in matrices with different types of anthropogenic land covers (Melo et al. 2013). Depending on the types and proportions of each land cover in the landscape (landscape composition), and on their spatial distribution (landscape configuration), such emerging landscapes can have a highly heterogeneous structure (Fahrig et al. 2011). Yet, the relative influence of the different aspects of landscape structure on tropical species is still poorly understood, limiting our ability to develop efficient conservation strategies (Fahrig 2003, Fahrig et al. 2011).

Different species can show different responses to changes in landscape structure (Gorresen and Willig 2004, Veter et al. 2011, Carrara et al. 2015, Arroyo-Rodríguez et al. 2016). Whereas many species can disappear in human-modified landscapes, other species tend to proliferate ('loser' and 'winner' species, respectively, sensu Tabarelli et al. 2012) or maintain stable populations. Defaunation – the human-driven decline of animal species – is a common process that negatively impacts biotic communities as well as ecosystem functioning in human-modified landscapes (Dirzo et al. 2014). Yet, some species, including some small rodents, can be highly resilient to the main drivers of defaunation, and even proliferate in these landscapes (Keesing and Young 2014, Galetti et al. 2015, Young et al. 2015, Rosin and Poulsen 2016). Proliferation of small rodents could be caused by the absence of predators or competitors, and/or by an increase in resource availability due to a higher productivity of forest edges (Dirzo et al. 2014, Mendes et al. 2015, Young et al. 2015). Yet, not all rodent species are equally resilient to disturbance (Trujano-Álvarez and Álvarez-Castañeda 2010, San-José et al. 2014, Howe and Davlantes 2017) and many species may be negatively impacted by habitat isolation in fragmented landscapes (Pardini et al. 2010, Banks-Leite et al. 2014).

Understanding the patterns and drivers of changes in rodent abundance in human-modified landscapes is urgently needed because these animals are involved in many biotic interactions (as prey, as competitors, as predators, as vectors), which are crucial for the maintenance and functioning of tropical forests (Andresen et al. 2018). For example, rodents play important roles in herbivory and seed dispersal (Dirzo et al. 2007, Wolff and Sherman 2007, Galetti et al. 2015), and hence, changes in population sizes could affect plant recruitment, potentially altering forest structure and diversity (Galetti and Dirzo 2013, Galetti et al. 2015, Rosin and Poulsen 2016).

Determining rodent population variations through time and the spatial determinants of such changes requires longitudinal studies, including several years and reproductive cycles. Although some studies include 2 to 3 years of rodent population analysis (e.g., Pardini et al. 2010, Lira et al. 2012, Banks-Leite et al. 2014, Young et al. 2015), longer studies are extremely rare (but see Isabirye-Basuta and Kasenene 1987, Fryxell et al. 1998, Gibson et al. 2013), thus limiting our understanding of population and community dynamics in human-modified landscapes (Fahrig and Merriam 1994, del Castillo 2015). Longitudinal studies could help us understand the relative importance of human-induced proliferation or decline of rodents and identify the landscape spatial attributes that might have an impact on these fluctuations. Here, we present the first longitudinal assessment of small rodent assemblages in the Lacandona rainforest – a species-rich region (Instituto Nacional de Ecología 2000) that harbors the highest diversity of mammals in Mexico (Medellín 1994). Covering about 1.3 million ha (Instituto Nacional de Ecología 2000), this region has suffered very high rates of forest loss, fragmentation and degradation in the last three decades due to the advance of the agricultural frontier (Carabias et al. 2015).

Previous studies in the region show that among the common terrestrial small rodent species, *Heteromys desmarestianu*s (Desmarest's Spiny Pocket Mouse) and *Peromyscus mexicanus* (Mexican Deer Mouse) are mainly found in conserved forests, while *Sigmodon toltecus* (Toltec Cotton Rat) is found in disturbed sites, and *Oryzomys* sp. (Rice Rat) in both types of vegetation (Medellín and Equihua 1998, Reid 2009). Yet, the local and landscape determinants of rodent abundances are largely unknown. To our knowledge, there is only one study that assesses the effects of landscape structure on the rodent community, but it uses a temporary static landscape approach to suggest species-specific responses to landscape structure (San-José et al. 2014). Yet, as the landscape structure in this region is not static but rather changes over time, longitudinal assessments are needed to accurately identify which rodent species may be proliferating in this region (i.e., 'winners'), which species may be declining in abundance (i.e., 'losers'), and what landscape structural attributes can predict these patterns.

Here, we evaluated (1) changes in landscape structure in the Lacandona region between 2010 and 2016; (2) temporal changes in the abundance of four terrestrial rodent species within 12 forest sites (sampling conducted in 2011, 2012, 2014 and 2016); and (3) the landscape structure variables as predictors of changes in rodent abundance through time. We measured four landscape structure variables, two compositional (forest cover and matrix contrast) and two configurational variables (fragmentation degree and forest edge density). We expected species-specific responses to changes in landscape structure, with populations of forest-specialist species (i.e., *H. desmarestianu*s and *Peromyscus mexicanus*) declining in more disturbed landscapes (i.e., more deforested, fragmented, and/or with higher forest edge density and matrix contrast). Yet, following previous studies in the region (Medellín and Equihua 1998, San-José et al. 2014), we predicted an increase in the abundance of more generalist, disturbance-adapted species (i.e., *S. toltecus* and *Oryzomys* sp.) through time, especially in more disturbed landscapes.

Methods

Study area

The Lacandona rainforest region is situated in the north-eastern portion of the Mexican State of Chiapas State (16º 05'N, 90º 25'W; Fig. 1). With a warm and humid climate (average monthly temperatures ranging from 24 to 26 °C, and mean annual precipitation ranging from 1500 to 3500 mm; Instituto Nacional de Ecología 2000), it was originally covered by mature tropical rainforest. This region is considered of highest conservation priority because of its exceptional biodiversity (Arriaga et al. 2000). Within this region, the Montes Azules Biosphere Reserve (MABR) encompasses an area of 331,200 ha of continuous rainforest (Instituto Nacional de Ecología 2000). South of the MABR, across the Lacantún River, the Marqués de Comillas Region (MCR) is comprised of 203,999 ha of fragmented forests embedded in a matrix dominated by agricultural lands and human settlements (Fig. 1). All the area is highly threatened by several human-related pressures, such as illegal flora and fauna extraction and land-use change (Carabias et al. 2015). The study was conducted inside the MABR (three continuous forest sites), as well as in forest patches outside the reserve, in the MCR (nine forest patches, ranging from 3 to 92 ha; Fig. 1). All sites were located at similar altitudes (0-200 m a.s.l.), and continuous forest sites were located at least 1 km from the nearest border of the Lacantún River (see further details in San-José et al. 2014).

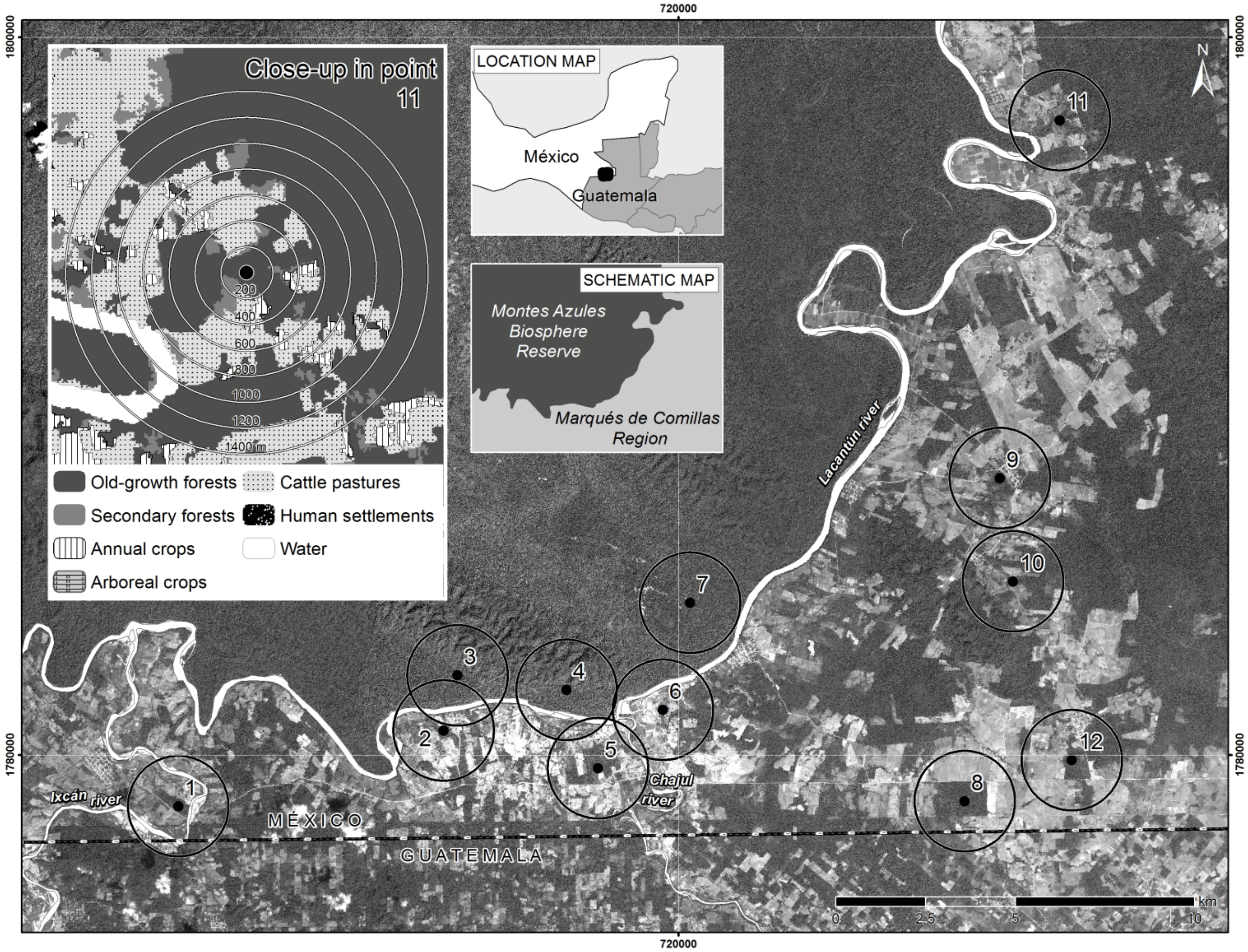


Figure 1. Location of the study sites in the Lacandona rainforest, Mexico. Points represent the center of each site, where rodent surveys were carried out. From the geographic center of each site we estimated the structure of seven different-sized landscapes (see example in the top left side of the map). Circles surrounding each point represent the largest buffer (1400-m radius).

Sampling design

We sampled small (<1 kg) terrestrial rodents within each site once a year, from April to September (including periods of both the dry and rainy seasons) in 2011, 2012, 2014 and 2016. In each year, we sampled the 12 sites following a random order to avoid potential confounding effects of temporal variations in resource availability and environmental conditions. In each site, we placed 120 Sherman traps in a grid of 90 x 110 m (distance between traps = 10 m). We located the grid in the center of each forest patch (avoiding tree-fall gaps). In continuous forest sites, the grid was located more than 1 km away from the nearest forest edge (i.e., the Lacantún river, Fig. 1). We baited each trap with a mixture of oats, sunflower seeds, and vanilla. In each site, we captured rodents for eight consecutive nights (960 trap-nights per site, 11,520 per field session, totaling 46,080 trap-nights). Animals were marked with gentian violet to account for recaptures within each year. This non-invasive short-term marking technique allows the identification of marked individuals for several months and has no adverse physiological effects on mammals (Silvy et al. 2005). We used the number of individuals captured as a proxy of abundance within each site. Ten species of small-sized rodents are reported for the area (Medellín and Equihua 1998); however, this study is only focused on the most common terrestrial species. We excluded from the analysis arboreal species (*Nyctomys sumichrasti*, *Ototylomys phyllotis* and *Tylomys nudicaudatus*). *Oryzomys* (=*Handleyomys*) species, were treated at the genus level because of inconsistent taxonomy in the region, and the non-invasive nature of this study (San-José et al. 2014).

Landscape metrics

We used a site-landscape approach (sensu Fahrig 2013), that is, response variables were recorded in the 12 forest sites, and landscape variables were measured in the surrounding landscape containing each site. We considered all sites as independent samples because they were separated from each other by at least 1.5 km (continuous forest sites were separated by at least 2.5 km), and small-sized rodents are known to have a very low vagility and are not likely to migrate between forest sites (McNab 1963, Maza et al. 1973). Independence also increased by measuring landscape predictors in non-overlapping landscape buffers (Eigenbrod et al. 2011). Note that the few landscapes that showed some spatial overlap were separated by large rivers, thus contributing to the independence between sites (Fig. 1). We used high resolution (10 m) satellite images from 2010 (SPOT 5) and 2016 (Sentinel 2A) – both sensors with similar radiometric characteristics (Hagolle et al. 2015) – to classify six different land-cover types using Spring 3.3 (Camara et al. 1996): old-growth forests, secondary forests, cattle pastures, annual crops (e.g., chili, corn), arboreal crops (e.g., rubber and palm plantations), and human settlements (e.g., houses, roads). Overall, classification accuracy was 80.0 percent in 2010 and 80.3 percent in 2016.

We then used Conefor software extensions (Saura and Torné 2009) to measure landscape metrics in 2010 and 2016. In particular, we measured two metrics of landscape composition (percentage of forest cover and matrix contrast), and two metrics of landscape configuration (number of forest patches and forest edge density). Forest cover included only old-growth forests, and matrix contrast (*sensu* Campbell et al. 2011) was the percentage of the matrix composed of open areas: cattle pastures, annual crops, and human settlements. Forest edge density was measured as the length of all old-growth forest edges divided by the total area of the landscape (m/ha; McGarigal et al. 2012). We selected these landscape predictors because: (1) rodents' abundance in the region seems to be related to landscape forest cover and matrix contrast (San-José et al. 2014); (2) forest fragmentation can shape population movements, migration dynamics and diversity patterns (Malcolm 1995, Bennett and Saunders 2010); and (3) edge density may affect resource availability and predation/competition interactions (Mendes et al. 2015).

Since the response of species to landscape structure can be scale-dependent (San-José et al. 2014, Smith et al. 2011, Galán-Acedo et al. 2018), we assessed each landscape metric within seven different-sized radii (200- to 1400-m radius, at 200-m intervals) from the center of each forest site to assess the scale of landscape effect (see below). The 1400-m radius was the largest radius until a minimum overlap between two buffers started to appear, thus avoiding dependence (i.e., pseudoreplication) problems in our analyses (Eigenbrod et al. 2011). To include continuous forest sites in regression models, we considered these sites as having 100 percent forest cover, 0 percent matrix contrast, no fragmentation (number of forest patches = 1), no edges (edge density = 0) and no isolation (mean inter-patch distance = 0).

Data analyses

We first used repeated measures models to test for differences between the first and last sampling year (Δ = 2016 value – 2010 value) in the value of each landscape metric at the largest scale (1400-m radius). We then used a similar statistical procedure to test for differences in the abundance of each rodent species among the four survey years (2011, 2012, 2014, and 2016). To identify the temporal changes in rodent abundance we summed up the data of all traps from each site and year and tested for variations (i.e., 4 survey years) in the abundance of each species through time within each site using Spearman correlations (i.e., correlation between abundance and time). The correlation coefficient of each species within each site was used as a measure of the average tendency of change in abundance, as it indicates whether a given rodent population is increasing ($r_s > 0$), decreasing ($r_s < 0$) or shows no trend ($r_s \sim 0$) through time in a given site. We then assessed the landscape drivers of these temporal changes in rodent abundance with generalized linear models. In particular, we related the obtained correlation coefficients in each site with the differences (Δ) between years (2016 - 2010) in each landscape metric. A positive Δ value indicates that a given metric is increasing through time in a given landscape, i.e., it shows a higher value in 2016 than in 2010, whereas a negative value indicates the opposite.

As we did not know *a priori* the landscape size that best predicts rodent responses to landscape patterns, we assessed the so-called "scale of effect" of each landscape metric following Jackson and Fahrig (2015). In brief, we used Spearman correlations to assess the association between each landscape metric (Δ values) and each response variable (changes in abundance) at each spatial scale (i.e., different-sized radii) to identify the scale that yields the strongest response-predictor relationship (i.e., the highest correlation coefficient; Table A1 in supplementary material). We then used a multimodel averaging approach (sensu Burnham and Anderson 2002) with generalized linear models to assess the effect of each landscape predictor (measured at the optimal scale; Table A1) on correlation coefficients with the 'glmulti' package (Calcagno and de Mazancourt 2010) for R version 3.3.3. To avoid multicollinearity problems in multiple models, we estimated the variance inflation factor (VIF) of each predictor using the 'car' package for R 3.3.3 (Fox and Weisberg 2011). VIF values for the number of forest patches (VIF = 13.0) and forest cover (VIF = 8.4) indicated collinearity between these two predictors (see Neter et al. 1996). Therefore, we excluded the former predictor from the analysis. For each response variable we constructed 8 models, which represent all combinations of three explanatory variables and the null model (which includes only the intercept). For each model, we calculated the Akaike's Information Criterion corrected for small samples (AICc). We ranked the models from the best (i.e., lowest AICc) to the worst (i.e., highest AICc). We then calculated the sum of Akaike weights ($\sum w_i$) of each landscape predictor, i.e., the sum of Akaike weights of the models in which each variable appeared. This metric represents the probability that each variable is within the true best model, and it was used to weight model-averaged parameter estimates (Burnham and Anderson 2002). To be conservative, we considered that the variation (Δ) in a given landscape attribute through time was an important explanatory variable for a given change in rodent abundance if the following three criteria were met: (1) it showed a high sum of Akaike weights; (2) the model-averaged unconditional variance was lower than the model-averaged parameter estimate (Burnham and Anderson 2002); and (3) the complete model showed a high percentage of explained deviance (i.e., high goodness-of-fit; Crawley 2007).

Results

Landscape structure showed important changes through time in each forest site (Fig. A1). For example, while some landscapes lost up to 10% of forest cover between 2010 and 2016, others actually showed an increase in forest cover of up to 40%. Thus, when averaged across all landscapes, we did not find significant differences in landscape metrics between the two years (Table 1). Yet, mean matrix contrast tended to increase over time, mostly due to the expansion of annual crops, such as corn.

Table 1. Landscape spatial structure surrounding 12 forest sites in 2010 and 2016 in the Lacandona rainforest, Mexico. Mean (± SD) values are indicated for a 1400-m radius landscape from the center of each forest site. Differences between years were evaluated with repeated measures models.

Landscape variable	2010	2016	*t (P)*
Landscape configuration			
Patch number (No)	17.3 ± 14.4	15.5 ± 12.0	-1.08 (0.30)
Edge density (m/ha)	58.9 ± 37.6	56.5 ± 37.0	-1.06 (0.31)
Landscape composition			
Forest cover (%)	57.8 ± 28.2	59.4 ± 26.4	1.13 (0.28)
Matrix contrast (%)	61.0 ± 37.0	64.2 ± 39.0	2.01 (0.07)

We recorded four species of small terrestrial rodents: *Heteromys desmarestianus* (Desmarest's Spiny Pocket Mouse), *Sigmodon toltecus* (Toltec Cotton Rat), *Peromyscus mexicanus* (Mexican Deer Mouse) and *Oryzomys* sp. (Rice Rat) in all years. In total, we collected 76 individuals in 2011, 82 in 2012, 49 in 2014 and 153 in 2016. The abundance of three species (*H. desmarestianus, Oryzomys* sp., and *P. mexicanus*) showed a significant temporal trend, but populations of *S. toltecus* remained stable through time (Table 2, Fig. A2 in supplementary material). In particular, the abundance of *H. desmarestianus* and *Oryzomys* sp. tended to increase through time, whereas the abundance of *P. mexicanus* tended to decrease.

Table 2. Mean (± SD) number of rodent individuals recorded in 12 forest sites in the Lacandona rainforest, Mexico. Differences among years were tested with repeated measures mixed models.

Species	2011	2012	2014	2016	*t (P)*
Oryzomys sp.	0.8 ± 1.1^{A}	2.8 ± 3.8^{A}	0.5 ± 1.2^{A}	5.1 ± 7.1^{B}	2.08 (0.045)
Heteromys desmarestianus	2.7 ± 3.3^{A}	2.1 ± 1.8^{A}	1.4 ± 1.2^{A}	5.3 ± 4.4^{B}	2.34 (0.026)
Sigmodon toltecus	1.4 ± 3.2	1.2 ± 2.3	1.4 ± 3.0	2.1 ± 2.6	0.86 (0.397)
Peromyscus mexicanus	1.4 ± 1.9^{A}	0.8 ± 1.5^{A}	0.8 ± 1.8^{A}	0.3 ± 0.9^{B}	-1.98 (0.049)

Significant differences between years are indicated with different letters.

Considering the scale of effect of each landscape variable on each response (Table A1), we found strong associations between temporal changes in landscape structure and changes in rodent abundance (36-50% of explained deviance), with each rodent species showing different responses to changes in each landscape metric (Fig. 2; Table 3). In particular, the abundance of *Oryzomys* sp. increased mainly in sites with decreasing forest edge density (Fig. 2; Table 3; Table A2 in supplementary material). Yet, the abundance of *H. desmarestianus* increased in sites surrounded by increasing matrix contrast. The abundance of *S. toltecus* mainly decreased in landscapes suffering a decrease in matrix contrast. Finally, the abundance of *P. mexicanus* increased in landscapes exposed to increasing matrix contrast and decreasing edge density (Table 3 and A2, Fig. 2).

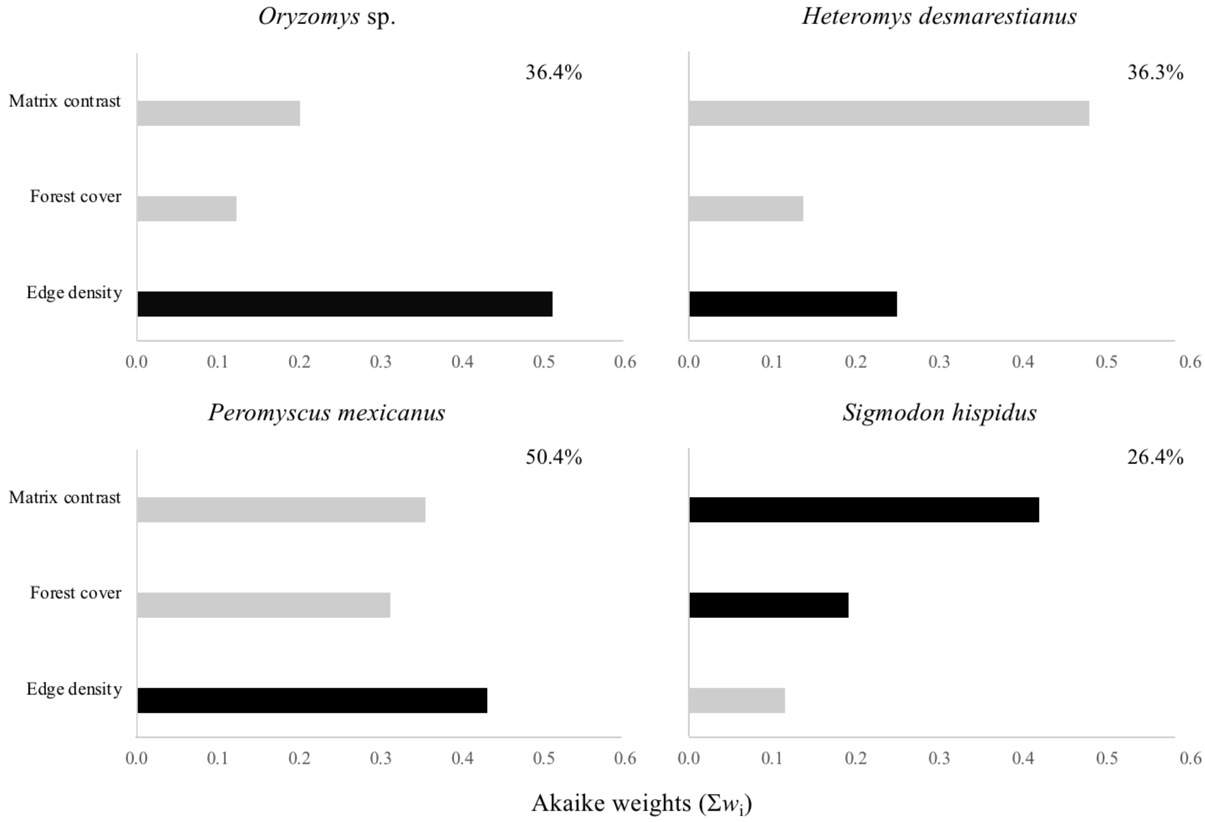


Figure 2. Effect of temporal (2016-2010) differences in landscape structure on temporal trends in rodent abundance in the Lacandona rainforest, Mexico. We show the sum of Akaike weights (Σwi) of each landscape predictor (bars). The sign (+/−) of parameter estimates are indicated with different colors: grey bars for positive responses, and black bars for negative responses (see averaged parameters and associated unconditional variances in Table 3). We also indicate values of pseudo-R2, i.e., the percentage of explained deviance by complete models. Each landscape metric was measured at the optimal scale (see Table A2 in supplementary material).

Table 3. Results of information-theoretic based model selection and multimodel inference for assessing the impact of the change in landscape metrics (considering the scale of effect; see scales in Table 4) on the changes in the abundance of four rodent species in the Lacandona rainforest, Mexico. We present model-averaged parameter estimates (β) and the unconditional variance (UV) for each landscape predictor. Note that all β estimates (i.e., slopes) are higher than their respective UV values, which suggests confidence in the estimation of β values (Burnham and Anderson 2002).

	Oryzomys sp.		*Heteromys desmarestianus*		*Peromyscus mexicanus*		*Sigmodon toltecus*	
Metrics	*β*	UV	*β*	UV	*β*	UV	*β*	UV
Edge density	-0.00795	0.00009	-0.00601	0.00019	-0.00767	0.00011	0.00031	0.00002
Matrix contrast	0.00602	0.00029	0.02830	0.00130	0.00620	0.00010	-0.01178	0.00030
Forest cover	0.00045	0.00002	0.00118	0.00004	0.01148	0.00045	-0.00834	0.00069

Discussion

To our knowledge, the present study is the first in assessing the patterns and potential landscape drivers of rodent populations using a longitudinal approach, covering several sampling years and reproductive cycles. With such an approach, we were able to demonstrate that the Lacandona rainforest – a relatively new agricultural frontier in southeastern Mexico (Meli et al. 2015) – is suffering a rapid process of land-use change that promotes high spatial variations in landscape structure. Such variations in landscape structure lead to species-specific changes in the abundance of small rodents. Although total rodent abundance was two times higher in 2016 than in 2011, the mean number of individuals in all sites was very low, probably because the region has not suffered a significant defaunation process (Garmendia et al. 2013), allowing a top-down control of rodent populations by natural predators (Dirzo et al. 2014, Bovendorp et al. 2018). However, as discussed below, if current annual deforestation rates continue in the region (-2.1% between 1990 and 2010; Courtier et al. 2012) we can expect significant changes in the abundance of small rodents in the near future, including the population increase of some species (winner species) and population decline (loser species) of others.

Our findings support previous studies on the contrasting responses of different rodent species to habitat disturbance (San-José et al. 2014). Whereas the abundance of *H. desmarestianus* and *Oryzomys* sp. increased through time in most sites, the abundance of *P. mexicanus* tended to decrease and populations of *S. toltecus* remained relatively stable through time. These population trends were strongly related to temporal changes in landscape structure in each site. For example, two out of four species (*H. desmarestianus* and *P. mexicanus*) increased their populations in forest sites that had experienced an increase in matrix contrast through time (i.e., higher percentage of open area in the matrix). As both species are forest specialists that mainly live in old-growth and secondary forests (Ceballos and Oliva 2005, Reid 2009), these patterns do not mean that they are benefited by increasing matrix contrast, but that individuals in landscapes with higher matrix contrast could be 'forced' to take refuge in the remaining forest patches, concentrating there. This ecological process has been demonstrated in other forest-specialist species, such as Australian tropical non-volant mammals (Laurance 1991) and howler monkeys (Arroyo-Rodríguez and Dias 2010). If this process is verified in future studies, these two species could be good candidates of 'loser' species (sensu Tabarelli et al. 2012), as it is well-known that forest-dependent species that avoid using the matrix are more prone to extinction in fragmented rainforests (Laurance 1991, 1994, Gascon et al. 1999, Veter et al. 2011, Carrara et al. 2015). This is not only related to resource scarcity in forest patches, but also to lower connectivity in landscapes with higher matrix contrast, which may promote population isolation and a limited gene flow (Bennett and Saunders 2010, Mech and Hallett 2001).

The abundance of three species (*Oryzomys* sp., *H. desmarestianus* and *P. mexicanus*) tended to increase in forest sites located in landscapes with decreasing forest edge density. This is consistent with Pardini (2004), who found a negative response of small terrestrial mammals to increasing forest edges in the Brazilian Atlantic forest. Pfeifer et al. (2017) also show that many forest-interior specialist species, including amphibians, reptiles, birds, and mammals, respond negatively to forest edges, reaching peak abundances only at sites farther than 200–400 m from sharp high-contrast forest edges. Such negative response can be related to both abiotic and biotic changes along forest edges. For example, forest temperature can increase at forest edges, especially in fragmented rainforests (Arroyo-Rodríguez et al. 2017), potentially making basic activity patterns, such as feeding and traveling, more energetically costly (Tuff et al. 2016). Also, predation pressures may be higher at forest edges, because these habitats are exposed to higher light incidence than forest interiors, making preys more easily located by predators at edges than interiors (e.g., Barbaro et al. 2014, and references therein). Whatever the proximate cause of these negative edge effects, these patterns support the hypothesis that *H. desmarestianus* and *P. mexicanus* may represent 'loser' species.

Besides forest-dependence and specialization, other species' ecological attributes and life history traits can help to explain the observed rodent responses to landscape structure. For example, extinction risk in human-modified landscapes has also been inversely related to reproductive rate, and directly associated with life span extension (Laurance 1991, Terborgh et al. 2001, Vetter et al. 2011). In this sense, both potentially 'loser' species (i.e., *H. desmarestianus* and *P. mexicanus*) have relatively lower reproductive rates and longer life expectancies, whereas the potentially 'winner' species (*Oryzomys* sp. and *S. toltecus*) have higher reproductive rates and lower life expectancies (Ceballos and Oliva 2005, Reid 2009). Additionally, *H. desmarestianus* feeds mainly on seeds and fruits, which could further increase its vulnerability to disturbance, compared with the other three species (all omnivores), as frugivory has been related with a higher sensitivity to habitat disturbance in fragmented landscapes (Laurance and Yensen 1991).

Species traits can also influence the scale of landscape effect, i.e., the landscape size that best predicts rodent responses to landscape structure (Jackson and Fahrig 2015). In particular, the scale of effect is expected to be higher in species with greater vagility, as they are expected to interact with its environment across larger spatial scales (Miguet et al. 2016). Here, the scale of effect varied from 200- to 1400-m radius, with *Oryzomys* sp. showing the lowest scale of effect, followed by *H. desmarestianus*, *S. toltecus* and *P. mexicanus* (Table A1). Following Miguet et al. (2016), this finding suggests that *Oryzomys* sp. may have lower vagility, which is reasonably expected for a generalist species that is able to find resources in both conserved and disturbed forests (Medellín and Equihua 1998). In other words, *Oryzomys* sp. probably does not need to move much to find enough resources, at least compared to *P. mexicanus*, which is a forest-specialist species, and probably need to move more frequently or larger distances to find adequate resources in the landscape. Unfortunately, we found no information on the ranging behavior or dispersal distances of these species, and thus, this represents an interesting avenue for future research.

Conclusions and conservation implications

The Lacandona rainforest is suffering a rapid process of land-use change, which is spatially variable (Fig. A1). Such spatial variations in landscape changes, however, did not result in a generalized increase in rodent abundance (i.e., 'rodentization', sensu Mendes 2014), but rather lead to species-specific responses to landscape structure. This can be related to the relatively short period of deforestation in the region (< 50 years ago), the relatively high amount of forest cover (~ 40%), and a highly heterogeneity matrix that includes different land covers, many of which can be used by small rodents as temporally or permanent habitat (Medellin 1994, Medellin and Equihua 1998). Whatever the cause of this pattern, it represents 'good news', as it suggests that the biotic interactions and ecological processes in which rodents are involved (e.g., seed dispersal, seed predation) have not suffered great alteration in the region. Yet, we cannot reject the hypothesis that populations of some rodent species will increase in the future, as the low values of final model-averaged parameter estimates (β estimates) suggest that the impact of landscape spatial changes on rodent population dynamics act at very low rates. In other words, it seems that the impact of landscape spatial changes on rodent communities will only be fully appreciated at the long-term.

In particular, if current land-use changes are maintained in the region, we can expect a population decline of forest specialist species (*P. mexicanus* and *H. desmarestianus*), and an increase in habitat generalist species (*S. toltecus* and *Oryzomys* sp.). *H. desmarestianus* showed an increase in abundance (not a decrease, as expected), but such increase seems to be 'forced' by increasing matrix contrast in the local landscape (see above). Regarding *S. toltecus*, their populations remained without significant changes, but given the tolerance of this species to human-induced disturbances (Medellin and Equihua 1998), they would probably benefit from future landscape disturbance.

Based on the empirical evidence available to date for this biodiversity hotspot (Medellín 1994, Medellín and Equihua 1998, San-José et al. 2014), preventing the expansion of open areas (e.g., cattle pastures and annual crops) in the region seems to be crucial for increasing landscape connectivity and resource availability for forest-dwelling rodent species, such as *P. mexicanus* and *H. desmarestianus*. Our findings also support the importance of preventing potential negative edge effects (Pardini 2004, Pfeifer et al. 2017), for example, by increasing forest cover (and thus, the amount of core areas) in the landscape. Although the percentage of forest cover showed a weaker effect than other landscape metrics, it showed a positive effect on both forest-specialist species, thus highlighting the importance of stopping forest loss and increasing forest cover through passive or active restoration.

References

Andresen, E., Arroyo-Rodríguez, V., Escobar, F. 2018. Tropical biodiversity: the roles of biotic interactions in its origin, maintenance, function and conservation. In: Dáttilo, W., Rico-Gray, V. (Eds.) Ecological networks in the tropics. Springer, New York, pp 1–13.

Arriaga, L., Espinoza, J., Aguilar, C., Martínez, E., Gómez, L., Loa, E. 2000. Regiones terrestres prioritarias de México. CONABIO, Mexico City.

Arroyo-Rodríguez, V, Dias, P.A.D. 2010. Effects of habitat fragmentation and disturbance on howler monkeys: a review. American Journal of Primatology 72: 1–16.

Arroyo-Rodríguez, V., Rojas, C., Saldaña-Vázquez, R.A., Stoner, K.E. 2016. Landscape composition is more important than landscape configuration for phyllostomid bat assemblages in a fragmented biodiversity hotspot. Biological Conservation 198: 84–92.

Arroyo-Rodríguez, V., Saldaña-Vázquez, R.A., Fahrig, L., Santos, B.A. 2017. Does forest fragmentation cause an increase in forest temperature? Ecological Research 32: 81–88.

Banks-Leite, C., Pardini, R., Tambosi, L.R., Pearse, W.D., Bueno, A.A., Bruscagin, R.T., Condez, T.H., Dixo, M., Igari, A.T., Martensen, A.C., Metzger, J.P. 2014. Using ecological thresholds to evaluate the costs and benefits of set-asides in a biodiversity hotspot. Science 345: 1041–1045.

Barbaro, L., Giffard, B., Charbonnier, Y., Van Halder, I., Brockerhoff, E.G. 2013. Bird functional diversity enhances insectivory at forest edges: a transcontinental experiment. Diversity and Distributions 20: 149–159.

Bennett, A.F., Saunders, D.A. 2010. Habitat fragmentation and landscape change. In: Sodhi, N.S., Ehrlich, P.R. (Eds) Conservation Biology for All. Oxford University Press, Oxford, pp 88–106.

Bovendorp, R.S., Brum, F.T., McCleery, R.A., Baiser, B., Loyola, R., Cianciaruso, M.V., Galetti, M. 2018. Defaunation and fragmentation erode small mammal diversity dimensions in tropical forests. Ecography 42: 23–35.

Burnham, K.P., Anderson, D.R. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Springer, New York.

Calcagno, V., de Mazancourt, C. 2010. Glmulti: An R package for easy automated model selection with (generalized) linear models. Journal of Statistical Software 34: 1–29.

Camara, G., Souza, R.C.M., Freitas, U.M., Garrido, J. 1996. SPRING: Integrating remote sensing and GIS by object-oriented data modelling. Computers & Graphics 20: 395–403.

Campbell, R.E., Harding, J.S., Ewers, R.M., Thorpe, S., Didham, R.K. 2011. Production land use alters edge response functions in remnant forest invertebrate communities. Ecological Applications 21: 3147–3161.

Carabias, J., de la Maza, J., Cadena, R. 2015. Conservación y desarrollo sustentable en la Selva Lacandona. 25 años de actividades y experiencias. Natura y Ecosistemas Mexicanos, Mexico City.

Carrara, E., Arroyo-Rodríguez, V., Vega-Rivera, J.H., Schondube, J.E., de Freitas, S.M., Fahrig, L. 2015. Impact of landscape composition and configuration on forest specialist and generalist bird species in the fragmented Lacandona rainforest, Mexico. Biological Conservaion 184: 117–126.

Ceballos, G., Oliva, G. 2005. Los mamíferos silvestres de México. CONABIO & Fondo de Cultura Económica, Mexico City.

Courtier, S., Núñez, J.M., Kolb, M. 2012. Measuring tropical deforestation with error margins: a method for REDD monitoring in south-eastern Mexico. In: Sudarshana, P. (Ed) Tropical forests. InTech, Shanghai, pp 269–296.

Crawley, M.J. 2007. The R Book. John Wiley & Sons Ltd., London.

Del Castillo, R.F. 2015. A conceptual framework to describe the ecology of fragmented landscapes and implications for conservation and management. Ecological Applications 25: 1447–1455.

Dirzo, R., Mendoza, E., Ortiz, P. 2007. Size-related differential seed predation in a heavily defaunated Neotropical rainforest. Biotropica 39: 355–362.

Dirzo, R., Young, H.S., Galetti, M., Ceballos, G., Isaac, N.J.B., Collen, B. 2014. Defaunation in the Anthropocene. Science 345: 401–406.

Eigenbrod, F., Hecnar, S.J., Fahrig, L. 2011. Sub-optimal study design has major impacts on landscape-scale inference. Biological Conservation 144: 298–305.

Fahrig, L. 2003. Effects of habitat fragmentation on biodiversity. Annual Review of Ecology, Evolution, and Systematics 34: 487–515.

Fahrig. L. 2013. Rethinking patch size and isolation effects: the habitat amount hypothesis. Journal of Biogeography 40: 1649–1663.

Fahrig, L., Baudry, J., Brotons, L., Burel, F.G., Crist, T.O., Fuller, R.J., Sirami, C., Siriwardena, G.M., Martin, J.L. 2011. Functional landscape heterogeneity and animal biodiversity in agricultural landscapes. Ecology Letters 14: 101–112.

Fahrig, L., Merriam, G. 1994. Conservation of fragmented populations. Conservation Biology 8: 50–59.

FAO. 2016. State of the World's Forests 2016. Forests and agriculture: land-use challenges and opportunities. FAO, Rome.

Fox, J., Weisberg, S. 2011. An {R} companion to applied regression, 2nd edn. SAGE publications Inc, Thousand Oaks.

Galán-Acedo, C., Arroyo-Rodríguez, V., Estrada, A., Ramos-Fernández, G. 2018. Drivers of the spatial scale that best predict primate responses to landscape structure. Ecography 41: 1–11.

Galetti, M., Bovendorp, R., Guevara, R. 2015. Defaunation of large mammals leads to an increase in seed predation in the Atlantic forests. Global Ecology and Conservation 3: 824–830.

Galetti, M., Dirzo, R. 2013. Ecological and evolutionary consequences of living in a defaunated world. Biological Conservation 163: 1–6.

Garmendia, A., Arroyo-Rodríguez, V., Estrada, A., Naranjo, E.J., Stoner, K.E. 2013. Landscape and patch attributes impacting medium- and large-sized terrestrial mammals in a fragmented rain forest. Journal of Tropical Ecology 29: 331–344.

Gascon, C., Lovejoy, T.E., Bierregaard, R.O.J., Malcolm, J.R., Stouffer, P.C., Vasconcelos, H.L., Laurance, W.F., Zimmerman, B., Tocher, M., Borges, S. 1999. Matrix habitat and species richness in tropical forest remnants. Biological Conservation 91: 223–229.

Gorresen, M., Willig, M.R. 2004. Landscape responses of bats to habitat fragmentation in Atlantic forest of Paraguay. Journal of Mammalogy 85: 688–697.

Hagolle, O., Sylvander, S., Huc, M., Claverie, M., Clesse, D., Dechoz, C., Lonjou, V., Poulain, V. 2015. SPOT-4 (Take 5): simulation of Sentinel-2 time series on 45 large sites. Remote Sensing 7: 12242–12264.

Howe, H.F., Davlantes, J. 2017. Waxing and waning of a cotton rat (*Sigmodon toltecus*) monoculture in early tropical restoration. Tropical Conservation Science 10: 1–11.

Instituto Nacional de Ecología. 2000. Programa de Manejo Reserva de la Biósfera Montes Azules. Secretaría de Medio Ambiente y Recursos Naturales, Mexico City.

Jackson, H.B., Fahrig, L. 2015. Are ecologists conducting research at the optimal scale? Global Ecology and Biogeography 24: 52–63.

Keesing, F., Young, T.P. 2014. Cascading consequences of the loss of large mammals in an African Savanna. BioScience 64: 487–495.

Krebs, C.J. 2013. Population fluctuations in rodents. The University of Chicago Press, Chicago.

Laurance, W.F. 1991. Ecological correlates of extinction proneness in Australian tropical rain forest mammals. Conservation Biology 5: 79–89.

Laurance, W.F. 1994. Rainforest fragmentation and the structure of small mammal communities in tropical Queensland. Biological Conservation 69: 23–32.

Malcolm, J.R. 1995. Forest structure and the abundance and diversity of Neotropical small mammals. In: Lowman, M.D., Nadkarni, N.M. (Ed.) Forest canopies. Academic Press, San Diego, pp 179–197.

Maza, B.G., French, N.R., Aschwanden, A.P. 1973. Home range dynamics in a population of heteromyid rodents. Journal of Mammalogy 54: 405–425.

McNab, B.K. 1963. Bioenergetics and the determination of home range size. American Naturalist 97: 133–140.

Mech, S.G., Hallett, J.G. 2001. Evaluating the effectiveness of corridors: a genetic approach. Conservation Biology 15: 467–474.

Medellín, R. 1994. Mammal diversity and conservation in the Selva Lacandona, Chiapas, Mexico. Conservation Biology 8: 780–799.

Medellín, R., Equihua, W. 1998. Mammal species richness and habitat use in rainforest and abandoned agricultural fields in Chiapas, Mexico. Journal of Applied Ecology 35: 13–23.

Meli, P., Hernández-Cárdenas, G., Carabias, J., Ruiz, L., Aguilar-Fernández, R., Toledo-Guzmán, A. 2015. La deforestación de los ecosistemas naturales en Marqués de Comillas. In: Carabias, J., de la Maza, J., Cadena, R. (Eds.) Conservación y desarrollo sustentable de la Selva Lacandona. Natura y Ecosistemas Mexicanos A.C., Mexico City, pp 247–259.

Melo, F., Arroyo-Rodríguez, V., Fahrig, L., Martínez-Ramos, M., Tabarelli, M. 2013. On the hope for biodiversity-friendly tropical landscapes. Trends Ecology and Evolution 28: 462–468.

Mendes, C. 2014. Patch size, shape and edge distance influences seed predation in a keystone palm in tropical rainforests. MS Thesis, Universidade Estadual Paulista, Instituto de Biociencias de Rio Claro, Rio Claro.

Mendes, C., Ribeiro, M.C., Galetti, M. 2015. Patch size, shape and edge distance influence seed predation on a palm species in the Atlantic forest. Ecography 38: 1–11.

Neter, J., Kutner, M.H., Nachtshein, C.J., Wasserman. 1996. Applied Linear Statistical Models, 4th edn. McGraw-Hill/Irwin, New York.

Pardini, R. 2004. Effects of forest fragmentation on small mammals in an Atlantic Forest landscape. Biodiversity and Conservation 13: 2567–2586.

Pardini, R., Bueno, A.A., Gardner, T.A., Prado, P.I., Metzger, J.P. 2010. Beyond the fragmentation threshold hypothesis: regime shifts in biodiversity across fragmented landscapes. PLoS ONE 5: e13666.

Pfeifer, M., Lefebvre, V., Peres, C.A., Banks-Leite, C., Wearn, O.R., Marsh, C.J., Butchart, H.M., Arroyo-Rodríguez, V., Balow, J., *et al*. 2017. Creation of forest edges has a global impact on forest vertebrates. Nature 551: 187–191.

Reid, F.A. 2009. A field guide to the mammals of Central America & Southeast Mexico. Oxford University Press, New York.

Rosin, C., Poulsen, J.R. 2016. Hunting-induced defaunation drives increased seed predation and decreased seedling establishment of commercially important tree species in an Afrotropical forest. Forest Ecology and Management 382: 206–213.

San-José, M., Arroyo-Rodríguez, V., Sánchez-Cordero, V. 2014. Association between small rodents and forest patch and landscape structure in the fragmented Lacandona rainforest, Mexico. Tropical Conservation Science 7: 403–422.

Saura, S., Torné, J. 2009. Conefor Sensinode 2.2: a software package for quantifying the importance of habitat patches for landscape connectivity. Environmental Modelling & Software 24: 135–139.

Silvy, N.J., López, R.R., Peterson, M.J. 2005. Wildlife marking techniques. In: Braun, E.E. (Ed.) Research and management techniques for wildlife and habitats. The Wildlife Society Inc., Bethesda pp 339–376.

Smith, A.C., Fahrig, L., Francis, C.M. 2011. Landscape size affects the relative importance of habitat amount, habitat fragmentation, and matrix quality on forest birds. Ecography 34: 103–113.

Tabarelli, M., Peres, C.A., Melo, F.P.L. 2012. The 'few winners and many losers' paradigm revisited: emerging prospects for tropical forest biodiversity. Biological Conservation 155: 136–140.

Terborgh, J., López, L., Nuñez, P., Rao, M., Shahabuddin, G., Orihuela, G., Riveros, M., Ascanio, R., Adler, G.H., Lambert, T.D., Balbas, L. 2001. Ecological meltdown in predator-free forest fragments. Science 294: 1923–1926.

Trujano-Álvarez, A.L., Álvarez-Castañeda, S.T. 2010. *Peromyscus mexicanus* (Rodentia: Cricetidae). Mammalian Species 42: 111–118.

Tuff, K.T., Tuff, T., Davies, K.F. 2016. A framework for integrating thermal biology into fragmentation research. Ecology Letters 19: 361–374.

Vetter, D., Hansbauer, M.M., Végvári, Z., Storch, I. 2011. Predictors of forest fragmentation sensitivity in Neotropical vertebrates: a quantitative review. Ecography 34: 1–8.

Wolff, P.W., Sherman, P.W. 2007. Rodent societies: an ecological & evolutionary perspective. The University of Chicago Press, Chicago.

Young, H.S., McCauley, D.J., Dirzo, R., Goheen, J.R., Agwanda, B., Brook, C., Otarola-Castillo, E., Ferguson, A.W., Kinyua, S.N. McDonough, M.M., Palmer, T.M., Pringle, R.M., Young, T.P., Helgen, K.M. 2015. Context-dependent effects of large-wildlife declines on small-mammal communities in central Kenya. Ecological Applications 25: 348–360.

Supplementary information

Table A1. Association (i.e., correlation coefficients, *r*-Spearman) between the temporal changes (2016-2010) in landscape structure and temporal changes in abundance of four small rodent species. Changes in landscape structure were measured considering seven different-sized radii to identify the landscape size (radius) at which the strongest association between each response variable and each predictor was observed (i.e., the scale of landscape effect, in bold).

Landscape predictor/scale	***Oryzomys* sp.**	***Heteromys desmarestianus***	***Sigmodon toltecus***	***Peromyscus mexicanus***
Δ Forest cover				
1400	0.085	0.108	**-0.470**	**0.598**
1200	0.134	0.045	-0.394	0.511
1000	0.138	0.047	-0.237	0.387
800	0.006	0.080	-0.127	0.308
600	-0.081	0.165	0.018	0.274
400	0.216	0.263	0.213	0.242
200	**0.252**	**0.389**	0.345	0.214
Δ Matrix contrast				
1400	-0.201	-0.001	-0.344	0.462
1200	-0.056	-0.029	-0.497	0.565
1000	0.011	-0.087	-0.535	0.518
800	0.006	0.062	-0.526	0.601
600	-0.321	0.101	**-0.568**	**0.612**
400	**0.400**	**0.542**	0.323	0.374
200	0.109	0.383	0.319	0.236
Δ Number of patches				
1400	-0.240	-0.334	-0.124	-0.538
1200	-0.100	-0.225	0.112	-0.501
1000	-0.195	-0.310	0.006	-0.374
800	-0.260	-0.382	**-0.414**	-0.261
600	-0.149	-0.417	-0.003	**-0.608**
400	**-0.388**	**-0.418**	-0.260	-0.376
200	0.057	0.302	-0.048	0.178
Δ Edge density				
1400	-0.020	-0.317	0.208	-0.584
1200	-0.197	**-0.400**	0.176	**-0.609**
1000	-0.404	-0.343	0.134	-0.544
800	-0.420	-0.182	0.224	-0.459
600	-0.300	-0.375	0.071	-0.539
400	**-0.555**	-0.224	**0.248**	-0.583
200	-0.127	-0.380	-0.177	-0.235

Table A2. Additive models assessing the effects of changes in landscape spatial structure (i.e., percentage of forest cover, percentage of matrix contrast and edge density) between 2016 and 2011, on temporal changes in abundance of four small rodent species in the Lacandona rainforest, Mexico.

Model			AICc	ΔAICc	w_i	% deviance explained	df
Ab_Oryzomys	~	1 + Edge_density	23.43	0.00	0.41	30.26	10
Ab_Oryzomys	~	1	24.17	0.75	0.28	0.00	11
Ab_Oryzomys	~	1 + Matrix_contrast	25.74	2.32	0.13	8.46	10
Ab_Oryzomys	~	1 + Forest_cover	27.05	3.63	0.07	2.46	10
Ab_Oryzomys	~	1 + Matrix_contrast + Edge_density	27.41	3.98	0.06	31.00	9
Ab_Oryzomys	~	1 + Forest_cover + Edge_density	28.08	4.65	0.04	33.16	9
Ab_Oryzomys	~	1 + Forest_cover + Matrix_contrast	30.44	7.01	0.01	8.46	9
Ab_Oryzomys	~	1+ Forest_cover + Matrix_contrast + Edge_density	33.16	9.74	0.00	36.43	8
Ab_Heteromys	~	1 + Matrix_contrast	28.82	0.00	0.38	31.18	10
Ab_Heteromys	~	1	29.64	0.82	0.25	0.00	11
Ab_Heteromys	~	1 + Edge_density	30.46	1.64	0.17	21.10	10
Ab_Heteromys	~	1 + Forest_cover	32.01	3.19	0.08	10.22	10
Ab_Heteromys	~	1 + Matrix_contrast + Edge_density	32.63	3.80	0.06	36.21	9
Ab_Heteromys	~	1 + Forest_cover + Matrix_contrast	33.53	4.71	0.04	31.20	9
Ab_Heteromys	~	1 + Forest_cover + Edge_density	34.78	5.95	0.02	23.71	9
Ab_Heteromys	~	1+ Forest_cover + Matrix_contrast + Edge_density	38.90	10.08	0.00	36.25	8
Ab_Peromyscus	~	1 + Edge_density	13.13	0.00	0.28	37.45	10
Ab_Peromyscus	~	1 + Matrix_contrast	13.28	0.15	0.26	36.65	10
Ab_Peromyscus	~	1 + Forest_cover	14.12	0.99	0.17	32.06	10
Ab_Peromyscus	~	1	15.09	1.96	0.10	0.00	11
Ab_Peromyscus	~	1 + Forest_cover + Edge_density	15.23	2.10	0.10	49.69	9
Ab_Peromyscus	~	1 + Matrix_contrast + Edge_density	16.47	3.34	0.05	44.21	9
Ab_Peromyscus	~	1 + Forest_cover + Matrix_contrast	16.93	3.80	0.04	42.02	9
Ab_Peromyscus	~	1+ Forest_cover + Matrix_contrast + Edge_density	21.35	8.23	0.00	50.36	8
Ab_Sigmodon	~	1	28.11	0.00	0.36	0.00	11
Ab_Sigmodon	~	1 + Matrix_contrast	28.17	0.06	0.35	25.96	10
Ab_Sigmodon	~	1 + Forest_cover	29.97	1.86	0.14	13.96	10
Ab_Sigmodon	~	1 + Edge_density	31.47	3.37	0.07	2.47	10
Ab_Sigmodon	~	1 + Forest_cover + Matrix_contrast	32.82	4.71	0.03	26.33	9
Ab_Sigmodon	~	1 + Matrix_contrast + Edge_density	32.88	4.77	0.03	25.97	9
Ab_Sigmodon	~	1 + Forest_cover + Edge_density	34.61	6.50	0.01	14.52	9
Ab_Sigmodon	~	1+ Forest_cover + Matrix_contrast + Edge_density	39.09	10.98	0.00	26.44	8

Figure A1 Temporal differences (2016-2010) in landscape structure measured in landscapes of 1400-m radius surrounding nine forest patches in the Lacandona rainforest, Mexico. Changes between years are indicated in percentage [i.e., (value in 2016 – value in 2010)*100/value in 2010]. Positive values indicate that a given landscape variable increased through time, whereas a negative value indicates the opposite. Site numbers in Y-axis correspond to those shown in Fig. 1 from the main text.

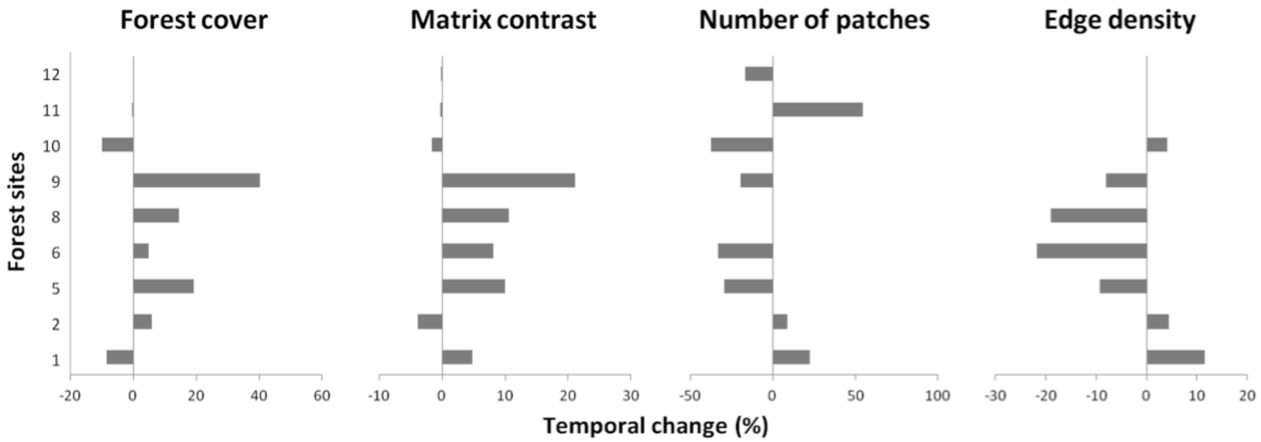
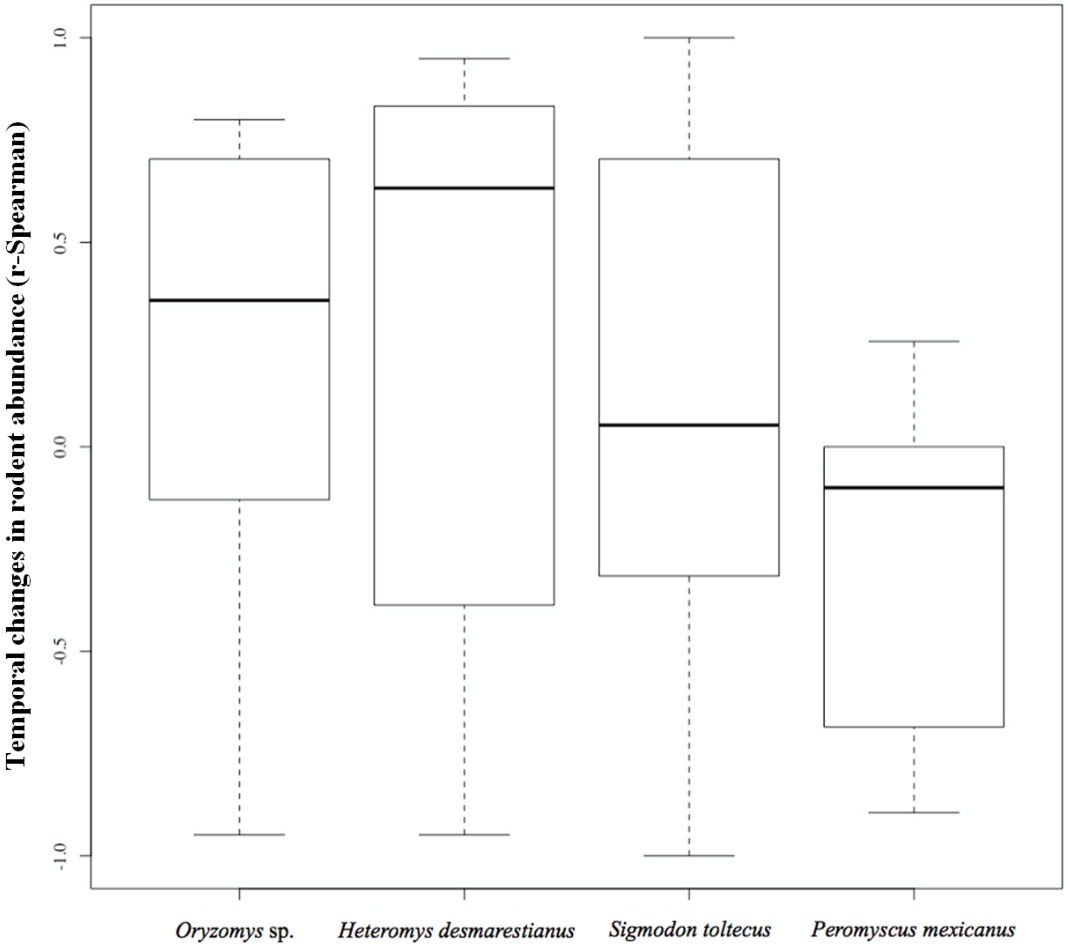


Figure A2. Temporal changes in the abundance of four rodent species in the Lacandona rainforest, Mexico. Temporal trends within each of the 12 study forest sites were assessed with Spearman correlations. In particular, we related the abundance of each species within each site to time (*i.e.*, four survey years, 2011, 2012, 2014 and 2016). Boxplots show median (central line), 25th and 75th percentiles (box), and outliers of correlation coefficients.



Capítulo 4.

Linking changes in landscape structure to population changes of an endangered primate

Norma P. Arce-Peña, Víctor Arroyo Rodríguez, Pedro A.D. Dias, Iván Franch Pardo, Ellen Andresen

Arce-Peña, NP, Arroyo-Rodríguez, V, Dias, PAD, Franch-Pardo, I., Andresen, E. 2019. Linking changes in landscape structure to population changes of an endangered primate. Landscape Ecology 34: 2687-2701.

Abstract

Context: Non-human primates are among the most threatened mammals on Earth. Although some species, such as howler monkeys, are thought to be resistant to initial phases of habitat disturbance, the lack of longitudinal studies prevents determining if this holds over time.

Objectives: We assessed temporal changes in landscape structure in the Lacandona rainforest, Mexico, and how these changes relate to population trends of black howler monkeys (*Alouatta pigra*).

Methods: We surveyed primates in 22 forest sites in 2011 and 2017, and related temporal changes in primate abundance and immature-to-female ratio with changes in the spatial structure of local landscapes (forest cover, matrix openness, number of forest patches, and forest edge density) using a multi-scale approach.

Results: Landscape changes occurring over a 6-year period were strongly associated with temporal changes in population parameters. Primate abundance increased as forest cover increased. Both primate abundance and immature-to-female ratio increased in sites located in landscapes where the number of patches increased over time, but where the proportion of open matrix decreased. Edge density showed a negative effect on immature-to-female ratio.

Conclusions: This endangered primate might not be as tolerant to landscape disturbance as generally thought. Allowing forest patches to increase in number and/or size through active or passive restoration (reverse fragmentation) and preventing forest loss and an increase in matrix openness are key management strategies to preserve howler monkeys in this biodiversity hotspot.

Keywords: Habitat loss, Habitat fragmentation, Human-modified landscape, Scale of effect, Tropical rainforest

Introduction

Deforestation of tropical forests represents one of the biggest threats to biodiversity (Gibson et al. 2011). Tropical forests are being rapidly converted to human modified landscapes, comprised of patches of native ecosystems surrounded by a matrix of anthropogenic land-cover types, such as crops, secondary forests and human settlements (Melo et al. 2013). Depending on the presence of different land-cover types and their proportions (i.e., landscape composition) as well as their spatial distribution and physiognomy (i.e., landscape configuration), landscapes can have a highly heterogeneous spatial structure, with variable impacts on wildlife (Fahrig et al. 2011). Whereas most species are negatively affected by the loss of forest cover, species' responses to other landscape attributes are highly variable (Fahrig 2003, 2017, Galán-Acedo et al. 2019a).

Human-modified landscapes are not only heterogeneous in their spatial dimension, but also temporally, as forest patches can increase or decrease in size, or change into another vegetation type (del Castillo 2015). However, few studies in anthropogenic landscapes have considered this temporal dynamism, which requires using longitudinal and multi-scale approaches (Ewers et al. 2013, Fahrig 2013). Longitudinal studies encompassing larger time periods are important for identifying lagged species' responses to changes in land-use and landscape structure (Metzger et al. 2009, Hanski 2013), particularly in the case of long-lived taxa, such as primates.

Primates play important ecological functions in the ecosystems they inhabit (da Silva et al. 2015, Andresen et al. 2018), but they are also among the most threatened groups of animals globally, mainly due to habitat loss, hunting and emergent diseases (Estrada et al. 2017). Several studies have assessed the importance of spatial characteristics of the habitat in determining primate abundance and distribution. These studies have found that both site-level variables (e.g., size, shape and isolation of forest patches; Anzures-Dadda and Manson 2007, Arroyo-Rodríguez et al. 2013, Benchimol and Peres 2013b, Puig-Lagunes et al. 2016), and landscape-level variables (e.g., forest cover, level of fragmentation, mean distance among patches and matrix quality; Arroyo-Rodríguez et al. 2013, Benchimol and Peres 2013b, da Silva et al. 2015, Galán-Acedo et al. 2019a), can affect the presence and/or abundance of primates. However, as most studies have been carried out at single temporal and spatial scales, additional assessments of primates' responses to spatial changes through time are needed to design effective long-term conservation strategies (Chapman et al. 2018, Galán-Acedo et al. 2019a).

Southern Mexico represents the northernmost distribution limit of Neotropical primates and is inhabited by three species: *Alouatta pigra, A. palliata and Ateles geoffroyi* (Estrada and Coates-Estrada 1996). Among these species, the black howler monkey (*A. pigra*) has the most restricted distribution (Horwich and Johnson 1986). Throughout the geographic range of this primate, rainforests have been degraded, fragmented and converted into agricultural lands, threatening their populations (Estrada et al. 2002). It has been suggested that all howler monkeys (*Alouatta* spp.) are relatively resistant to the initial phases of habitat disturbance, due to their flexible diet and small area requirements (Silver et al. 1998, Kowalewski and Zunino 1999, Rangel-Negrín et al. 2014). However, they can be negatively affected by ongoing habitat loss and degradation, potentially becoming locally or regionally extinct in the long run (e.g., Van Belle and Estrada 2005, Dias et al. 2015, Puig-Lagunes et al. 2016). Potential negative effects of habitat disturbance on black howler monkeys include altered dispersal and reproductive patterns, and increased endogamy, stress levels, disease incidence and mortality rates (Arroyo-Rodríguez and Dias 2010).

Although longitudinal studies on primate responses to habitat changes—and in particular for howler monkeys—are scarce, they are becoming more frequent. One patch-scale study of *Alouatta caraya* in northern Argentina used a longitudinal approach (1984–1995) and concluded that these primates were resilient to deforestation (Kowalewski and Zunino 1999). Similarly, Cristóbal-Azkarate et al. (2017) showed that between 2000 and 2011 there was an increase in the number of individuals of *A. palliata* in forest patches at Los Tuxtlas, Mexico. However, a 7-year study of *A. pigra* in Campeche, Mexico, showed that population growth and infant survival were negatively related to habitat disturbance (Dias et al. 2015). Yet, to our knowledge, no study to date has linked the temporal changes in landscape-scale spatial patterns to changes in population parameters of these primates. As primates in general (Galán-Acedo et al. 2019a, b) and howler monkeys in particular (e.g., Asensio et al. 2009, Pozo-Montuy et al. 2013) can travel in and out of habitat patches, they may be more strongly affected by the spatial structure of surrounding landscapes than by the characteristics of individual patches (see Fahrig 2013). Therefore, additional longitudinal landscape-scale studies are needed to better understand the impact of land-use change on this forest-specialist species.

Here, we present the first longitudinal assessment of the effects of landscape changes on black howler monkeys in the Lacandona rainforest, a biodiversity hotspot that maintains the highest mammal biodiversity in Mexico (Medellín 1994). Despite its great ecological importance, the region has undergone an intense and continuous process of land-use change, with high deforestation and degradation rates throughout the last three decades, mainly due to agriculture (Carabias et al. 2015). In a period of 6 years we quantified structural landscape changes in terms of both its composition (i.e., forest cover and matrix openness) and configuration (i.e., number of forest patches and edge density). We then related these changes to those recorded in two important black howler monkey population parameters (i.e., number of individuals and immature-to-female ratio). Due to the relatively recent history of deforestation in the region, we expected to find high variability in the change of all landscape variables, as well as in the change of population parameters among study sites. We expected to find a positive effect of forest cover on both population parameters because this landscape metric is a proxy of resource availability and landscape connectivity. Number of patches (fragmentation level) and forest edge density are also predicted to have positive effects on both population parameters because these two metrics are negatively related to mean patch isolation distance (Fahrig 2003, 2017), and can therefore favor inter-patch animal movements and food availability through landscape supplementation dynamics (Dunning et al. 1992, Asensio et al. 2009). Following a similar rationale, we expected to find a negative impact of an increase in the proportion of the matrix covered by open (i.e., treeless) land uses because such increase is expected to limit landscape connectivity and resource availability for arboreal primates (Galán-Acedo et al. 2019a, b).

Methods

Compliance with ethical standards

This research is based on observational data. It adhered to national and international guidelines and was conducted in accordance with the legal requirements of the National Autonomous University of Mexico (UNAM), and the country of Mexico (NOM-059: SEMARNAT 2010). We were granted access to all study sites by landowners and authorities.

Study area

The Lacandona rainforest, located in the northeast of the Mexican state of Chiapas (16º 05'N, 90º 25'W; Fig. 1), has a warm-humid climate, with average temperatures ranging from 24 to 26 ºC and annual mean rainfall ranging from 2,500 to 3,500 mm (Instituto Nacional de Ecología 2000). The region, originally covered by old-growth tropical rainforest, has a high biodiversity and is considered of high conservation priority in Mexico (Arriaga et al. 2000). However, the area is highly threatened by anthropic pressures, such as land-use change and illegal extraction of fauna and flora (Carabias et al. 2015). To protect its biodiversity, the Montes Azules Biosphere Reserve was established in the northern part of the region, encompassing 331,200 ha of continuous tropical rainforest (Instituto Nacional de Ecología 2000). However, south from this reserve, the Marqués de Comillas Region comprises 203,999 ha of anthropic lands, where different-sized forest patches are surrounded by a matrix of agricultural lands, successional vegetation and human settlements. We conducted this study in 22 forest sites located at similar altitude (1-200 m a.s.l.): 19 forest patches (3-92 ha) in Marqués de Comillas and three continuous forest sites inside the biosphere reserve (Fig. 1).

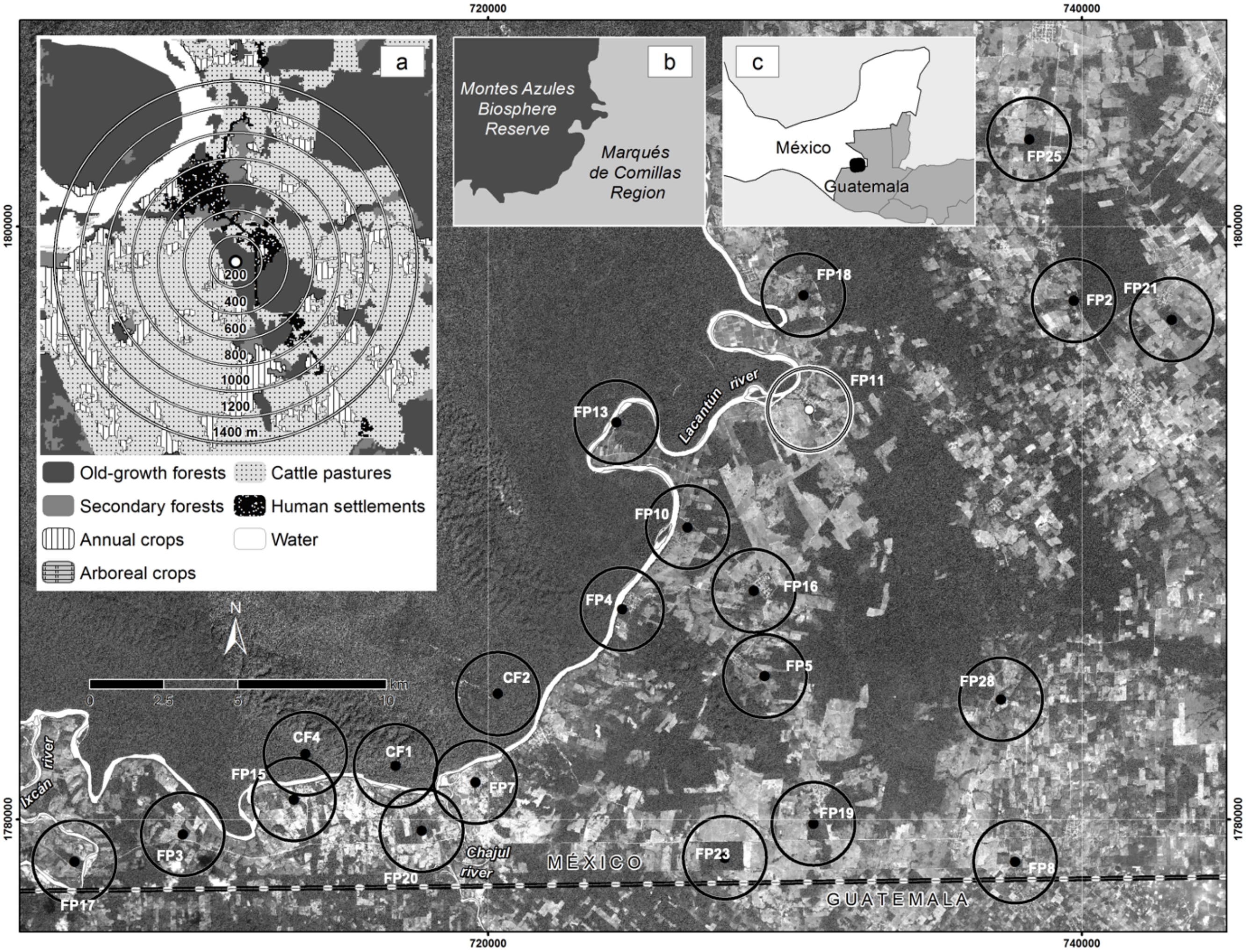


Figure 1. Location of the 22 forest sites in the Lacandona rainforest, Mexico. Points represent the center of each site. From the center of each site we estimated the spatial structure of seven different-sized landscapes. Circles surrounding each point represent the largest buffer, i.e. 1400-m radius. (a) Close-up in white point, representing the land-cover classification used (i.e. old-growth forests, secondary forests, annual crops, arboreal crops, cattle pastures, human settlements and water) and the different-sized landscapes surrounding each site (radii of 200 m to 1,400 m, at 200-m

intervals, from the center of each forest site). (b) Schematic map, showing the Montes Azules Biosphere Reserve, and the Marqués de Comillas region. (c) Location map.

Study species

The black howler monkey (*Alouatta pigra*) has a restricted distribution, being endemic to Mexico, Belize and Guatemala. It mainly inhabits primary tropical forests but can also be found in disturbed forests (Arroyo-Rodríguez et al. 2013; Dias et al. 2015). Its diet is flexible (from highly folivorous to highly frugivorous, depending on food availability; Dias and Rangel-Negrín 2015). Group sizes range from 2 to 12 individuals (Crockett and Eisenberg 1987; Van Belle and Estrada 2008). According to the IUCN's Red List and Mexico's legislation, the species is considered Endangered, with declining populations (SEMARNAT 2010; Marsh et al. 2008).

Landscape metrics

We used a patch-landscape approach (*sensu* Fahrig 2013), in which we measured response variables in the 22 forest sites, whereas the explanatory variables were measured in the local landscapes containing each site. Given a home range size for black howler monkeys of 6.3 ± 1.1 ha (mean ± SD) and a daily ranging distance of 393 ± 74 m (Fortes et al. 2015), we considered sites as independent, as forest patches were separated by more than 1.5 km and continuous forest sites by more than 2.5 km. We used high resolution (10 m) satellite images from 2010 (SPOT 5) and 2016 (Sentinel 2 A), produced by sensors with comparable radiometric features (Hagolle et al. 2015). Using Spring 3.3 (Camara et al. 1996), we identified six land-cover types: old-growth forest, secondary forest, cattle pasture, annual crop (e.g. chili pepper, corn), arboreal crop (e.g. rubber, oil palm), and human settlement (e.g. houses, roads) (see Step 1, Fig. A1). Following the map validation procedure proposed by Olofsson et al. (2014), we obtained a classification accuracy of 80.0% in 2010 and 80.3% in 2016, with inaccuracies mainly caused by the differentiation between annual crops and pastures. As these two land cover types were pooled in our analyses, such inaccuracies did not affect our results.

We characterized landscape structure using five variables: three configurational variables (number of forest patches, edge density and mean inter-patch distance) and two compositional variables (percentage of forest cover and matrix openness in the landscapes containing each patch) (Step 2, Fig. A1). We tested these landscape predictors because they can have strong effects on primate populations

(Galán-Acedo et al. 2019a), especially on black howler monkey abundance in the region (Arroyo-Rodríguez et al. 2013). The description and ecological justification of the selected landscape metrics are presented in Table 1. As species' responses to landscape structure may be scale-dependent (Jackson and Fahrig 2015), we assessed the effect of each landscape metric in seven different-sized landscapes containing each forest site (radii from 200 m to 1,400 m, at 200-m intervals, from the center of each site), to determine the scale of effect (see below). Except in two cases, the 1,400 m radius was the largest radius that still avoided spatial overlap between the buffers of two sites, thus increasing independence between sample units (Eigenbrod et al. 2011). The smaller scales (200- and 400-m radius) were included following Jackson & Fahrig (2015), who recommend that to avoid measuring landscape structure at suboptimal scales, the scales at which landscape variables are measured should range widely, from the size of a single territory to well above the average dispersal distance. As stated above, the home range size of howler monkeys averages 6.3 ha, but larger sizes have been reported (reviewed by Galán-Acedo et al. 2019c). Therefore, the 200-m radius (12.6 ha) can represent the territory size of a black howler monkeys' group. Although relatively small, this landscape size was large enough to show a high variation in all explanatory variables (Supplementary Material, Table A1), which is needed to make accurate landscape-scale inferences (Eigenbrod et al. 2011). In eight fragmented sites close to the river, some buffers included a portion of the biosphere reserve, whereas buffers of two continuous forest sites presented some overlap with the fragmented area (Fig. 1). In all these cases, as the river represents a barrier for howler monkey populations, we excluded the spatial information from the other side of the river, i.e. for the forest patches whose buffers included the continuous forest, we excluded the area covered by continuous forest from the spatial characterization of the patches' matrix, and vice versa for the two continuous forest sites whose buffers included the fragmented region.

Table 1. Definition and ecological justification of the landscape metrics assessed in the study.

Landscape metric	Metric description	Ecological interpretation	Refs.^{a}
Forest cover	Percentage of landscape area covered by old-growth forest cover	A proxy of landscape-scale habitat amount, resource availability and landscape connectivity	1,2,3
Matrix openness	Percentage of the matrix composed of treeless areas (i.e. cattle pastures, annual crops and human settlements)	Open-area matrices increase negative edge effects and limit inter-patch movements. These matrices also limit landscape supplementation dynamics	2,3,4
Number of patches	Number of forest patches in the landscape	Positively related to landscape connectedness and the number of subpopulations in the landscape. Also, landscape supplementation dynamics May be enhanced in landscapes with more patches	2,5
Edge density	Length of all old-growth forest edges divided by total landscape area (m/ha)	Positively related to landscape connectedness and availability of pioneer tree species (which can be important food resources for howler monkeys, such as *Cecropia obtusifolia*). But it can also have negative impacts on primates through negative edge effects, such as an increased mortality of emergent trees at forest edges	2,5,6
Inter-patch distance	Average value (m) of the shortest edge-to-edge distance between all possible pairs of patches in the landscape	Inversely related to landscape connectedness, with potential negative effects on inter-patch animal movements	2,6

^{a}References: 1. Fahrig (2003), 2. McGarigal et al. (2012), 3. Fahrig (2017), 4. Galán-Acedo et al (2019a), 5. Dunning et al. (1992), 6. Bennet and Saunders (2010).

Primate surveys

We conducted surveys between April and October in 2011 and 2017, using the same methods applied in previous research on the species (e.g. Rosales-Meda et al. 2007, Arroyo-Rodríguez et al. 2013). Briefly, two people walked slowly (1 km/hr) inside and around each forest site, starting at 6:00 h, looking for groups and locating them by their long-distance vocalizations. Survey duration in each site varied according to area: 2 days for 3-4 hours each day in small patches (<10 ha), 3 days for 5-6 hours daily in medium-sized patches (10-50 ha), 4 days for 7-8 hours daily in larger patches (>50 ha), and 5 days for 9-10 hours daily in continuous forest sites. Surveys in the continuous forest sites were restricted to an area of approximately 100 ha to standardize sampling area. Once we established visual contact with howler monkeys, we registered the geographical position of the group with a GPS and counted individuals, classifying each one as adult male, adult female, juvenile or infant (Rosales-Meda et al. 2007). We then obtained primate abundance from the total number of individuals observed during the surveys and calculated the immature-to-female ratio as the number of infants and juveniles divided by the number of adult females. The ratio of immatures to females is a measure of successful reproduction commonly used in howler monkey studies (e.g. Arroyo-Rodríguez et al. 2008, Cristóbal-Azkarate et al. 2005); yet, it is not only affected by female reproductive output and immature survival, but also by variations in the abundance of adult females.

Data analyses

All analyses were carried out using R version 3.5.1 (R Core Team 2018). We first tested for differences in population parameters between continuous forest sites and forest patches with t-Student tests. We then obtained the differences between years (2016 values – 2010 values) for each landscape metric (forest cover, matrix openness, number of patches, edge density and mean inter-patch distance; Table A1) and used generalized linear mixed models to evaluate such differences at the largest scale (1,400-m radius landscape; Fig. A2). We used the same analysis for assessing differences in each primate population parameter (primate abundance and immature-to-female ratio) between years (2011–2017). For percentage of forest cover and matrix openness we selected a binomial distribution with a logit link-function. All other variables were log-transformed to normalize their residuals and analyzed with a normal error distribution and identity link-function. We assessed model fit with a Shapiro-Wilk test on model residuals. For all models, we used year as a fixed factor, and site ID as a random factor. To assess whether complete models (i.e. with both fixed and random factors) were a better fit for dependent variables than solely the random factors, we used likelihood ratio tests. In these tests we compared null models including only the random factor with the complete models (Pinheiro and Bates 2000). We evaluated the change in landscape drivers (landscape Δs = 2016 values – 2010 values) and the changes in howler monkeys' demographic attributes (primate Δs = 2017 values – 2011 values) (Steps 3-4, Fig. A1). Positive delta values (Δ) indicate that a variable increased through time, i.e. it showed a higher value in 2017/2016 than in 2011/2010, whereas negative values indicate the opposite.

As we did not know *a priori* the landscape size that better predicted primate population responses to changes in landscape structure, we followed Jackson and Fahrig (2015) to determine the scale of effect of each landscape metric change (Step 5, Fig. A1). We used generalized linear models to quantify the association between the change in each landscape metric (landscape Δs) and the change in each demographic attribute (primate Δs). We obtained the AIC (Akaike's Information Criterion) and the percentage of explained deviance of each univariate model to identify the spatial scale (i.e. length of the radius of the circular landscape, measured from the center of each forest site) at which the strongest relationship occurred (lowest AIC and highest percentage of explained deviance). Most scales of effect were relatively small (Table A2). In 3 out of 8 cases, monkeys responded most strongly to landscape metrics measured at the 200-m radius, and in another 3 cases, to metrics measured at the 400-m radius. These scales of effect are within the range reported in other studies (Ordóñez-Gómez et al. 2015, Galán-Acedo et al. 2018, Gestich et al. 2019) and can be related to the relatively small home-range size of the species.

Finally, we used a multimodel averaging approach (Burnham and Anderson 2002) with generalized linear models to assess the relationship between the landscape Δs (measured at their scale of effect; Table A2) and the primates Δs (Step 6, Fig. A1). We used the 'glmulti' package (Calcagno and de Mazancourt 2010), selecting a normal distribution with an identity-link function. To avoid multicollinearity among multiple models, we estimated the Variance Inflation Factor (VIF) for each predictor, using the 'car' package (Fox and Weiberg 2011). In several cases VIF values for mean inter-patch distance were higher than 4, indicating collinearity (Neter et al. 1996). Since this landscape predictor was negatively correlated with forest cover (r = -0.91), we excluded it from analyses. For each response variable (primate Δs) we then constructed 16 models, representing all combinations of the four explanatory variables (Δforest cover, Δmatrix openness, Δedge density and Δnumber of patches) and the null model (which includes only the intercept). We calculated the Akaike Information Criterion of each model corrected for small samples (AICc) and arranged the models from best to worst (i.e. lowest to highest AICc). We obtained model-averaged parameter estimates using Akaike weights (w_i). Then, we calculated the sum of Akaike weights ($\sum w_i$) of each Δ landscape predictor, which represents the probability that this predictor is within the true best model (Burnham and Anderson 2002). To be conservative, we considered a landscape attribute as an important explanatory variable if the following three criteria were met: (i) it showed a relatively high sum of Akaike weights; (ii) the model-averaged unconditional variance was lower than the model-averaged parameter estimate; and (iii) the complete model showed a relatively high percentage of explained deviance (i.e. relatively high goodness-of-fit; Burnham and Anderson 2002).

Results

Population parameters did not differ between continuous and fragmented forests (primate abundance: t = 0.39, p = 0.70; immature-to-female ratio: t = 0.56, p = 0.58). Landscape structure changed through time, with high variability in those changes among sites (Table A1; Fig. A2). The percentage of forest cover (full model *vs.* null model: $\chi^2 = 5.6$, $p < 0.02$) and matrix openness ($\chi^2 = 7.5$, $p < 0.01$), showed a significant increase from 2010 to 2016 (Table 2). Total primate abundance ($\chi^2 = 4.2$, $p < 0.04$) and the immature-to-female ratio ($\chi^2 = 11.3$, $p < 0.001$) also differed between years, with an increase of 27% in the number of monkeys between 2011 and 2017, and a decrease of 35% in the immature-to-female ratio (Tables 2 and 3). Three forest patches did not present any individuals in both years (Table 3).

Table 2. Landscape composition and configuration metrics and *Alouatta pigra* population parameters sampled in two different years in the Lacandona rainforest, Mexico. Mean (± SD) values are indicated. Landscape metrics were recorded in buffers with 1,400-m radii measured from the center of each forest site (N = 22). Demographic attributes come only from forest sites occupied by howler monkeys (N = 19). Differences between years were evaluated with generalized linear mixed models and a likelihood ratio test. We show the β-estimate and standard error (SE) of each model.

Variables	**Year**		***β***	***SE***	***t***	**p**
Landscape metrics	**2010**	**2016**				
Compositional metrics						
Forest cover (%)	52.5 ± 23.9	53.5 ± 23.1	0.011	0.005	2.36	0.02
Matrix openness (%)	70.4 ± 29.6	73.0 ± 31.7	0.081	0.008	10.7	<0.001
Configurational metrics						
Number of patches	18.0 ± 12.5	16.5 ± 10.7	-0.371	0.192	-1.94	0.07
Edge density (m/ha)	65.9 ± 30.1	64.1 ± 34.1	-0.009	0.008	-1.06	0.30
Demographic attributes	***2011***	***2017***				
Number of individuals	11.7 ± 8.7	16.0 ± 10.9	0.045	0.021	2.14	0.047
Immature-to-female ratio	0.9 ± 0.5	0.6 ± 0.4	-0.105	0.029	-3.67	0.002

We found clear associations between the temporal changes in landscape structure (measured at their scale of effect, Table A2) and the temporal changes in primate population parameters (Fig. 2). Yet, based on the goodness-of-fit of the models, changes in the immature-to-female ratio (59% of explained deviance) were better predicted by changes in landscape structure than changes in primate abundance (34%). All model-averaged parameter estimates (slopes) were higher than their respective unconditional variances, suggesting confidence in the estimations (Table A3). Considering the sum of Akaike weights ($\sum w_i$), changes in howler monkey populations were better predicted by changes in the number of patches and changes in forest edge density than by changes in matrix openness and forest cover. In particular, both demographic variables increased in forest sites found in landscapes where the number of forest patches increased through time (Fig. 2a-b). Yet, the immature-to-female ratio decreased in sites found in landscapes in which the density of forest edges increased (Fig. 2b; Table 4). Changes in matrix openness were also negatively related to changes in immature-to-female ratio (Fig. 2a-b; Table A2). The association between changes in forest cover and changes in population parameters was positive, being more important for primate abundance than for immature-to-female ratio (Fig. 2a; Table 4).

Table 3. Results of *Alouatta pigra* population monitoring in the Lacandona rainforest in 2011 and 2017, and the deltas between years (2017 values – 2011 values) in three continuous forest sites (CF) and 19 forest patches (FP). Sites IDs correspond to those showed in Fig. 1 and Table A1. AM = adult males, AF = adult females, J = juveniles, IN = infants, I/F = immature-to-female ratio, TA = total abundance.

	2011						**2017**						**Deltas**					
Site	*AM*	*AF*	*J*	*IN*	*I/F*	*TA*	*AM*	*AF*	*J*	*IN*	*I/F*	*TA*	*AM*	*AF*	*J*	*IN*	*I/F*	*TA*
CF1	4	3	1	1	0.67	9	2	2	1	0	0.5	5	-2	-1	0	-1	-0.2	-4
CF3	6	3	3	0	1	12	4	5	1	0	0.2	10	-2	2	-2	0	-0.8	-2
CF4	4	3	2	1	1	10	9	9	6	0	0.67	24	5	6	4	-1	-0.3	14
FP2	2	3	2	1	1	8	6	4	2	1	0.75	13	4	1	0	0	-0.3	5
FP3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FP4	3	2	0	0	0	5	7	4	3	1	1	15	4	2	3	1	1	10
FP5	3	2	3	0	1.5	8	2	2	2	1	1.5	7	-1	0	-1	1	0	-1
FP7	2	1	1	0	1	4	1	3	1	0	0.33	5	-1	2	0	0	-0.7	1
FP8	0	0	0	0	0	0	1	4	1	0	0.25	6	1	4	1	0	0.25	6
FP10	4	1	2	0	2	7	3	4	2	0	0.5	9	-1	3	0	0	-1.5	2
FP11	8	7	5	3	1.14	23	6	8	1	1	0.25	16	-2	1	-4	-2	-0.9	-7
FP13	3	3	3	1	1.33	10	5	5	1	1	0.4	12	2	2	-2	0	-0.9	2
FP15	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FP16	1	2	0	1	0.5	4	7	5	6	3	1.8	21	6	3	6	2	1.3	17
FP17	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FP18	10	12	11	2	1.08	35	11	15	8	2	0.67	36	1	3	-3	0	-0.4	1
FP19	2	6	2	0	0.33	10	5	9	1	1	0.22	16	3	3	-1	1	-0.1	6
FP20	5	3	2	0	0.67	10	4	7	1	2	0.43	14	-1	4	-1	2	-0.2	4
FP21	8	10	5	2	0.7	25	19	13	6	1	0.54	39	11	3	1	-1	-0.2	14
FP23	2	5	3	2	1	12	3	7	1	2	0.43	13	1	2	-2	0	-0.6	1
FP25	7	9	5	2	0.78	23	14	15	6	2	0.53	37	7	6	1	0	-0.2	14
FP28	3	1	1	1	2	6	2	2	1	0	0.5	5	-1	1	0	-1	-1.5	-1

Table 4. Additive models assessing the relationship between changes in the abundance of howler monkeys and immature-to-female ratio (primate Δs = 2017 values – 2011values), and changes in landscape structure (landscape Δs = 2016 values – 2010 values). We show the five best models for both primate response variables. We present results of Akaikes' Information Criterion for small samples (AICc), the sum of Akaike Weights (w_i), the difference between each model and the best model (ΔAICc), and the percentage of deviance explained by each model (%ED). Forest cover = FC, number of patches = NP, matrix openness = MO, and edge density = ED.

Model			**AICc**	w_i	**ΔAICc**	**%ED**
Primate abundance	~	1+FC+NP	146.76	0.21	0	26.73
Primate abundance	~	1+FC	147.77	0.12	1.01	11.99
Primate abundance	~	1	147.88	0.12	1.12	0
Primate abundance	~	1+FC+NP+ED	148.36	0.09	1.6	32.47
Primate abundance	~	1+NP	148.61	0.08	1.85	8.56
Immature-to-female ratio	~	1+ NP+MO+ED	37.87	0.46	0	58.09
Immature-to-female ratio	~	1+NP+ED	39.75	0.18	1.88	46.48
Immature-to-female ratio	~	1+MO+ED	40.76	0.11	2.89	43.92
Immature-to-female ratio	~	1+FC+NP+MO+ED	41.06	0.09	3.19	59.36
Immature-to-female ratio	~	1+FC+NP+ED	42.71	0.04	4.84	47.55

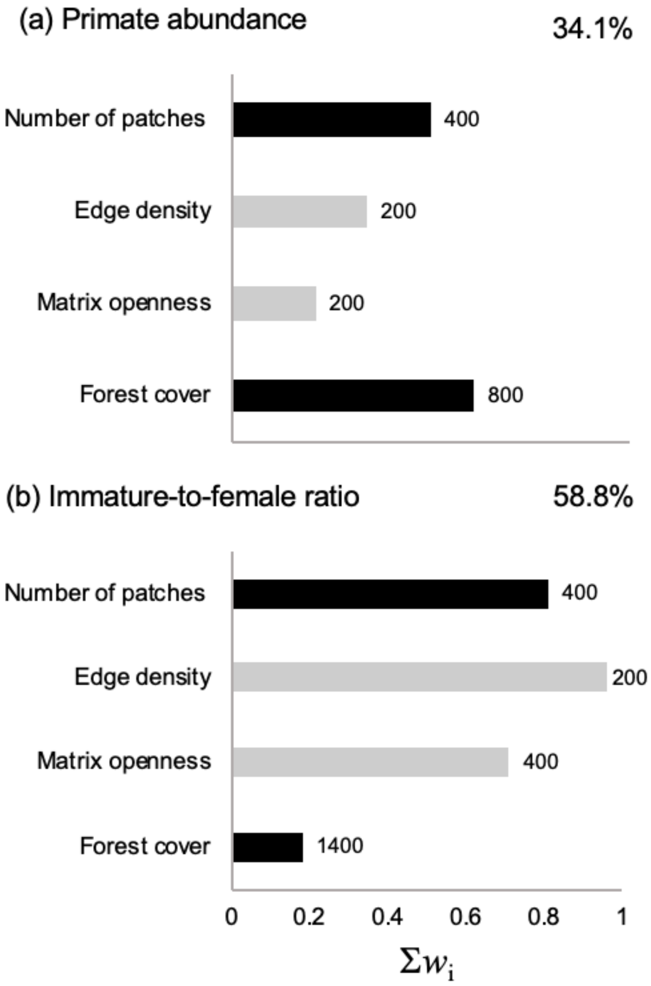


Figure 2. Effect of landscape structure change (landscape Δs) between 2016 and 2010 on changes in population parameters (primate Δs) of black howler monkeys (*Alouatta pigra*) between 2017 and 2011 in the Lacandona rainforest, Mexico. We assessed changes in primate abundance (a), and immature-to-female ratio (b). We present the sum of Akaike weights (Σw_i) of each landscape predictor, showing both positive parameter estimates (black), and negative parameter estimates (grey). We also indicate the values of pseudo-R^2, i.e. the percentage of deviance explained by complete models. Values at the right side of each bar are the scale of effects (i.e. radius in meters of landscape buffers) of each landscape metric on each response (see details in Table A2).

Discussion

This longitudinal study is the first to assess the effects of temporal and spatial changes in landscape structure on demographic attributes of the black howler monkey – an endangered primate with a highly restricted distribution (Marsh et al. 2008). Our findings indicate that the Mexican portion of the Lacandona rainforest is highly dynamic, with different sites undergoing contrasting changes in landscape structure through time. Howler monkeys responded strongly to such changes, including those describing landscape configuration (i.e. number of forest patches and forest edge density) and those associated with landscape composition (i.e. forest cover and matrix openness). As predicted, the number of individuals increased in sites located in landscapes in which forest cover increased. Additionally, both the number of individuals and immature-to-female ratio increased in sites surrounded by landscapes with increasing number of patches over time, but where the proportion of treeless land decreased in the matrix. Yet, in contrast to our predictions, the immature-to-female ratio decreased in sites with an increasing density of forest edges. These novel findings indicate that this primate species might not be as tolerant to landscape disturbance as generally thought (e.g. Silver et al. 1998, Rangel-Negrín et al. 2014), as both population parameters were clearly associated with landscape changes occurring over a relatively short (6 years) time period.

The number of individuals increased through time. This finding is unexpected because this species has a relatively long lifespan (>30 years: Glander 2004) and a slow life-history (e.g. mean interbirth interval = 18 months: Dias et al. 2016) – attributes that can result in time-lagged responses to habitat disturbance (Metzger et al. 2009). Such a relatively rapid increase can be related to two non-exclusive mechanisms. First, the continuous deforestation in the region could be pushing the remaining individuals to take refuge in remnant forest patches, causing them to concentrate there. This phenomenon is known as the ‘crowding effect’ and has been shown to occur in forest-specialist species, including insects (Grez et al. 2004), terrestrial mammals (Laurance 1991, Arce-Peña et al. 2019), and howler monkeys (Arroyo-Rodríguez and Dias 2010). The second mechanism is related to the social system of this primate. Howler monkeys live in groups that constantly move around the landscape in the search of resources (Estrada 1984, Crockett and Eisenberg 1987). Both males and females immigrate from their natal groups to enter other groups or form new groups (Crockett and Eisenberg 1987). Thus, it could be possible that individuals in forest patches are not being able to disperse from their natal group due to an increasingly open and inhospitable matrix (Arroyo-Rodríguez and Dias 2010). Whatever the cause of such accumulation of individuals, it could have negative impacts on the long-term persistence of howler monkey populations. For example, high population densities can cause a reduction in food availability and an increase in competition (Cristóbal-Azkarate and Arroyo-Rodríguez 2007). Furthermore, high densities can cause higher levels of disease and parasitism (Arroyo-Rodríguez and Dias 2010), which are important mortality causes in howler monkeys (Holzmann et al. 2010). Therefore, increasing landscape connectedness can be critical for primate conservation in the region (see below).

The disruption of female emigration from natal groups could explain the observed decrease in immature-to-female ratio. The number of immature individuals was similar in both years, averaging 3.6 individuals in 2011 and 2017 (Table 3). Yet, the mean number of adult females was 38% higher in 2017 (6.5 individuals) than 2011 (4 individuals) (Table 3). Dias et al. (2015) show that the number of immature individuals is usually stable through time in a fragmented forest, and that females migrate from natal groups at the age of ~4 years. Thus, the observed decrease in immature-to-female ratio in our study could be caused by a lack of female migration due to spatial changes in landscape structure, such as the increase in matrix openness. Consistent with this idea, the number of females increased more in forest patches surrounded by increasing matrix openness (Table A1). However, the number of females also increased in two continuous sites where dispersal movements are not limited. In these cases, the increase in female abundance could actually be associated to immigrations of females from other landscapes.

The number of individuals, but more importantly the immature-to-female ratio, increased with increasing the number of fragments, i.e. increasing fragmentation. These results support a recent review of species' responses to habitat fragmentation *per se* by Fahrig (2017), which suggests that significant responses to fragmentation are mostly positive. Galán-Acedo et al. (2019a) also found a similar pattern in a review of primate responses to fragmentation, and other case studies indicate that howler monkeys are not the exception (Anzures-Dadda and Manson 2007, Arroyo-Rodríguez et al. 2013). Therefore, our findings support that mechanisms resulting in positive responses to fragmentation may be more important than those resulting in negative responses (reviewed by Fahrig et al. 2019). For example, a high number of patches remaining in the landscape can reduce inter-patch isolation distances and facilitate animal movements between patches (Anzures-Dadda and Manson 2007, Fahrig 2017). Decreasing isolation distances can also reduce movement-related risks and favor landscape-scale processes critical for population maintenance in fragmented landscapes, such as source/sink dynamics and landscape supplementation dynamics (*sensu* Dunning et al. 1992). Finally, as the number of patches increases, the number of sub-populations can also increase, which can facilitate metapopulation persistence (Hanski 1999). Therefore, increasing the number of forest patches while simultaneously maintaining or increasing forest cover in the landscape could favor primate conservation in the region. Of course, this does not mean that we should break apart the remaining patches because this would result in habitat loss – a critical threat to howler monkeys (present study), and other primates (Galán-Acedo et al. 2019a). We rather suggest increasing the number of forest patches through active or passive restoration (the so-called 'reverse fragmentation'; sensu del Castillo 2015), which would result in an increase in both habitat amount and landscape connectedness.

The fact that the number of individuals increased in sites that showed an increase in forest cover over time is not surprising. For arboreal primates, forest cover is a proxy of habitat amount in the landscape, as they depend on forest for finding food, shelter, and sites for reproduction (Silva et al. 2015). Arroyo-Rodríguez et al. (2008) also report that landscapes with higher forest cover have a higher number of howler monkeys (*A. palliata*) in the Los Tuxtlas rainforest, Mexico. In fact, this landscape variable is an important predictor of primate distribution, abundance and richness in fragmented forests across the world (da Silva et al. 2015, Dias et al. 2015, Puig-Lagunes et al. 2016, Galán-Acedo et al. 2019a). Percentage of forest cover also has positive effects on many other forest-dependent taxa (Benchimol and Peres 2013a, Morante-Filho et al. 2018), probably due to its positive association with landscape connectedness and resource availability (Fahrig 2003, 2013). Therefore, prevention of forest loss and increase in forest cover (e.g. through restoration) are needed to preserve howler monkeys.

Our findings also highlight the key role played by matrix quality in maintaining howler monkey populations. Matrix openness was negatively related to both population parameters, but more importantly to the immature-to-female ratio. The importance of the matrix for primate populations had been reported in a previous study of black howlers in the region (Arroyo-Rodríguez et al. 2013), as well as in a global review of primate responses to landscape structure (Galán-Acedo et al. 2019a). As other primates (Arroyo-Rodríguez et al. 2017, Galán-Acedo et al. 2019b), black howler monkeys can use the matrix for feeding and traveling, but such use depends on matrix quality, which in this case was related to the availability of trees in the matrix (Arroyo-Rodríguez et al. 2017). Thus, the increase of treeless areas in the matrix limits resource availability and landscape connectedness, and 'forces' primates to inhabit the remaining forest patches (Dias et al. 2015). Although howler monkeys can move through highly disturbed matrices to reach isolated food patches (Fortes et al. 2015), these movements involve risks such as road kills, predation, and hunting, especially for immature individuals. Therefore, consistent with previous studies (Arroyo-Rodríguez et al. 2017, Galán-Acedo et al. 2019a, 2019b), matrix enrichment with native food-plant trees and creation of wooded corridors may be critical for primate conservation. Decreasing matrix openness by changing open-area matrices (e.g. annual crops, cattle pastures) to different arboreal crops (e.g. mango, guava) and agroforests (e.g. shade coffee and cacao plantations) can have numerous benefits for both primates and humans (see Arroyo-Rodríguez et al. 2017).

Finally, in contrast to our prediction, the immature-to-female ratio decreased in landscapes where edge density increased through time. This result could represent two non-exclusive effects of edge density on primate populations: (i) a positive effect on the number of adult females, and (ii) a negative effect on the number of immatures. Positive effects on adult individuals have been previously reported (Arroyo-Rodríguez et al. 2013), probably because sites surrounded by higher edge density can be better connected to other patches. In particular, edge density is higher in landscapes dominated by patches with more complex shapes, and such patches can be more frequently colonized by dispersing fauna (Ewers and Didham 2006). Edge density can also increase food availability through landscape supplementation dynamics (Dunning et al. 1992, Asensio et al. 2009), as the amount of forest that is in contact with the anthropogenic matrix increases with edge density. In fact, forest edges are typically dominated by fast-growing light-demanding tree species, and these highly productive trees (e.g. *Cecropia*, *Ficus*) are known to be top food species for howler monkeys (Dias and Rangel-Negrín 2015). Yet, immature individuals could be negatively affected by increasing edge density because of an increased vulnerability to predation and human-related activities (e.g. hunting, extraction for illegal trade, road-kills) at forest edges (Michalski and Peres 2005). Accurately testing the relative importance of these processes is necessary to better understand the role of edge density in maintaining primate populations, and thus improving conservation strategies.

Conclusions

The rapid response of howler monkeys to landscape spatial changes suggests that this species may not be as tolerant to landscape disturbance as previously proposed (Silver et al. 1998, Rangel-Negrín et al. 2014). Although we did not assess temporal changes in patch-scale characteristics such as patch size, quality and history – a very interesting topic that needs to be assessed in future studies – our research indicates that relatively short-term landscape-scale changes can have important effects on black howler monkey populations. To improve landscape quality for this endangered primate species, conservation actions should include: (i) preventing forest loss and increasing forest cover (passive or active restoration); (ii) generating or increasing the size of forest patches in the landscape (i.e. reverse fragmentation); and (iii) decreasing the amount of treeless areas by enriching the matrix with native tree species, wooded corridors and different arboreal crops and agroforests. Overall, these management strategies can contribute to increasing both resource availability and landscape connectedness for howler monkeys and many other forest-dependent species in this important but vanishing biodiversity hotspot.

References

Andresen, E., Arroyo-Rodríguez, V., Ramos-Robles, M. 2018. Primate seed dispersal: old and new challenges. International Journal of Primatology 39: 443–465.

Anzures-Dadda, A., Manson, R.H. 2007. Patch- and landscape-scale effects on howler monkey distribution and abundance in rainforest fragments. Animal Conservation 10: 69–76.

Arce-Peña, N.P., Arroyo-Rodríguez, V., San-José, M., Jiménez-González, D., Franch-Pardo, I., Andresen, E., Ávila-Cabadilla, L.D. 2019. Landscape predictors of rodent dynamics in fragmented rainforests. Biodiversity and Conservation 28: 655–669.

Arriaga, L., Espinoza, J., Aguilar, C., Martínez, E., Gómez, L., Loa, E. 2000. Regiones terrestres prioritarias de México. CONABIO, Mexico City.

Arroyo-Rodríguez, V., Dias, P.A.D. 2010. Effects of habitat fragmentation and disturbance on howler monkeys: a review. American Journal of Primatology 72: 1–16.

Arroyo-Rodríguez, V., González-Perez, I.M., Garmendia, A., Solà, M., Estrada, A. 2013. The relative impact of forest patch and landscape attributes on black howler monkey populations in the fragmented Lacandona rainforest, Mexico. Landscape Ecology 8: 1717–1727.

Arroyo-Rodríguez, V., Mandujano, S., Benítez-Malvido, J. 2008. Landscape attributes affecting patch occupancy by howler monkeys (*Alouatta palliata mexicana*) at Los Tuxtlas, Mexico. American Journal of Primatology 70: 69–77.

Arroyo-Rodríguez, V., Pérez-Elissetche, G.K., Ordóñez-Gómez, J.D., González-Zamora, A., Chaves, O.M., Sánchez-López, S., Chapman, C.A., Morales-Hernández, K., Pablo-Rodríguez, M., Ramos-Fernández, G. 2017. Spider monkeys in human-modified landscapes: the importance of the matrix. Tropical Conservation Science 10: 1–30.

Asensio, N., Arroyo-Rodríguez, V., Dunn, J.C., Cristobal-Azkarate, J. 2009. Conservation value of landscape supplementation for howler monkeys living in forest patches. Biotropica 41: 768–773.

Benchimol, M., Peres, C.A. 2013a. Anthropogenic modulators of species-area relationships in Neotropical primates: a continental-scale analysis of fragmented forest landscapes. Diversity and Distributions 19: 1339–1352.

Benchimol, M., Peres, C.A. 2013b. Predicting primate local extinctions within “real-world” forest fragments: A pan-neotropical analysis. American Journal of Primatology 76: 289–302.

Bennet, A.F., Saunders, D.A. 2010. Habitat fragmentation and landscape change. In: Sodhi, N.S., Ehrlich, P.R. (Eds.) Conservation biology for all. Oxford University Press, Oxford, pp 88–106.

Burnham, K.P., Anderson, D.R. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Springer, New York.

Calcagno, V., de Mazancourt, C. 2010. Glmulti: An R package for easy automated model selection with (generalized) linear models. Journal of Statistical Software 34: 1–29.

Camara, G., Souza, R.C.M., Freitas, U.M., Garrido, J. 1996. SPRING: Integrating remote sensing and GIS by object-oriented data modelling. Computers and Graphics 20: 395–403.

Carabias, J., de la Maza, J., Cadena, R. 2015. Conservación y desarrollo sustentable en la Selva Lacandona. 25 años de actividades y experiencias. Natura y Ecosistemas Mexicanos, Mexico City.

Chapman, C.A., Bortolamiol, S., Matsuda, I., Omeja, P.A., Paim, F.P., Reyna-Hurtado, R., Sengupta, R., Valenta, K. 2018. Primate population dynamics: variation in abundance over space and time. Biodiversity and Conservation 27: 1221–1238.

Cristóbal-Azkarate, J., Arroyo-Rodríguez, V. 2007. Diet and activity pattern of howler monkeys (*Alouatta palliata*) in Los Tuxtlas, Mexico: effects of habitat fragmentation and implications for conservation. American Journal of Primatology 69: 1013–1029.

Cristóbal-Azkarate, J., Dunn, J.C., Domingo-Balcells, C., Veá-Baró, J. 2017. A demographic history of a population of howler monkeys (*Alouatta palliata*) living in a fragmented landscape in Mexico. PeerJ 5: e3547.

Cristóbal-Askarate, J., Veá, J., Asensio, N., Rodríguez-Luna, E. 2005. Biogeographical and floristic predictors of the presence and abundance of mantled howlers (*Alouatta palliata mexicana*) in rainforest fragments at Los Tuxtlas, Mexico. American Journal of Primatology 67: 209–222.

Crockett, C.M., Eisenberg, J.F. 1987. Howlers: Variations in group size and demography. In: Smuts, B.B., Cheney, D.L., Seyfarth, R.M., Wrangham, R.W., Struhsaker, T.T. (Eds.) Primate societies. The University of Chicago Press, Chicago, pp 54–68.

Da Silva, L.G., Ribeiro, M.C., Hasui, E., da Costa, C.A., Da Cunha, R.G.T. 2015. Patch size, functional isolation, visibility and matrix permeability influences neotropical primate occurrence within highly fragmented landscapes. PLoS ONE 10: e0114025.

Del Castillo, R.F. 2015. A conceptual framework to describe the ecology of fragmented landscapes and implications for conservation and management. Ecological Applications 25: 1447–1455.

Dias, P.A.D., Coyohua-Fuentes, A., Canales-Espinosa, D., Rangel-Negrín, A. 2015. Group structure and dynamics in black howlers (*Alouatta pigra*): a 7-year perspective. International Journal of Primatology 36: 311–331.

Dias, P.A.D., Coyohua-Fuentes, A., Canales-Espinosa, D., Rangel-Negrín, A. 2016. Factors influencing the reproductive success of female black howlers (*Alouatta pigra*). International Journal of Primatology 37: 638–655.

Dias, P.A.D., Rangel-Negrín, A. 2015. Diets of howler monkeys. In: Kowaleski, M.M., Garber, P.A., Cortés-Ortíz, L., Urbani, B., Youlatos, D. (Eds.) Howler monkeys: behavior, ecology and conservation. Springer Science+Business Media, New York, pp 21–56.

Dunning, J.B., Danielson, B.J., Pulliam, R. 1992. Ecological processes that affect populations in complex landscapes. Oikos 65: 169–175.

Eigenbrod, F., Hecnar, S.J., Fahrig, L. 2011. Sub-optimal study design has major impacts on landscape-scale inference. Biological Conservation 144: 298–305.

Estrada, A., Coates-Estrada, R. 1996. Tropical rain forest fragmentation and wild populations of primates at Los Tuxtlas, Mexico. International Journal of Primatology 17: 759–783.

Estrada, A., Garber, P.A., Rylands, A.B., Roos, C., Fernandez-Duque, E., Di Fiore, A., Nekaris, K.A.I., Nijman, V., Heymann, E.W., Lambert, J.E., Rovero, F., Barelli, C., Setchell, J.M., Gillespie, T.R., Mittermeier, R.A., Arregoitia, L.V., de Guinea, M., Gouveia, S., Dobrovolski, R., Shanee, S., Shanee, N., Boyle, S.A., Fuentes, A., MacKinnon, K.C., Amato, K.R., Meyer, A.L.S., Wich, S., Sussman, R.W., Pan, R., Kone, I., Li, B. 2017. Impending extinction crisis of the world's primates: why primates matter. Science Advances 3: e1600946.

Estrada, A., Mendoza, A., Castellanos, L., Pacheco, R., Van Belle, S., García, Y., Muñoz, D. 2002. Population of the black howler monkey (*Alouatta pigra*) in a fragmented landscape in Palenque, Chiapas, Mexico. American Journal of Primatology 58: 45–55.

Ewers, R.M., Didham, R.K. 2006. Confounding factors in the detection of species responses to habitat fragmentation. Biological Reviews 81: 117–142.

Ewers, R.M., Didham, R.K., Pearse, W.D., Lefebvre, V., Rosa, I.M.D., Carreiras, J.M.B., Lucas, R.M., Reuman, D.C. 2013. Using landscape history to predict biodiversity patterns in fragmented landscapes. Ecology Letters 16: 1221–1233.

Fahrig. L. 2003. Effects of habitat fragmentation on biodiversity. Annual Review of Ecology, Evolution, and Systematics 34: 487–515.

Fahrig, L. 2013. Rethinking patch size and isolation effects: the habitat amount hypothesis. Journal of Biogeography 40: 1649–1663.

Fahrig, L. 2017. Ecological responses to habitat fragmentation per se. Annual Review of Ecology, Evolution, and Systematics 48: 1–23.

Fahrig, L., Arroyo-Rodríguez, V., Bennett, J., Boucher-Lalonde, V., Cazeta, E., Currie, D., Eigenbrod, F., Ford, A., Jaeger, J., Koper, N., Martin, A., Metzger, J.P., Morrison, P., Rhodes, J., Saunders, D., Simberloff, D., Smith, A., Tischendorf, L., Vellend, M., Watling, J. 2019. Is habitat fragmentation bad for biodiversity? Biological Conservation 230: 179–186.

Fahrig, L., Baudry, J., Brotons, L., Burel, F.G., Crist, T.O., Fuller, R.J., Sirami, C., Siriwardena, G.M., Martin, J.L. 2011. Functional landscape heterogeneity and animal biodiversity in agricultural landscapes. Ecology Letters 14: 101–112.

Fortes, V.B., Bicca-Marques, J.C., Urbani, B., Fernández, V.A., da S. Pereira, T. 2015. Ranging behavior and spatial cognition of howler monkeys. In: Kowalewski, M.M., Garber, P.A., Cortés-Ortiz, L., Urbani, B., Youlatos, D. (Eds.) Howler monkeys: Behavior, ecology, and conservation. Springer, New York, pp 219–255.

Fox, J., Weisberg, S. 2011. An {R} companion to applied regression, second edition. SAGE publications Inc, Thousand Oaks.

Galán-Acedo, C., Arroyo-Rodríguez, V., Estrada, A., Ramos-Fernández, G. 2018. Drivers of the spatial scale that best predict primate responses to landscape structure. Ecography 41: 1–11.

Galán-Acedo, C., Arroyo-Rodríguez, V., Cudney-Valenzuela, S., Fahrig, L. 2019a. A global assessment of primate responses to landscape structure. Biological Review 94: 1605–1618.

Galán-Acedo, C., Arroyo-Rodríguez, V., Andresen, E., Arregoitia, L.V., Veja, E., Peres, C.A., Ewers, R.M. 2019b. The conservation value of human-modified landscapes for the world's primates. Nature Communications 10: 152.

Galán-Acedo, C., Arroyo-Rodríguez, V., Arasa-Gisbert, R., Andresen, E. 2019c. Ecological traits of the world's primates. Sci Data 6: 55.

Gestich, C.C., Arroyo-Rodríguez, V., Ribeiro, M.C., da Cunha, R.G.T., Setz, E.Z.F. 2019. Unraveling the scales of effect of landscape structure on primate species richness and density of titi monkeys (*Callicebus nigrifrons*). Ecological Research 34: 150–159.

Gibson, L., Ming-Lee, T., Pin-Koh, L., Brook, B.W., Gardner, T.A., Barlow, J., Peres, C.A., Bradshaw, C.J.A., Laurance, W.F., Lovejoy, T.E., Sodhi, N.S. 2011. Primary forests are irreplaceable for sustaining tropical biodiversity. Nature 478: 378–383.

Grez, A., Zaviezo, T., Tischendorf, L., Fahrig, L. 2004. A transient, positive effect of habitat fragmentation on insect population densities. Oecologia 141: 444–451.

Hagolle, O., Sylvander, S., Huc, M., Claverie, M., Clesse, D., Dechoz, C., Lonjou, V., Poulain, V. 2015. SPOT-4 (Take 5): simulation of Sentinel-2 time series on 45 large sites. Remote Sensing 7: 12242–12264.

Hanski, I. 1999. Habitat connectivity, habitat continuity, and metapopulations in dynamic landscapes. Oikos 87: 209–219.

Hanski, I. 2013. Extinction debt at different spatial scales. Animal Conservation 16: 12–13.

Holzmann, I., Agostini, I., Areta, J.I., Ferreyra, H., Beldomenico, P., Di Biteti, M.S. 2010. Impact of yellow fever outbreaks on two howler monkey species (*Alouatta guariba clamitans* and *A. caraya*) in Misiones, Argentina. American Journal of Primatology 72: 475–480.

Horwich, R.H., Johnson, E.D. 1986. Geographical distribution of the black howler (*Alouatta pigra*) in Central America. Primates 27: 53–62.

Instituto Nacional de Ecología. 2000. Programa de Manejo Reserva de la Biósfera Montes Azules. Secretaría de Medio Ambiente y Recursos Naturales, Mexico City.

Jackson, H.B., Fahrig, L. 2015. Are ecologists conducting research at the optimal scale? Global Ecology and Biogeography 24:52–63.

Kowalewski, M.M., Zunino, G.E. 1999. Impact of deforestation on a population of *Alouatta caraya* in Northern Argentina. Folia Primatologica 70: 163–166.

Laurance, W.F. 1991. Ecological correlates of extinction proneness in Australian tropical rain forest mammals. Conservation Biology 5: 79–89.

Marsh, L.K., Cuarón, A.D., Cortés-Ortíz, L., Shedden, A., Rodríguez-Luna, E., de Grammont, P.C. 2008. *Alouatta pigra*. The IUCN Red List of Threatened Species 2008: e.T914A13094441. http://dx.doi.org/10.2305/IUCN.UK.2008.RLTS.T914A13094441.en

Medellín, R. 1994. Mammal diversity and conservation in the Selva Lacandona, Chiapas, Mexico. Conservation Biology 8: 780–799.

Melo, F., Arroyo-Rodríguez, V., Fahrig, L., Martínez-Ramos, M., Tabarelli, M. 2013. On the hope for biodiversity-friendly tropical landscapes. Trends in Ecology and Evolution 28: 462–468.

Metzger, J.P., Camargo, A.M., Dixo, M., Bernacci, L.C., Ribeiro, M.C., Godoy, A.M.T., Pardini, R. 2009. Time-lag in biological responses to landscape changes in a highly dynamic Atlantic forest region. Biological Conservation 142: 1166–1177.

Michalski, F., Peres, C. 2005. Anthropogenic determinants of primate and carnivore local extinctions in a fragmented forest landscape of southern Amazonia. Biological Conservation 124: 383–396.

Morante-Filho, J.C., Arroyo-Rodríguez, V., Pessoa, M.S., Cazetta, E., Faria, D. 2018. Direct and cascading effects of landscape structure on tropical forest and non-forest frugivorous birds. Ecological Applications 28: 2024–2032

Neter, J., Kutner, M.H., Nachtshein, C.J., Wasserman, W. 1996. Applied Linear Statistical Models, 4th Edn. McGraw-Hill/Irwin, New York.

Olofsson, P., Foody, G.M., Herold, M., Stehman, S.V., Woodcock, C.E., Wulder, M.A. 2014. Good practices for estimating area and assessing accuracy of land change. Remote Sensing of Environment 148: 42–57.

Ordóñez-Gómez, J.D., Arroyo-Rodríguez, V., Nicasio-Arzeta, S., Cristóbal-Azkarate, J. 2015. Which is the appropriate scale to assess the impact of landscape spatial configuration on the diet and behavior of spider monkeys? American Journal of Primatology 77: 56–65.

Pinheiro, J., Bates, D. 2000. Mixed-effects models in s and S-plus. Springer, New York.

Pozo-Montuy, G., Serio-Silva, J.C., Chapman, C.A., Bonilla-Sánchez, Y.M. 2013. Resource use in a landscape matrix by an arboreal primate: evidence of supplementation in black howlers (*Alouatta pigra*). International Journal of Primatology 34: 714–731.

Puig-Lagunes, A.A., Canales-Espinosa, D., Rangel-Negrín, A., Dias, P.A.D. 2016. The influence of spatial attributes on fragment occupancy and population structure in the Mexican mantled howler (*Alouatta palliata mexicana*). International Journal of Primatology 6: 656–670.

R Core Team. 2018. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org/.

Rangel-Negrín, A., Coyohua-Fuentes, A., Canales-Espinosa, D., Dias, P.A.D. 2014. Mammal assemblages in forest fragments and landscapes occupied by black howler monkeys. Primates 55: 345–352.

Rosales-Meda, M., Estrada, A., López, A.E. 2008. Demographic survey of black howler monkey (*Alouatta pigra*) in the Lachuá eco-region in Alta Verapaz, Guatemala. American Journal of Primatology 70: 231–237.

SEMARNAT. 2010. NOM-059-SEMARNAT-2010. Protección ambiental- Especies nativas de México de flora y fauna silvestres- Categorías de riesgo y especificaciones para su inclusión, exclusión o cambio- Lista de especies en riesgo. Diario Oficial de la Federación, December 30, 2010.

Silver, S.C., Ostro, L.E.T., Yeager, C.P., Horwich, R. 1998. Feeding ecology of the black howler monkey (*Alouatta pigra*) in Northern Belize. American Journal of Primatology 45: 262–279.

Van Belle, S., Estrada, A. 2005. Demographic features of *Alouatta pigra* populations in extensive and fragmented forests. In: Estrada, A., Garber, P.A., Pavelka, M.S.M., Luecke, L. (Eds.) New perspectives in the study of Mesoamerican primates: distribution, ecology, behavior, and conservation. Springer, New York, pp 121–142.

Van Belle, S., Estrada, A. 2008. Group size and composition influence male and female reproductive success in black howler monkeys (*Alouatta pigra*). American Journal of Primatology 70: 613–619.

Supplementary material

Table A1. Delta values (Δ = 2016 – 2010) of landscape features at the 1,400 m, 400 m and 200 m scales. CF = continuous forest sites, FP = forest patches.

Site	ΔForest cover (%)			ΔMatrix openness (%)			ΔNumber of patches			ΔEdge density (m/ha)		
	1400 m	400 m	200 m	1400 m	400 m	200 m	1400 m	400 m	200 m	1400 m	400 m	200 m
CF1	0.0	0.0	0.0	0.0	0.0	0.0	0	0	0	0.0	0.0	0.0
CF2	0.0	0.0	0.0	0.0	0.0	0.0	0	0	0	0.0	0.0	0.0
CF4	0.0	0.0	0.0	0.0	0.0	0.0	0	0	0	0.0	0.0	0.0
FP2	1.5	16.9	18.6	3.4	4.1	-46.7	8	1	1	23.2	83.5	-33.9
FP3	-1.0	-10.6	-12.2	20.2	14.5	49.9	-12	-3	0	14.8	-49.9	-67.8
FP4	2.2	-1.1	16.0	13.0	34.6	25.2	-1	3	-3	-20.5	-25.9	-203.8
FP5	-6.9	-3.2	7.7	-1.4	6.7	16.7	-3	-1	0	2.7	28.6	9.9
FP7	10.8	28.7	51.6	11.4	19.6	52.3	3	-9	-1	-27.0	-38.3	-71.1
FP8	12.1	2.9	2.5	-7.1	-26.0	-7.7	-1	2	1	35.2	9.8	-55.9
FP10	2.5	35.5	13.0	12.4	14.3	23.1	-10	-6	0	-23.7	-3.9	-41.2
FP11	-6.1	-1.7	-7.7	11.5	17.8	10.8	-7	-3	-2	-24.7	-35.4	-33.0
FP13	12.1	8.2	16.6	7.5	54.0	99.0	-1	-1	1	16.3	11.8	0.5
FP15	3.1	-1.7	29.5	2.0	16.2	25.8	0	0	-1	-0.8	-43.8	-74.0
FP16	12.6	14.7	19.5	15.3	11.3	50.0	-6	-1	-2	-7.3	-14.3	-94.3
FP17	-2.5	-1.9	7.3	4.1	-7.2	13.3	6	0	-3	10.9	1.4	13.2
FP18	-4.3	-13.8	-11.7	28.7	12.9	26.2	-5	1	0	-6.7	-2.6	0.0
FP19	0.0	-0.4	0.0	-0.1	-0.8	0.0	-3	0	0	0.0	0.0	0.0
FP20	4.2	5.2	-12.2	15.9	22.0	0.5	-11	-2	2	1.0	-21.6	60.0
FP21	-5.4	-0.3	0.8	9.1	9.4	-100.0	-4	1	0	-2.7	-10.7	4.1
FP23	4.9	-2.0	0.0	9.2	-9.2	0.0	0	0	0	-11.0	-8.3	0.0
FP25	2.1	0.1	-5.0	2.1	16.7	61.5	-8	0	0	-15.5	-37.8	-23.0
FP28	0.5	-8.0	-8.3	-13.3	100.0	0.0	6	0	0	-22.4	-12.6	23.6

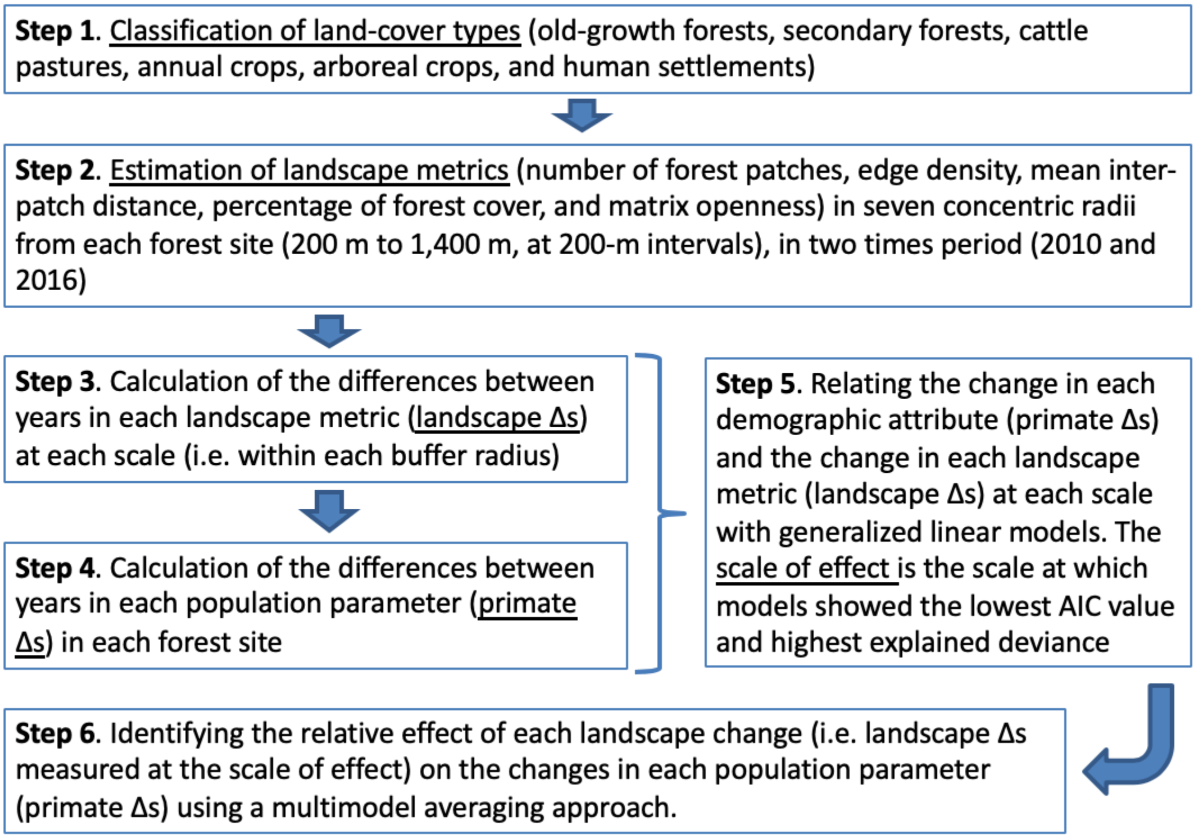
Table A2. Association between temporal changes in primate population parameters (i.e. primate abundance and immature-to-female ratio; primate Δs = 2017 values – 2011 values) and temporal changes in landscape structure (landscape Δs = 2016 values – 2010 values). We measured changes in landscape structure considering 7 different-sized radii (200 m – 1400 m) to identify the landscape size that yields the strongest predictor-response association (i.e. scale of effect). We conducted generalized linear models and obtained the AIC value and the percentage of explained deviance (%ED). Values in bold represent the best model (lowest AIC and highest percentage of explained deviance), indicating the selected scale of effect for each predictor-response association.

	ΔNumber of patches		ΔForest cover		ΔMatrix openness		ΔEdge density	
	% ED	AIC	% ED	AIC	% ED	AIC	% ED	AIC
ΔPrimate abundance								
1400	2.02	148.80	7.92	147.40	0.32	149.20	0.20	149.20
1200	4.69	148.20	9.05	147.20	0.01	149.20	0.22	149.20
1000	0.36	149.20	8.91	147.20	0.14	149.20	0.06	149.20
800	0.01	149.20	**11.99**	**146.40**	0.98	149.00	0.45	149.10
600	0.10	149.20	9.58	147.00	0.25	149.20	0.00	149.20
400	**8.56**	**147.30**	2.10	148.80	1.26	149.00	0.01	149.20
200	0.06	149.20	0.73	149.10	**1.29**	**149.00**	**7.01**	**147.60**
ΔImmature-to-female ratio								
1400	0.68	48.84	**3.10**	**48.29**	3.56	48.19	8.03	47.14
1200	6.46	47.52	1.64	48.62	0.15	48.95	3.10	48.29
1000	1.32	48.69	0.00	48.98	2.64	48.40	0.01	48.98
800	0.90	48.79	0.00	48.98	1.08	48.75	5.16	47.82
600	0.85	48.80	0.00	48.98	3.60	48.18	0.99	48.77
400	**18.18**	**44.57**	2.86	48.32	**14.52**	**45.43**	0.22	48.89
200	14.37	45.57	2.24	48.49	0.01	48.98	**29.08**	**41.42**

Table A3. Results of information-theoretic based model selection and multimodel inference for assessing the impact of landscape structure on two population parameters of black howler monkeys (i.e. primate abundance and immature-to-female ratio), while accounting for the scale of effect (see scales in Table A1). We show the results obtained when assessing the impact of landscape structure change (landscape Δs = 2016 values – 2010 values) on population parameters change (primate Δs = 2017 values – 2011 values). We present model-averaged parameter estimates (β) and the unconditional variance (UV) for each landscape predictor. All β estimates (i.e. slopes) are higher than their respective UV values, which suggests confidence in the estimation of β values (Burnham and Anderson 2002).

	Primate abundance		**Immature ratio**	
Metrics	β	UV	Β	UV
Number of patches	0.44259	0.33201	0.07992	0.00286
Forest cover	0.19921	0.04321	0.00231	0.00010
Matrix openness	-0.00473	0.00039	-0.00653	0.00003
Edge density	-0.01060	0.00043	-0.00610	0.00001

Figure A1. Conceptual design of our methodological approach.



Step 1. Classification of land-cover types (old-growth forests, secondary forests, cattle pastures, annual crops, arboreal crops, and human settlements)

Step 2. Estimation of landscape metrics (number of forest patches, edge density, mean inter-patch distance, percentage of forest cover, and matrix openness) in seven concentric radii from each forest site (200 m to 1,400 m, at 200-m intervals), in two times period (2010 and 2016)

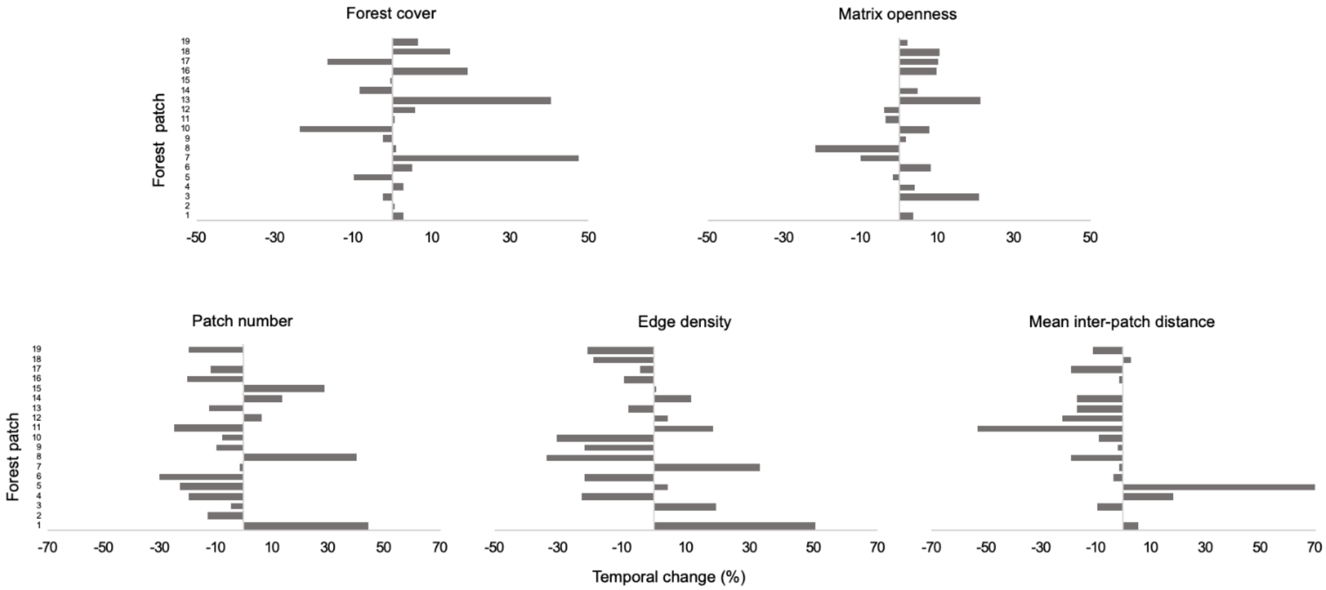
Step 3. Calculation of the differences between years in each landscape metric (landscape Δs) at each scale (i.e. within each buffer radius)

Step 4. Calculation of the differences between years in each population parameter (primate Δs) in each forest site

Step 5. Relating the change in each demographic attribute (primate Δs) and the change in each landscape metric (landscape Δs) at each scale with generalized linear models. The scale of effect is the scale at which models showed the lowest AIC value and highest explained deviance

Step 6. Identifying the relative effect of each landscape change (i.e. landscape Δs measured at the scale of effect) on the changes in each population parameter (primate Δs) using a multimodel averaging approach.

Figure A2. Temporal differences (2016-2010) in the structure of landscapes (1400-m radius from the center of each patch) containing 19 forest patches in the Lacandona rainforest, Mexico. Changes between years are indicated in percentages: i.e. (2016 value – 2010 value) *100/2010 value. Positive values indicate an increase in a given landscape metric, whereas negative values indicate the opposite. Forest patches are arranged according to their original size (2010), from the smallest (1) to the largest (19).



Capítulo 5.

Homogenization of terrestrial mammals in fragmented rainforests: the loss of species turnover and its landscape drivers

Norma P. Arce Peña, Víctor Arroyo Rodríguez, Luis Daniel Avila Cabadilla, Claudia E. Moreno, Ellen Andresen

Abstract

Understanding the factors and mechanisms shaping differences in species composition across space and time (β-diversity) in human-modified landscapes has key ecological and applied implications. This topic is, however, challenging because landscape disturbance can promote either decreases (biotic homogenization) or increases (biotic differentiation) in β-diversity. We assessed temporal differences in inter-site β-diversity of medium- and large-bodied mammals in the fragmented Lacandona rainforest, Mexico. We hypothesized that given the relatively short history of land-use changes in the region, and the gain and loss of some species caused by landscape spatial changes, β-diversity is increasing through time, especially its nestedness component. We estimated β-diversity between 24 forest sites (22 forest patches and two continuous forest sites) in 2011 and 2017 to assess whether β-diversity is decreasing or increasing in the region, and calculated its turnover and nestedness components to understand the mechanisms responsible for changes in β-diversity, separately assessing mammal groups with different body mass, feeding guild, and habitat specialization. We then related such temporal changes in β-diversity to temporal changes in five landscape variables (forest cover, matrix openness, number of patches, edge density and inter-patch distance) to identify the landscape drivers of β-diversity. In contrast to our expectations, β-diversity decreased over time, suggesting an ongoing biotic homogenization process. This pattern was mostly driven by a decrease in species turnover in all mammal groups, especially in landscapes with decreasing forest cover and increasing treed matrices. Although the nestedness component showed a 3-fold increase through time, species turnover was 22 and 6 times higher than nestedness in 2011 and 2017, respectively. The decreased turnover appears to be driven by an increase in the dispersal (i.e., spillover) of native species among patches. The prevalence of species turnover over nestedness indicates that different forest sites have a fairly distinct subset of species (i.e., high complementarity in species composition). Therefore, conserving all the remaining forest patches and increasing forest cover is of utmost importance to effectively maintain β-diversity and conserve the total diversity (γ) of mammal assemblages in this Mesoamerican biodiversity hotspot.

Key words: β-diversity; defaunation; habitat amount; landscape structure; matrix quality; nestedness; scale of effect.

Introduction

Habitat loss and degradation are major causes of the contemporary biodiversity crisis (Gibson et al. 2011). Such crisis is particularly strong in tropical forests – the most species-rich terrestrial ecosystem on Earth (Hillebrand 2004) and also the most deforested and fragmented (Hansen et al. 2013, Taubert et al. 2018). The remaining biotic assemblages are forced to inhabit forest patches embedded in matrices composed of anthropogenic land covers, such as human settlements, crops, and cattle pastures (Arroyo-Rodríguez et al. 2020). The responses to such conditions can be highly variable among species (Pfeifer et al. 2017, Betts et al. 2019). Yet, as most studies in human-modified landscapes assess changes in within-site diversity patterns (i.e., α-diversity), our understanding on the impact of landscape changes on between-site differences in species composition (i.e., β-diversity) across space and time remains very limited.

β-diversity is essential for understanding how species diversity is organized and maintained (Condit et al. 2002, Socolar et al. 2016). β-diversity can be partitioned into two components, the species turnover (i.e., the substitution of species in one site by different species in another site), and nestedness (i.e., the non-random loss of species that results in a poorer assemblage being a subset of a richer one) (Baselga and Orme 2012). However, not only has β-diversity received relatively low attention (but see McGill et al. 2015, Solar et al. 2015), it is also usually measured at one point in time, so temporal changes in spatial β-diversity have been largely overlooked (but see Lôbo et al. 2011, Baselga et al. 2015).

Changes in β-diversity can be caused by either a process of biotic homogenization or a process of biotic differentiation (Baselga 2010, Socolar et al. 2016). Biotic homogenization refers to a decrease over time in compositional dissimilarity across space (i.e., lower spatial β-diversity along time) (McKinney and Lockwood 1999, Solar et al. 2015). In contrast, biotic differentiation refers to the opposite process – an increased spatial β-diversity along time (Baiser et al. 2012). Both processes can be part of a continuum of changes in β-diversity along the human disturbance gradient (Socolar et al. 2016). For example, in low impacted landscapes, the arrival of disturbance-adapted species and/or invasive species to some sites and the extirpation of some native species from others can cause an increase in β-diversity (Socolar et al. 2016). Yet, in intermediate to high impacted landscapes, some invasive or disturbance-adapted native species can become ubiquitous and many native species can become extinct, promoting a loss of β-diversity (Tabarelli et al. 2012, Socolar et al. 2016).

These changes in β-diversity depend on several processes and mechanisms that alter the distribution and abundance of species; for example, species' dispersion ability (Baselga 2012). These mechanisms, in turn, may be caused (e.g., species introduction) or exacerbated (e.g., competitive exclusion) by human activities (Solar et al. 2015). Furthermore, other factors such as the spatial heterogeneity of the landscape, the degree of connectivity, environmental conditions, and the patterns of disturbance, can also influence biotic homogenization and differentiation processes (Tscharntke et al. 2012, Solar et al. 2015). Understanding which factors and mechanisms can lead to biotic homogenization or differentiation is a fundamental, yet understudied topic for biodiversity management and conservation in anthropogenic landscapes (Socolar et al. 2016). In fact, the few available studies on this topic are centered on tropical trees (Lôbo et al. 2011, Arroyo-Rodríguez et al. 2013*b*), insects (Solar et al. 2015), birds (Morante-Filho et al. 2016), and small mammals (Püttker et al. 2015), and do not assess other vulnerable groups of organisms, such as medium- and large-bodied terrestrial mammals.

Mammals are a very important component of tropical forests, where they play key ecosystem functions (Schipper et al. 2008, Dirzo et al. 2014). However, many species are being negatively affected by anthropogenic disturbances, such as habitat loss and hunting (Schipper et al. 2008, Ceballos et al. 2015, Barlow et al. 2016). Here, we present the first longitudinal assessment of β-diversity of medium and large mammal communities in the Lacandona rainforest, a biodiversity hotspot within the Mesoamerican Biological Corridor (Medellín 1994). We evaluated the changes in landscape structure in the region between 2010 and 2016 (*objective i*). We then compared inter-site β-diversity of mammals between 2011 and 2017 to identify whether biotic homogenization or differentiation is occurring in the region (*objective ii*). We partitioned β-diversity into its turnover and nestedness components and described the frequency distribution of species occurring in the sampling sites, and its change over time, to give some light on the mechanisms responsible for changes in β-diversity (*objective iii*). Furthermore, we assessed which changes in landscape attributes (i.e., forest cover, matrix openness, edge density, number of patches, and mean inter-patch distance) were more strongly associated with the observed temporal shifts in spatial β-diversity (*objective iv*). Finally (*objective v*), we assessed whether changes in β-diversity and its components are consistent across mammal groups with different ecological traits (body mass, diet and habitat specialization).

Following the model proposed by Socolar et al. (2016), and given the relatively recent history of land-use change (i.e., around 50 years) in the Lacandona region (Carabias et al. 2015), we hypothesized that the undergoing landscape spatial changes in the region are probably causing the loss of some species and the gain of others, potentially promoting an increase in β-diversity between study sites through time (biotic differentiation), especially the nestedness component of β-diversity. We also hypothesize that such increase in β-diversity is likely to be more evident in habitat-specialists, carnivores and large-bodied species than in habitat generalists, omnivore and mid-bodied species, because the former groups are expected to be more sensitive to landscape spatial changes (Dirzo et al. 2014, Bogoni et al. 2016).

Materials and Methods

Study area

Fieldwork was conducted in the Lacandona rainforest, Chiapas, Mexico (16º 05'N, 90º 25'W; Fig. 1). It has a warm and humid climate, with average monthly temperatures ranging from 26 to 36 ºC, and mean annual precipitation ranging from 1500 to 3500 mm (Instituto Nacional de Ecología 2000). This region is considered of high conservation priority in Mexico (Arriaga et al. 2000) and harbors the highest mammal diversity in the country (Medellín 1994). However, the Lacandona rainforest is suffering a rapid process of land-use change, mainly due to expanding agriculture, which is threatening mammal populations in the region (primates: Arroyo-Rodríguez et al. 2013*a*, Arce-Peña et al. 2019*a*; medium and large-sized mammals: Garmendia et al. 2013; small rodents: Arce-Peña et al. 2019*b*).

We collected data in two different areas: the Montes Azules Biosphere Reserve, which consists of 331,200 ha of continuous tropical rainforest (Instituto Nacional de Ecología 2000), and the Marqués de Comillas Region, which comprises 203,999 ha of anthropic land, with forest patches immersed in a matrix of agricultural lands and human settlements. We chose 22 forest patches in the Marqués de Comillas Region (3-92 ha; Fig. 1) and 4 continuous forest sites in the Montes Azules Biosphere Reserve, all located at similar altitudes (1-200 m a.s.l.). To ensure independence, forest patches were separated by at least 1.5 km, and continuous forest sites by at least 2.5 km.

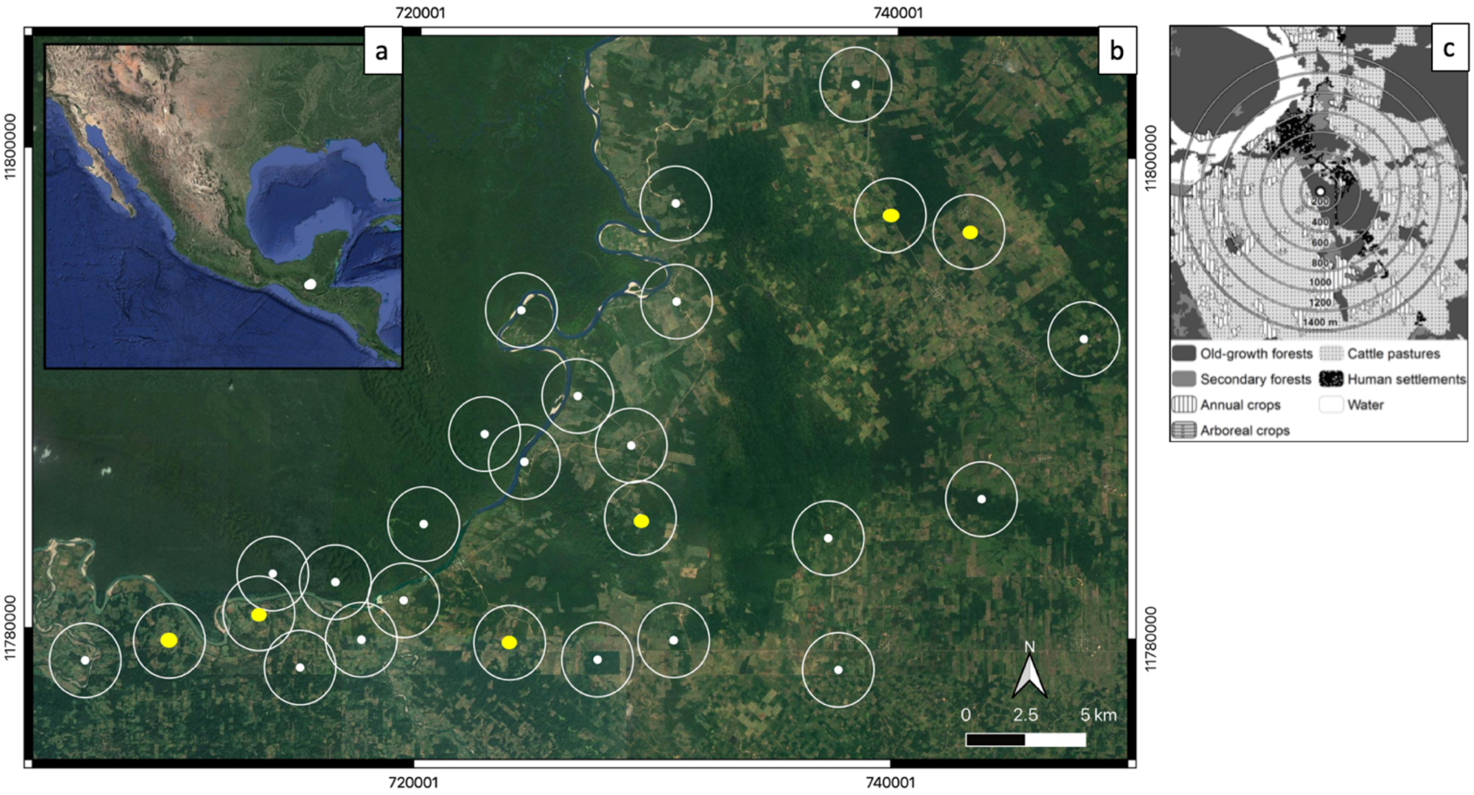


Figure 1. Location of the Lacandona region, Mexico (a), and forest sites studied in the Montes Azules Biosphere Reserve (large forest area in the upper left) and Marqués de Comillas region (right side), which are separated by the Lacantún River (b). We sampled terrestrial mammals in 22 forest patches and 4 continuous forest sites (white points in b), but 6 patches (in yellow) were excluded from the analysis because they showed a low sample coverage (see Methods). We measured landscape variables in different-sized landscapes surrounding each site (200-1,400-m radius, at 200-m intervals, from the center of each site) (c). White circles in (b) represent the largest landscape size.

Mammal sampling

We sampled mammals in 2011 and 2017, between April and October, using strictly the same methods described by Garmendia et al. (2013), including the same field assistant. We sampled mammals using camera-traps, ground tracks and direct sightings. We used three different sampling methods, as they provide complementary information (Silveira et al. 2003), allowing us to more accurately estimate mammal diversity within each site. We used one motion-activated camera-trap (Cuddeback Capture or Cuddeback Capture-IR Plus; recovery time of 30 s per photograph) in each forest site, placing it in locations favorable for mammal detection (i.e., with signs of use by mammals). Every 30 days we changed the location of the camera within the same site (0.06 – 1.1 km) and repeated this procedure for five months (i.e., 30 d x 5 mo = 150 camera-trap nights per site, with five sample points in each site). To register footprints and/or direct sightings, two people walked at a speed of 1 km h-1, between 6:00 and 16:00 h. Footprints were identified following Aranda-Sánchez (2012). We conducted these surveys once a month, for 6 months (i.e., 6 surveys per site). Duration of the survey in each site was determined by its area: 3-4 hr in small-sized patches (< 10 ha), 5-6 hr in medium-sized patches (10 - 50 ha), 7-8 hr in large-sized patches (> 50 ha), and 9-10 hr in continuous forest sites. Finally, we classified mammal species according to their size (medium = 0.5 to 20 kg, large > 20.0 kg), degree of forest specialization, and their feeding guild = carnivore (including insectivores), herbivore (including frugivores) and omnivore (Jones et al. 2009, IUCN 2019).

Landscape metrics

We followed a patch-landscape approach (sensu Fahrig 2013), i.e., we measured the landscape metrics within a given radius (buffer or landscape) measured from the geographic centroid of each of the sampled sites. We included both forest patches and continuous forest sites to get the broadest range possible of landscape spatial variables, from well-preserved sites (i.e., continuous forest sites) to highly disturbed ones (i.e., high-deforested landscapes). We obtained high-resolution (10 m) satellite images from 2010 (SPOT-5) and 2016 (Sentinel-2A), whose sensors have comparable radiometric features (Hagolle et al. 2015). We classified six different land-cover types using Spring 3.3 (Camara et al. 1996): old-growth forest, secondary forest, cattle pasture, annual crop, arboreal crop, and human settlement. Following Olofsson et al. (2014), we analyzed classification accuracy and obtained a very high accuracy (80%) in both years.

For each site, we measured metrics of landscape composition (i.e., percentage of forest cover and matrix openness) and landscape configuration (i.e., number of patches, edge density and mean inter-patch distance). Forest cover, the percentage of old-growth forest in the landscape, is a proxy of landscape-scale habitat amount, and is positively related to connectedness and resource availability (Fahrig 2003). Following previous studies in the region (Arce-Peña et al. 2019*a*, 2019*b*), matrix openness was measured as the percentage of the matrix area (not the landscape) covered by open areas (cattle pastures, annual crops and human settlements), a measure of the proportion of high contrast matrix, which is a concept widely used in related literature. An open matrix can increase negative edge effects, limit inter-patch movements, limit landscape supplementation dynamics, and increase the susceptibility of species to forest loss (Arroyo-Rodríguez et al. 2020, Boesing et al. 2018). The number of forest patches in the landscape is a measure of fragmentation, positively related to landscape connectedness and the number of subpopulations in the landscape (McGarigal et al. 2012). Edge density (m/ha), the length of all old-growth forest-patch edges divided by the total area of the landscape may have negative impacts in mammals through negative edge effects (Dunning et al. 1992, McGarigal et al. 2012). Finally, mean inter-patch distance was measured as the average value of the shortest distance between all pairs of patches in the landscape (McGarigal et al. 2012); it is inversely related to landscape connectedness, with potential negative effects on inter-patch movements (Bennet and Saunders 2010, McGarigal et al. 2012).

To avoid measuring landscape metrics at suboptimal scales (Jackson and Fahrig 2015), we evaluated the effect of each landscape metric on the response variables in seven different-sized landscapes containing each forest patch (radii of 200 m to 1,400 m, at 200-m intervals, from the center of each patch). As mammals hardly cross the 100-m wide Lacantún river (Arce-Peña et al. 2019*a*), we only characterized each landscape in the side of the river where the focal forest site was located (i.e., we excluded the spatial information from the other side of the river in the case of landscapes that encompass both areas; Fig. 1).

Data analysis

All analyses were carried out using R-version 3.5.1 (R-Core Team 2018). We generated a matrix of mammal abundances in each forest site, for 2011 and 2017, adding up the information obtained from the camera-traps, track surveys and direct sightings. Following previous camera-trap methodology (e.g., Kinnaird et al. 2003), we defined independent events as (i) consecutive photos of different species, (ii) consecutive photographs of different individuals of the same species taken more than 30 minutes apart, or (iii) non-consecutive photos of individuals of the same species. We considered footprints as independent events if they were separated by at least 300 m apart from each other or from the camera, and/or did not appear to belong to the same individual (e.g., two different-sized footprints). As unequal levels of effort, replication, and sample completeness make comparisons of richness and β-diversity problematic (Beck et al. 2013), we applied the same levels of effort and replication during the two sampling years. We analyzed sample completeness in each site, separately for 2011 and 2017, using the sample coverage estimator proposed by Chao and Shen (2010) using the 'iNext' package for R (Hsieh et al. 2019). Sample coverage was low ($C_n < 0.65$) in six forest patches, so we removed these sites from the analyses to avoid statistical type II error. Thus, the analyses that are described below are based on 20 forest sites (16 patches and 4 continuous forest sites).

Objective i: Landscape spatial changes

We used Generalized Linear Mixed Models to evaluate the differences between years (2016 value – 2010 value) for each landscape metric (forest cover, matrix openness, number of patches, edge density and mean inter-patch distance) at the largest scale (1,400-m radius landscape) in the 16 forest patches. Forest cover and matrix openness were analyzed with a binomial distribution and a logit-link-function. All other variables were analyzed with a normal error distribution and identity-link function. We assessed model fit with Shapiro-Wilk tests on model residuals. For all models, we used year as a fixed factor, and site ID as a random factor. We used likelihood ratio tests, in which we compared the complete models (i.e., with both fixed and random factors) with the null models (i.e., including only the random factor) to see if the former ones were a better fit for dependent variables (Pinheiro and Bates 2000).

Objectives ii and iii: Beta-diversity changes over time

We calculated changes in β-diversity from 2017 to 2011 and decomposed it into its turnover and nestedness components using R-package 'betapart' (Baselga et al. 2018). For this, we built a presence-absence matrix, and calculated total β-diversity using the multi-site Jaccard dissimilarity index β_{JAC}. Then, we partitioned the β_{JAC} into its components β_{JTU} (species turnover) and β_{JNE} (nestedness) for both time periods. We used Jaccard dissimilarity index (1-Jaccard similarity) because it is a linear transformation of the true beta diversity of order zero ($^0\beta$) for two-equally-weighted samples, and ranges from 0 to 1, thus facilitating subsequent comparisons between regions with different numbers of communities (Jost 2007). Also, it is the most commonly reported measure of change in similarity and dissimilarity, thus allowing comparisons with other studies (Olden et al. 2011). The change in β-diversity (Δ β-diversity) was measured as the difference between 2017 values and the 2011 values. We calculated P-values, by assessing the proportion of samples for which the expected results (compared to the observed one) was obtained by chance. For future comparison purposes, we also calculated the multi-site Sorensen dissimilarity indices β_{SOR} and its components β_{SIM} (turnover) and β_{SNE} (nestedness). Sorensen dissimilarity indices showed the same tendencies as the Jaccard dissimilarity indices (Appendix 1: Table S1). To interpret the observed patterns of β-diversity, we also analyzed the frequency of species that occurred in 0 to 16 forest patches for each year (Arroyo-Rodríguez et al. 2009).

Objective iv: Landscape predictors of beta-diversity

We analyzed the association between changes in landscape variables and changes in β-diversity using the 'betapart' R-package (Baselga et al. 2018). First, we built a matrix of β-diversity between pairs of sites for each year (i.e., one matrix for 2011 = β_{2011} and one for 2017 = β_{2017}), using the incidence-based pairwise Jaccard dissimilarity index. We built one matrix for β_{JAC}, β_{JTU} and β_{JNE} for both time periods. Then, we built a matrix of changes (deltas Δ) in β-diversity through time (i.e., $\Delta = \beta_{2017} - \beta_{2011}$). Using the same procedure, we built a matrix of pairwise differences in each landscape attribute between sites for each year, and matrices of deltas of landscape spatial differences between sites (i.e., Δ = 2016 value – 2010 value; Δ forest cover, Δ matrix openness, Δ number of patches, Δ edge density, and Δ mean inter-patch distance). We tested collinearity between predictors using Mantel tests and found no significant correlations between predictors. Then, using Mantel tests, we assessed the relationships between the Δ β-diversity matrices and the Δ landscape metrics matrices (Arroyo-Rodríguez et al. 2013*b*, Rosenblad and Sax 2016). Following Jackson and Fahrig (2015), we determined the scale of effect of each landscape metric change on spatial β-diversity change. To do so, we quantified the association between the change in each landscape metric and the change in β-diversity, at each spatial scale. We selected the spatial scale at which the strongest relationship occurred (highest Mantel *r* statistic; Appendix 1: Table S2).

Objective v: β-diversity of mammal ecological groups

We evaluated changes in β-diversity within ecological groups through time considering different ecological traits of the species (body mass, diet, and habitat specialization; Appendix 1: Table S3), obtaining multi-site Jaccard and Sorensen dissimilarity indices and their components. We assessed the significance of differences between 2011 and 2017 with the same procedure described in *Objective ii*.

Results

Objective i: Landscape spatial changes

The percentage of forest cover and matrix openness increased from 2010 to 2016, whereas mean inter-patch distance decreased (Table 1; Appendix 1: Table S4). The number of patches and edge density tended to decrease through time (Table 1; Appendix 1: Table S4). The likelihood ratio tests indicated that complete models were a better fit for the dependent variables than the null model ($P < 0.05$, in all cases).

Table 1. Landscape spatial changes (mean ± SD) from 2010 to 2016 in the Lacandona rainforest. Spatial metrics were assessed in 1,400-m radius landscapes (N = 16). Differences between years were evaluated with generalized linear mixed models and a likelihood ratio test.

Landscape metrics	**2010**	**2016**	**P**
Forest cover (%)	42.8 ± 13.8	46.7 ± 13.7	<0.001
Matrix openness (%)	73.4 ± 8.2	80.2 ± 14.8	<0.001
Number of patches	21.1 ± 11.2	18.4 ± 10.1	0.059
Edge density (m/ha)	94.0 ± 21.8	84.8 ± 27.9	0.062
Mean inter-patch distance (m)	1022.6 ± 153.9	934.7 ± 197.0	0.041

Objectives ii and iii: Beta-diversity changes over time

We recorded the same 21 mammal species in both years (Appendix 1: Table S3); eight species (38%) classified as endangered and 2 (10%) as threatened by the Mexican government. β-diversity significantly decreased from 2011 to 2017. Regarding changes in β-diversity (Δ β-diversity), the multiple-site Jaccard dissimilarity (β_{JAC}) across the total 20 forest sites was 0.92 for 2011 and 0.86 for 2017, resulting in a decrease in β-diversity of 6.5%. The turnover component of β-diversity (β_{JTU}) also decreased (13.6%) and accounted for most of the total dissimilarity, but the dissimilarity due to nestedness (β_{JNE}) increased by 200% (Table 2). Sorensen indices presented the same tendency as Jaccard indices (Appendix 1: Table S1).

Table 2. Results of Baselga's multi-site dissimilarity indices based on Jaccard's index. We show the values for 2011 and 2017, and the Δ β-diversity (2017 values - 2011 values). Negative Δ values indicate a decrease in β-diversity through time. Significant differences are indicated with asterisks (* $P < 0.05$, ** $P < 0.005$).

Index	2011	2017	Δ
Beta-JAC (total)	0.92	0.86	-0.06**
Beta-JTU (turnover)	0.88	0.76	-0.12**
Beta-JNE (nestedness)	0.04	0.12	0.08*

Only one species (*Tayassu pecari*) was restricted to continuous forest sites in both years, and the rest (20 species) occurred in both continuous forest sites and forest patches. Most species in 2011 were recorded in 1-4 patches, whereas in 2017 the species were more widely distributed across forest patches (Fig. 2; Appendix 1: Table S3).

Objective iv: Beta and landscape variables

The temporal changes in total β-diversity (ΔJAC) were not significantly associated with changes in any landscape metric. Yet, species turnover (ΔJTU) increased in those forest sites where both forest cover and matrix openness increased through time. The nestedness component of β-diversity (ΔJNE) was also significantly related to landscape changes, increasing in forest sites with increasing number of patches, edge density and inter-patch distance (Table 3).

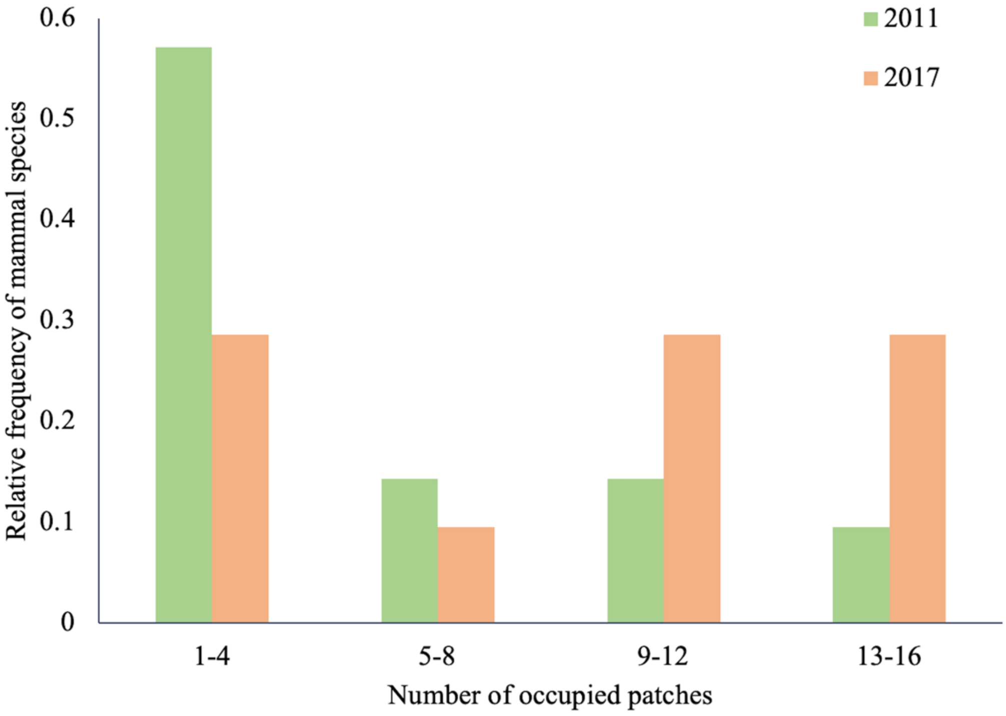


Figure 2. Relative frequency distribution of medium and large terrestrial mammal species across forest patches (n = 16) in the Lacandona rainforest, Mexico. We sampled mammals in the same sites in 2011 and 2017, registering the same 21 species in both years.

Table 3. Correlation coefficients (Mantel tests) between Baselga's pair-wise dissimilarity indices and changes in landscape spatial attributes through time. Positive coefficients indicate that increases in a given landscape variable promote an increase in dissimilarity through time (* $P < 0.1$, ** $P < 0.05$). Numbers within parentheses show the scale of effect, i.e., the landscape radius (m) that yields the strongest correlation coefficients.

Index	**ΔForest cover**	**ΔMatrix openness**	**ΔNumber of patches**	**ΔInter-patch distance**	**ΔEdge density**
ΔJAC	0.21	0.14	-0.20	-0.28	-0.20
	(600)	(200)	(1200)	(1200)	(200)
ΔJTU	0.22*	0.25**	-0.27	-0.31	-0.28
	(200)	(200)	(200)	(1000)	(200)
ΔJNE	-0.17	-0.21	0.25**	0.22**	0.20**
	(200)	(200)	(200)	(800)	(200)

Objective v: β-diversity and mammal ecological groups

Total β-diversity and the turnover component decreased through time in all ecological groups (Table 4; Appendix 1: Table S5). However, the nestedness component increased through time, but only in large-bodied, non-specialist, herbivore and omnivore species (Table 4; Appendix 1: Table S5).

Table 4. Differences (Δ) in β-diversity (i.e., based on Jaccard indices) between 2011 and 2017 in 20 forest sites from the Lacandona rainforest, separately assessing mammal species within different ecological groups. Negative Δ values indicate a decrease in β-diversity through time. We classified mammal species into ecological groups according to the following traits (Appendix 1: Table S3): body mass (medium = 0.5 to 20 kg, large > 20 kg), diet (carnivore, omnivore, herbivore), and whether they are forest specialists or not. Significant differences between years are indicated with asterisks (* $P < 0.05$, ** $P < 0.005$).

Ecological trait	**Δβ-JAC (total)**	**Δ β-JTU (turnover)**	**Δβ-JNE (nestedness)**
Body mass			
Medium (*n* = 14)	-0.073*	-0.081*	0.008
Large (*n* = 7)	-0.043*	-0.265*	0.221*
Diet			
Carnivores (*n* = 9)	-0.060*	-0.140*	0.085
Herbivores (*n* = 5)	-0.067*	-0.351*	0.284*
Omnivores (*n* = 7)	-0.099*	-0.258*	0.159*
Habitat specialization			
Forest specialists (*n* = 4)	-0.057*	-0.073	0.016
Non-specialists (*n* = 17)	-0.054*	-0.506*	0.448*

Discussion

The present assessment of the temporal changes in landscape structure and spatial β-diversity of terrestrial mammal assemblages indicates that the Lacandona rainforest is highly dynamic. In a relatively short time period, we found significant differences in landscape structure between 2010 and 2016, and a notable increase in between-site similarity in species composition (i.e., loss of β-diversity), thus suggesting that there is an ongoing biotic homogenization process in the region. Such a loss of β-diversity was mostly driven by a decrease in species turnover in all mammal groups, especially in landscapes with decreasing forest cover and increasing treed matrices over time. Although species turnover was 6 to 22 times higher than nestedness, the nestedness component of β-diversity showed a 3-fold increase from 2011 to 2017, especially in large-bodied, non-specialist, herbivore and omnivore species. The increase in nestedness was significantly higher in forest sites with an increasing number of patches, forest edge density and mean inter-patch distance over time. These findings have critical ecological implications of high applied value for the long-term conservation of terrestrial mammals in human-modified tropical landscapes.

Landscape structure is rapidly changing in the Mexican portion of the Lacandona rainforest. We found a significant increase in matrix openness caused by the conversion of treed matrices such as arboreal crops to open areas (e.g., annual crops, pastures and human settlements). Although this landscape spatial change could limit inter-patch animal movements (reviewed by Arroyo-Rodríguez et al. 2020), this potential loss of landscape connectivity was likely offset by the significant increase in forest cover and decrease of inter-patch isolation distances. In fact, some forest patches merged through secondary forests, leading to the observed decrease in the number of patches and forest edge density through time. As argued below, these landscape changes can enhance the spillover of organisms, helping to explain the observed loss of mammal β-diversity.

Contrary to our hypothesis, the region seems to be experiencing an ongoing biotic homogenization process. This is consistent with previous studies of different taxa (Baiser et al. 2012, Karp et al. 2012, Solar et al. 2015, Rosenblad and Sax 2016), including tropical mammals in other human-modified landscapes (Spear and Chown 2008, Beca et al. 2017, Longman et al. 2018, Alves et al. 2020). Such a loss of β-diversity was mainly related to the loss of species turnover in all studied mammal groups, which also support previous studies (Solar et al. 2015, Beca et al. 2017, Longman et al. 2018, Regolin et al. 2020). This suggests that the loss of β-diversity is likely being caused by an increased movement of individuals from native species among forest sites, and not by the extinction of natives or the colonization of invasive species, as found in other studies (e.g., Spear and Chown 2008, Beca et al. 2017, Longman et al. 2018, Alves et al. 2020). In fact, the proportion of species with restricted distribution (e.g., limited to 1-4 sites) fell by half in 2017 compared to 2011, and most species in 2017 were widely distributed across forest patches. Also, we recorded no extinctions, and we did not register any exotic species within the forest sites. Therefore, the observed loss of β-diversity is not as worrying as described in other studies

(McKinney and Lockwood 1999, Olden et al. 2004, Tabarelli et al. 2012), as it seems to be related to the spillover of organisms across forest sites, and not to the taxonomic or functional impoverishment of remaining assemblages.

The spillover hypothesis is particularly plausible in light of the observed relationships between species turnover and landscape structure. Species turnover tended to decrease with decreasing forest cover and increasing treed matrices. The negative effect of landscape forest loss on tropical biodiversity (including terrestrial mammals) is well documented (Benchimol and Peres 2013, Banks-Leite et al. 2014, Arce-Peña et al. 2019*b*, Watling et al. 2020), possibly because of its negative effect on resource availability (Fahrig 2003, 2013). Thus, forest loss may 'force' organisms to move more among forest sites to find complementary and/or supplementary resources. Such movements can be facilitated or even enhanced in landscapes with increasing treed land covers in the matrix, as these land covers are known to increase the quality and permeability of the matrix (reviewed by Arroyo-Rodríguez et al. 2020).

The prevalence of species turnover over nestedness has important ecological and applied implications. Species turnover was 22 and 6 times higher than nestedness in 2011 and 2017, respectively. This supports a recent meta-analysis on the prevalence of species turnover over nestedness across wide ranges of ecosystems (Soininen et al. 2018). As the turnover component of β-diversity reflects changes in species identities between sites (Baselga 2012), the observed pattern indicates that different forest patches present a fairly distinct subset of species (i.e., high complementarity in species composition; Beca et al. 2017). This is not surprising, as plant species composition in tropical forests is known to be highly variable across space, largely due to the patchy distribution of most species (e.g., Condit et al. 2002, Arroyo-Rodríguez et al. 2013*b*), which can in turn promote an increase in the species turnover of herbivore and predator assemblages. Therefore, consistent with recent proposals for designing biodiversity-friendly landscapes (Arroyo-Rodríguez et al. 2020), this finding suggests that conserving all the remaining forest sites is of utmost importance to effectively conserve mammal assemblages.

Despite the prevalence of turnover over nestedness, we found a 3-fold increase in nestedness, especially in forest sites found in landscapes where the number of patches, forest edge density and mean inter-patch distance increased through time. Nestedness occurs when the biotas of sites with smaller species richness are subsets of the biotas at richer sites (Baselga 2010), and usually increases along the disturbance gradient because of the deterministic loss of some native species (Baselga 2010, Baiser et al. 2012). In this sense, as the observed increase in all landscape configuration variables is caused by forest loss, our findings suggest that the fragmentation process (dependent of forest cover), not fragmentation per se (sensu Fahrig 2003) can be causing the extirpation of some species. In particular, the significant temporal increase in nestedness of large-bodied, non-specialist, herbivore and omnivore species suggests that such a native extinction (sensu Baselga 2010) might be more important in species from these groups – a topic that merits further investigation.

Conclusion

Taken together, our findings have important applied implications that can be used to preserve terrestrial mammal assemblages in this and other rainforest regions. First, the observed loss of β-diversity is likely being caused by an increased movement of individuals among forest sites, and not by the extinction of natives or invasion of exotic species. Thus, there is still a great opportunity for implementing time- and cost-effective measures that allow the conservation of all native species and prevent potential negative effects from the arrival of exotic species. Second, to prevent species loss, it is of utmost importance to maintain and increase the forest cover in the landscape and convert the existing treeless areas in the matrix to land covers more similar to the original forest. High forest covers and treed land covers increase the quality and permeability of the landscape, facilitating and enhancing species movements through the matrix and the remaining forest sites (Arroyo-Rodríguez et al. 2020). Increasing landscape connectivity is also highly valuable, for example, by allowing forest patches to increase in number and/or size through active or passive restoration (reverse fragmentation; sensu del Castillo 2015), protecting/restoring riparian corridors and promoting semi-natural treed elements (e.g., living fences, hedgerows and single standing trees) in the matrix (Arroyo-Rodríguez et al. 2020). These measures will ensure landscape connectedness and resource availability for forest-dependent mammals, promoting dispersal, gene-flow and the maintenance of a high β-diversity in the region. Although these measures will probably enhance inter-patch movements and thus decrease beta diversity at the regional scale, there is strong evidence on their positive effect on local (alpha) diversity (e.g., Reider et al. 2018, Watling et al. 2020). Finally, it is important to note that β-diversity was mostly driven by species turnover. Therefore, the maintenance of all the remaining forest sites is of great importance to effectively conserve mammal assemblages.

Acknowledgements

We thank financial support provided by Rufford Small Grants (22049-1), SEP-CONACyT (2015-253946), and DGAPA-UNAM (IA-203111). NPAP obtained a CONACyT scholarship. This paper constitutes a partial fulfillment of the PhD program of the Posgrado en Ciencias Biológicas, UNAM. We thank Adriana Garmendia for allowing the use of her data, Iván Franch-Pardo for technical support in GIS, Marqués de Comillas landowners for allowing us to collect data on their properties, and CONANP. Finally, we thank Natura y Ecosistemas Mexicanos and the Chajul Biological Station for providing logistical support. A special acknowledgement to Adolfo Jamangapé. This research is based on observational data. It adhered to national and international guidelines and was conducted in accordance with the legal requirements of UNAM and Mexico (NOM-059: SEMARNAT 2010).

Author's contributions

N.P.A.-P. and V.A.-R. conceived the study. N.P.A.-P. did the field work and analyzed the data with significant advice from V.A.-R., C.E.M., L.D.A.-C. and E.A. N.P.A.-P. prepared the first draft and all co-authors made significant contributions to the final manuscript. All authors gave final approval for publication.

Data Availability

Data is available at Figshare: https://doi.org/10.6084/m9.figshare.129782

References

Alves, T.S., Alvarado, F., Arroyo-Rodríguez, V., Santos, B.A. 2017. Landscape-scale patterns and drivers of novel mammalian communities in a human-modified protected area. Landscape Ecology 5: 619–1633.

Aranda-Sánchez, J.M. 2012. Manual para el rastreo de mamíferos silvestres de México. CONABIO, Mexico City, Mexico.

Arce-Peña, N.P., Arroyo-Rodríguez, V., Dias, P.A.D., Franch-Pardo, I., Andresen, E. 2019a. Linking changes in landscape structure to population changes of an endangered primate. Landscape Ecology 34: 2687–2701.

Arce-Peña, N.P., Arroyo-Rodríguez, V., San-José, M., Jiménez-González, D., Franch-Pardo, I., Andresen, E., Avila-Cabadilla, L.D. 2019b. Landscape predictors of rodent dynamics in fragmented rainforests. Biodiversity and Conservation 28: 655–669.

Arriaga, L., Espinoza, J., Aguilar, C., Martínez, E., Gómez, L., Loa, E. 2000. Regiones terrestres prioritarias de México. CONABIO, Mexico City, Mexico.

Arroyo-Rodríguez, V., Fahrig, L., Tabarelli, M., Watling, J.I., Tischendorf, L., Benchimol, M., Cazetta, E., Faria, D., Leal, I.R., Melo, F.P.L, Morante-Filho, J.C., Santos, B.A., Arasa-Gisbert, R., Arce-Peña, N., Cervantes-López, M.J., Cudney-Valenzuela, S., Galán-Acedo, C., San-José, M., Vieira, I.C.G., Slik, J.W.F., Nowakowski, J., Tscharntke, T. 2020. Designing optimal human-modified landscapes for forest biodiversity conservation. Ecology Letters 23: 1404–1420.

Arroyo-Rodríguez, V., González-Perez, I.M., Garmendia, A., Solà, M., Estrada, A. 2013a. The relative impact of forest patch and landscape attributes on black howler monkey populations in the fragmented Lacandona rainforest, Mexico. Landscape Ecology 8: 1717–1727.

Arroyo-Rodríguez, V., Pineda, E., Escobar, F., Benítez-Malvido, J. 2009. Value of small patches in the conservation of plant-species diversity in highly fragmented rainforest. Conservation Biology 23: 729–739.

Arroyo-Rodríguez, V., Rös, M., Escobar, F., Melo, F.P.L., Santos, B.A., Tabarelli, M., Chazdon, R. 2013b. Plant β-diversity in fragmented rain forests: testing floristic homogenization and differentiation hypotheses. Journal of Ecology 101: 1449–1458.

Baiser, B., Olden, J.D., Record, S., Lockwood, J.L., McKinney, M.L. 2012. Pattern and process of biotic homogenization in the New Pangaea. Proceedings of the Royal Society B 279: 4772–4777.

Banks-Leite, C., Pardini, R., Tambosi, L.R., Pearse, W.D., Bueno, A.A., Bruscagin, R.T., Condez, T.H., Dixo, M., Igari, A.T., Martensen, A.C., Metzger, J.P. 2014. Using ecological thresholds to evaluate the costs and benefits of set-asides in a biodiversity hotspot. Science 345: 1041–1045.

Barlow, J., Lennox, G.D., Ferreira, J., Berenguer, E., Lees, A.C., Mac Nally, R., Thomson, J.R., de Barros Ferraz, S.F., Louzada, J., et al. 2016. Anthropogenic disturbance in tropical forests can double biodiversity loss from deforestation. Nature 535: 144–147.

Baselga, A. 2010. Partitioning the turnover and nestedness components of beta diversity. Global Ecology and Biogeography 19: 134–143.

Baselga, A. 2012. The relationship between species replacement, dissimilarity derived from nestedness, and nestedness. Global Ecology and Biogeography 21: 1223–1232.

Baselga, A., Bonthoux, S., Balent, G. 2015. Temporal beta diversity of bird assemblages in agricultural landscapes: land cover change vs. stochastic processes. PLoS ONE 10: e0127913.

Baselga, A., Orme, D. 2012. Betapart: an R package for the study of beta diversity. Methods in Ecology and Evolution 3: 808–812.

Baselga, A., Orme, D., Villeger, S., De Bortoli, J., Leprieur, F., Logez, M., Henriques-Silva, R. 2018. Betapart: partitioning beta diversity into turnover and nestedness components. R-package version 1.5.1. https://CRAN.R-project.org/package=betapart (accessed on August 28th, 2019).

Beca, G., Vancine, M.H., Carvalho, C.S., Pedrosa, F., Alves, R.A.C., Buscariol, D., Peres, C.A., Ribeiro, M.C., Galetti, M. 2017. High mammal species turnover in forest patches immersed in biofuel plantations. Biological Conservation 210: 352–359.

Beck, H., Snodgradd, J.W., Thebpanya, P. 2013. Long-term exclosure of large terrestrial vertebrates: implications of defaunation for seedling demographics in the Amazon rainforest. Biological Conservation 163: 115–121.

Benchimol, M., Peres, C.A. 2013. Anthropogenic modulators of species-area relationships in Neotropical primates: a continental-scale analysis of fragmented forest landscapes. Diversity and Distributions 19: 1339–1352.

Bennett, A. F., Saunders, D.A. 2010. Habitat fragmentation and landscape change. In: Sodhi, N.S., Ehrlich, P.R. (Eds) Conservation Biology for All. Oxford University Press, pp 88–106.

Betts, M.G., Wolf, C., Pfeifer, M., Banks-Leite, C., Arroyo-Rodríguez, V., Bandini Ribeiro, D., Barlow, J., Eigenbrod, F., Faria, D., et al. 2019. Extinction filters mediate the global effects of habitat fragmentation on animals. Science 366: 1236–1239.

Boesing, A.L., Nichols, E., Metzger, J.P. 2018. Biodiversity extinction thresholds are modulated by matrix type. Ecography 41: 1520–1533.

Bogoni, J.A., Cherem, J.J., Hettwer-Giehl, E.L., Oliveira-Santos, L.G., de Castilho, P.V., Filho, V.P., Fantacini, F.M., Tortato, M.A., Ribeiro-Luiz, M.R., Rizzaro, R., Graipel, M.E. 2016. Landscape features lead to shifts in communities of medium-to large-bodied mammals in subtropical Atlantic Forest. Journal of Mammalogy 97: 713–725.

Camara, G., Souza, R.C.M., Freitas, U.M., Garrido, J. 1996. SPRING: Integrating remote sensing and GIS by object-oriented data modelling. Computers and Graphics 20: 395–403.

Carabias, J., de la Maza, J., Cadena, R. 2015. Conservación y desarrollo sustentable en la Selva Lacandona, 25 años de actividades y experiencias. Natura y Ecosistemas Mexicanos, Mexico City, Mexico.

Ceballos, G., Ehrlich, P.R., Barnosky, A.D, García, A., Pringle, R.M., Palmer, T.M. 2015. Accelerated modern human-induced species losses: entering the sixth mass extinction. Science Advances 1: e1400253.

Chao, A., Shen, T.J. 2010. Program SPADE: Species Prediction and Diversity Estimation. Program and user's guide. http://chao.stat.nthu.edu.tw/softwareCE.html (accessed on August 28th, 2019).

Condit, R., Pitman, N., Leigh, E.G.Jr., Chave, J., Terborgh, J., Foster, R.B., Núñez, P., Aguilar, S., Valencia, R., Villa, G., Muller-Landau, H.C., Losos, E., Hubbell, S.P. 2002. Beta-diversity in tropical forest trees. Science 295: 666–669.

Del Castillo, R.F. 2015. A conceptual framework to describe the ecology of fragmented landscapes and implications for conservation and management. Ecological Applications 25: 1447–1455.

Dirzo, R., Young, H.S., Galetti, M., Ceballos, G., Isaac, N.J.B., Collen, B. 2014. Defaunation in the Anthropocene. Science 345: 401–406.

Dunning, J.B., Danielson, B.J., Pulliam, R. 1992. Ecological processes that affect populations in complex landscapes. Oikos 65: 169–175.

Fahrig, L. 2003. Effects of habitat fragmentation on biodiversity. Annual Review of Ecology, Evolution and Systematics 34: 487–515.

Fahrig, L. 2013. Rethinking patch size and isolation effects: the habitat amount hypothesis. Journal of Biogeography 40: 1649–1663.

Fahrig, L. 2017. Ecological responses to habitat fragmentation *per se*. Annual Review of Ecology, Evolution, and Systematics 48: 1–23.

Garmendia, A., Arroyo-Rodríguez, V., Estrada, A., Naranjo, E., Stoner, K.E. 2013. Landscape and patch attributes impacting medium- and large-sized terrestrial mammals in a fragmented rain forest. Journal of Tropical Ecology 29: 331–344.

Gibson, L., Ming-Lee, T., Koh, L.P., Brook, B.W., Gardner, T.A., Barlow, J., Peres, C.A., Bradshaw, C.J.A., Laurance, W.F., Lovejoy, T.E., Sodhi, N.S. 2011. Primary forests are irreplaceable for sustaining tropical biodiversity. Nature 478: 378–383.

Hagolle, O., Sylvander, S., Huc, M., Claverie, M., Clesse, D., Dechoz, C., Lonjou, V., Poulain, V. 2015. SPOT-4 (Take 5): simulation of Sentinel-2 time series on 45 large sites. Remote Sensing 7: 12242–12264.

Hansen, M.C., Potapov, P.V., Moore, R., Hancher, M., Turubanova, S.A., Tyukavina, A., Thau, D., Stehman, S.V., Goetz, S.J., Loveland, T.R., Kommareddy, A., Egorov, A., Chini, L., Justice, C.O., Townshend, J.R.G. 2013. High-resolution global maps of 21st century forest cover change. Science 342: 850–853.

Hillebrand, H. 2004. On the generality of the latitudinal diversity gradient. The American Naturalist 163: 192–211.

Hsieh, T C., Ma, K.H., Chao, A. 2019. iNEXT: iNterpolation and EXTrapolation for species diversity. R package version 2.0.19. http://chao.stat.nthu.edu.tw/blog/software-download/ (accessed on August 28th, 2019).

Instituto Nacional de Ecología. 2000. Programa de Manejo Reserva de la Biósfera Montes Azules. SEMARNAT, Mexico City, Mexico.

IUCN. 2019. The IUCN Red List of Threatened Species. Version 2019-1. https://www.iucnredlist.org (accessed on August 2th, 2019).

Jackson, H.B., Fahrig, L. 2015. Are ecologists conducting research at the optimal scale? Global Ecology and Biogeography 24: 52–63.

Jones, K.E., Bielby, J., Cardillo, M., Fritz, S.A., O´Dell, J., Orme, C.D.L., Safi, K., Sechrest, W., Boakes, E.H., Carbone, C., Connolly, C., et al. 2009. PanTHERIA: a species-level database of life history, ecology, and geography of extant and recently extinct mammals. Ecology 90: 2648–2648.

Jost, L. 2007. Partitioning diversity into independent alpha and beta components. Ecology 88: 2427–2439.

Karp, D.S., Rominger, A.J., Zook, J., Ranganathan, J., Ehrlich, P.R., Daily, G.C. 2012. Intensive agriculture erodes β-diversity at large scales. Ecology Letters 15: 963–970.

Kinnaird, M.F., Sanderson, E.W., O'Brien, T.G., Wibisono, H.T., Woolmer, G. 2003. Deforestation trends in a tropical landscape and implications for endangered large mammals. Conservation Biology 17: 245–257.

Lôbo, D., Leao, T., Melo, F.P.L., Santos, A.M.M., Tabarelli, M. 2011. Forest fragmentation drives Atlantic forest of northeastern Brazil to biotic homogenization. Diversity and Distributions 17: 287–296.

Longman, E.K., Rosenblad, K., Sax, D.F. 2018. Extreme homogenization: the past, present and future of mammal assemblages on islands. Ecology and Biogeography 27: 77–95.

McGarigal, K., Cushman, S.A., Ene, E. 2012. FRAGSTATS v4: Spatial Pattern Analysis Program for Categorical and Continuous Maps. Computer software program produced by the authors at the University of Massachusetts, Amherst. http://www.umass.edu/landeco/research/fragstats/fragstats.html (accessed on October 14th, 2019).

McGill, B.J., Dornelas, M., Gotelli, N.J., Magurran, A.E. 2015. Fifteen forms of biodiversity trend in the Anthropocene. Trends in Ecology and Evolution 30: 104–113.

McKinney, M.L., Lockwood, J.L. 1999. Biotic homogenization: a few winners replacing many losers in the next mass extinction. Trends in Ecology and Evolution 14: 450–453.

Medellín, R. 1994. Mammal diversity and conservation in the Selva Lacandona, Chiapas, Mexico. Conservation Biology 8: 780–799.

Morante-Filho, J.C., Arroyo-Rodríguez, V., Faria, D. 2016. Patterns and predictors of β-diversity in the fragmented Brazilian Atlantic forest: A multiscale analysis of forest specialist and generalist birds. Journal of Animal Ecology 85: 240–250.

Olden, J.D., Poff, N.L., Douglas, M.R., Douglas, M.E., Fausch, K.D. 2004. Ecological and evolutionary consequences of biotic homogenization. Trends in Ecology and Evolution 19: 18–24.

Olden, J.D., Lockwood, J.L., Parr, C.L. 2011. Biological invasions and the homogenization of faunas and floras. In: Ladle, P.R., Whittaker, R.J. (Eds) Conservation Biogeography. John Wiley and Sons, pp 224–243.

Olofsson, P., Foody, G.M., Herold, M., Stehman, S.V., Woodcock, C.E., Wulder, M.A. 2014. Good practices for estimating area and assessing accuracy of land change. Remote Sensing of Environment 148: 42–57.

Pfeifer, M., Lefebvre, V., Peres, C.A., Banks-Leite, C., Wearn, O.R., Marsh, C.J., Butchart, S.H.M., Arroyo-Rodríguez, V., Barlow, J., Cerezo, A., Cisneros, L., et al. 2017. Creation of forest edges has a global impact on forest vertebrates. Nature 551: 187–195.

Pinheiro, J., Bates, D. 2000. Mixed-effects models in S and S-plus. Springer, New York, USA.

Püttker, T., Bueno, A.A., Prado, P.I., Pardini, R. 2015. Ecological filtering or random extinction? Beta-diversity patterns and the importance of niche-based and neutral processes following habitat loss. OIKOS 124: 206–215.

R-Core Team. 2018. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org/ (accessed on September 23rd, 2019).

Reider, I.J., Donnelly, M.A., Watling, J.I. 2018. The influence of matrix quality on species richness in remnant forest. Landscape Ecology 33: 1147–1157.

Regolin, A.L., Ribeiro, M.C., Martello, F., Melo, G.L., Sponchiado, J., de Castro-Campanha, L.F., Moreira-Sugai, L.S., Freire-Silva, T.S., Cáceres, N.C. 2020. Spatial heterogeneity and habitat configuration overcome habitat composition influences on alpha and beta mammal diversity. Biotropica 52: 969–980.

Rosenblad, K.C., Sax, D.F. 2016. A new framework for investigating biotic homogenization and exploring future trajectories: oceanic island plant and bird assemblages as a case study. Ecography 39: 1–10.

Schipper, J., Chanson, J.S., Chiozza, F., Cox, N.A., Hoffmann, M., Katariya, V., Young, B.E. 2008. The status of the world's land and marine mammals: diversity, threat, and knowledge. Science 322: 225–230.

Silveira, L., Jácomo, A.T., Diniz-Filho, J.A. 2003. Camera trap, line transect census and track surveys: a comparative evaluation. Biological Conservation 114: 351–355.

Socolar, J.B., Gilroy, J.J., Kunin, W.E., Edwards, D.P. 2016. How should beta-diversity inform biodiversity conservation? Trends in Ecology and Evolution 31: 67–80.

Soininen, J., Heino, J., Wang, J. 2018. A meta-analysis of nestedness and turnover components of beta diversity across organisms and ecosystems. Global Ecology and Biogeography 27: 96–109.

Solar, R.R.D., Barlow, J., Ferreira, J., Berenguer, E., Lees, A.C., Thomson, J.R., Louzada, J., Maués, M., Moura, N.G., Oliveira, V.H.F., Chaul, J.C.M., Schroereder, J.H., Guimarães-Vieira, I.C., Mac-Nally, R., Gardner, T.A. 2015. How pervasive is biotic homogenization in human-modified tropical forest landscapes? Ecology Letters 18: 1108–1118.

Spear, D., Chown, S.L. 2008. Taxonomic homogenization in ungulates: patterns and mechanisms at local and global scales. Journal of Biogeography 35: 1962–1975.

Tabarelli, M., Peres, C.A., Melo, F.P.L. 2012. The 'few winners and many losers' paradigm revisited: emerging prospects for tropical forest biodiversity. Biological Conservation 155: 136–140.

Taubert, F., Fischer, R., Groeneveld, J., Lehmann, S., Müller, M.S., Rödig, E., Wiegand, T., Huth, A. 2018. Global patterns of tropical forest fragmentation. Nature 554: 519–522.

Tscharntke, T., Tylianakis, J.M., Rand, T.A., Didhma, R.K., Fahrig, L., Batáry, P., Bengtsson, J., et al. 2012. Landscape moderation of biodiversity patterns and processes – eight hypotheses. Biological Reviews 87: 661–685.

Watling J.I., Arroyo-Rodríguez, V., Pfeifer, M., Baeten, L., Banks-Leite, C., Cisneros, L.M., Fang, R., Hamel-Leigue, A.C., Lachat, T., Leal, I.R., Lens, L., Possingham, H.P., Raheem, D.C., Ribeiro, D.B., Slade, E.M., Urbina-Cardona, J.N., Wood, E.M., Fahrig, L. 2020. Support for the habitat amount hypothesis from a global synthesis of species density studies. Ecology Letters 23: 674–681.

Supplementary material

Table S1. Baselga's multi-site indices based on Sorensen's index. We show the obtained values for 2011 and 2017, and the Δ-β-diversity (2017 values - 2011 values). For the deltas, negative values indicate a decrease in dissimilarity through time. Significant differences between years are indicated with asterisks (* $P < 0.05$, ** $P < 0.005$).

Index	**2011**	**2017**	**Δ**
Beta-SOR (total)	0.85	0.75	-0.1**
Beta-SIM (turnover)	0.78	0.61	-0.17**
Beta-SNE (nestedness)	0.07	0.14	0.07*

Table S2. Association between Baselga's multi-site dissimilarity indices and changes in landscape spatial attributes through time (2016 values – 2010 values). We assessed the scale of effect, measuring changes in landscape structure considering 7 different-sized radii (200 m – 1400 m) to identify the landscape size that yields the strongest predictor-response association. We conducted Mantel tests and obtained the Mantel statistic r. Values in bold indicate the selected scale of effect (highest r-value) for each predictor-response association. Significant differences between years are indicated with asterisks (* $P < 0.05$, ** $P < 0.005$).

	ΔForest Cover	**ΔMatrix Openness**	**ΔNumber of patches**	**ΔEdge Density**	**ΔInter-Patch Distance**
ΔJAC					
1400	0.121	0.086	-0.129	-0.133	-0.125
1200	0.126	0.065	**-0.201**	-0.051	**-0.279**
1000	0.119	0.057	-0.051	0.014	-0.247
800	0.144	0.045	-0.056	0.025	-0.044
600	**0.208**	0.105	-0.095	-0.046	0.077
400	0.177	0.006	-0.151	-0.193	-0.192
200	0.145	**0.144**	-0.128	**-0.197**	-0.202
ΔJTU					
1400	0.034	0.184	0.03	-0.11	-0.181
1200	0.024	0.143	-0.174	0.047	-0.239
1000	0.006	0.151	-0.045	0.104	**-0.309**
800	0.005	0.119	-0.109	0.031	-0.19
600	0.047	0.085	-0.0003	-0.02	0.016
400	0.059	0.127	-0.01	-0.101	-0.095
200	**0.223**	**0.253***	**-0.267**	**-0.278**	-0.295
ΔJNE					
1400	0.07	-0.172	-0.017	0.023	0.131
1200	0.088	-0.136	0.047	-0.115	0.061
1000	0.108	-0.154	0.012	-0.131	0.189
800	0.132	-0.122	0.097	-0.019	**0.222***
600	0.138	-0.016	-0.091	-0.017	0.052
400	0.09	-0.17	-0.013	-0.047	-0.055
200	**-0.17**	**-0.212**	**0.249***	**0.195***	0.214*

Table S3. Mammal species registered in 2011 and 2017 in the Lacandona rainforest, Mexico. We show their conservation status according to the IUCN (2019) and to the Mexican government (SEMARNAT, 2010). DD = Data Deficient, LC = Least Concern, NT = Near Threatened, VU = Vulnerable, EN = Endangered, SP = Special Protection, TH = Threatened. We present the number of forest fragments (FF) and continuous forest sites (CF) occupied by each species in 2011 and in 2017. We classify mammal species according to their body mass (medium: 0.5 to 20 kg, large: > 20.0 kg), whether they are forest specialists, and their feeding guild = carnivore (insectivore/carnivore), herbivore (frugivore/herbivore) and omnivore. Data was obtained from the IUCN Red List.

Species	**Status IUCN**	**Status Mexico**	**No. sites 2011**		**No. sites 2017**		**Body mass**	**Forest specialist**	**Diet**
			FF	**CF**	**FF**	**CF**			
Cabassous centralis[1]	DD	EN	3	0	3	0	Medium	No	Carnivore
Conepatus semistriatus[2]	LC	SP	1	0	13	4	Medium	No	Carnivore
Cuniculus paca[3]	LC	-	14	2	15	4	Medium	Yes	Herbivore
Dasyprocta punctata[4]	LC	-	2	0	12	3	Medium	No	Herbivore
Dasypus novemcinctus[5]	LC	-	15	3	16	4	Medium	No	Omnivore
Eira barbara[6]	LC	EN	4	0	9	1	Medium	No	Omnivore
Herpailurus yagouaroundi[7]	LC	TH	1	0	5	0	Medium	No	Carnivore
Leopardus pardalis[8]	LC	EN	6	2	11	4	Medium	No	Carnivore
Leopardus wiedii[9]	NT	EN	4	0	10	3	Medium	Yes	Carnivore
Mazama temama[10]	DD	-	9	3	5	4	Large	No	Herbivore
Nasua narica[11]	LC	TH	5	1	13	4	Medium	No	Omnivore
Odocoileus virginianus[12]	LC	-	9	1	14	4	Large	No	Herbivore
Panthera onca[13]	NT	EN	1	2	4	3	Large	No	Carnivore
Pecari tajacu [14]	LC	-	11	3	16	4	Large	No	Omnivore
Philander oposum[15]	LC	-	1	0	2	0	Medium	No	Omnivore
Procyon lotor[16]	LC	-	7	0	11	3	Medium	No	Omnivore
Puma concolor[17]	LC	-	2	1	3	4	Large	No	Carnivore
Tamandua mexicana[18]	LC	EN	1	0	10	2	Medium	No	Carnivore
Tapirus bairdii[19]	EN	EN	2	4	3	4	Large	Yes	Herbivore
Tayasu pecari[20]	VU	EN	0	2	0	3	Large	Yes	Omnivore
Urocyon cinereoargenteus[21]	LC	-	1	0	1	0	Medium	No	Carnivore

[1] Tirira et al., 2014; [2]Cuarón et al., 2016*a*; [3]Emmons, 2016*a*; [4]Emmons, 2016*b*; [5] Loughry et al., 2014; [6] Cuarón et al., 2016*c*; [7]Caso et al., 2015; [8] Paviolo et al., 2015; [9] de Oliveira et al., 2015; [10] Bello et al., 2016; [11] Cuarón et al., 2016*b*; [12] Gallina and Lopez-Arevalo, 2016; [13]Quidley et al., 2017; [14]Gongora et al., 2011; [15]De la Sancha et al., 2016; [16]Timm et al., 2016; [17]Nielsen et al., 2015; [18]Ortega-Reyes et al., 2014; [19]García et al., 2016; [20]Keuroghlian et al., 2013; [21]Roemer et al., 2016.

Supplementary References

Bello, J., Reyna, R., Schipper, J. 2016. *Mazama temama*. The IUCN Red List of Threatened Species 2016: e.T136290A22164644 (accessed on September 2nd, 2019).

Caso, A., de Oliveira, T., Carvajal, S.V. 2015. *Herpailurus yagouaroundi*. The IUCN Red List of Threatened Species 2015: e.T9948A50653167 (accessed on September 2nd, 2019).

Cuarón, A.D., Helgen, K., Reid, F. 2016a. *Conepatus semistriatus*. The IUCN Red List of Threatened Species 2016: e.T41633A45210987 (accessed on September 2nd, 2019).

Cuarón, A.D., Helgen, K., Reid, F., Pino, J., González-Maya, J.F. 2016b. *Nasua narica*. The IUCN Red List of Threatened Species 2016: e.T41683A45216060 (accessed on September 2nd, 2019).

Cuarón, A.D., Reid, F., Helgen, K., González-Maya, J.F. 2016c. *Eira barbara*. The IUCN Red List of Threatened Species 2016: e.T41644A45212151 (accessed on September 2nd, 2019).

De la Sancha, N., Pérez-Hernandez, R., Costa, L.P., Brito, D., Cáceres, N. 2016. Philander opossum. The IUCN Red List of Threatened Species 2016: e.T40516A22176779 (accessed on September 2nd, 2019).

De Oliveira, T., Paviolo, A., Schipper, J., Bianchi, R., Payan, E., Carvajal, S.V. 2015. Leopardus wiedii. The IUCN Red List of Threatened Species 2015: e.T11511A50654216 (accessed on September 2nd, 2019).

Emmons, L. 2016a. *Cuniculus paca.* The IUCN Red List of Threatened Species 2016: e.T699A22197347. http://dx.doi.org/10.2305/IUCN.UK.2016-2.RLTS.T699A22197347.en (accessed on September 2nd, 2019).

Emmons, L. 2016b. *Dasyprocta punctata*. The IUCN Red List of Threatened Species 2016: e.T89497686A78319610 (accessed on September 2nd, 2019).

Gallina, S., Lopez-Arevalo, H. 2016. *Odocoileus virginianus*. The IUCN Red List of Threatened Species 2016: e.T42394A22162580 (accessed on September 2nd, 2019).

García, M., et al. 2016. *Tapirus bairdii*. The IUCN Red List of Threatened Species 2016: e.T21471A45173340 (accessed on September 2nd, 2019).

Gongora, J., Reyna-Hurtado, R., Beck, H., Taber, A., Altrichter, M., Keuroghlian, A. 2011. *Pecari tajacu*. The IUCN Red List of Threatened Species 2011: e.T41777A10562361 (accessed on September 2nd, 2019).

Keuroghlian, A., Desbiez, A., Reyna-Hurtado R., Altrichter, M., Beck, H., Taber, A., Fragoso, J.M.V. 2013. *Tayassu pecari*. The IUCN Red List of Threatened Species 2013: e.T41778A44051115 (accessed on September 2nd, 2019).

Loughry, J., McDonough, C., Abba, A.M. 2014. *Dasypus novemcinctus*. The IUCN Red List of Threatened Species 2014: e.T6290A47440785 (accessed on September 2nd, 2019).

Nielsen, C., Thompson, D., Kelly, M., Lopez-Gonzalez, C.A. 2015. *Puma concolor* (errata version published in 2016). The IUCN Red List of Threatened Species 2015: e.T18868A97216466 (accessed on September 2nd, 2019).

Ortega-Reyes, J., Tirira, D.G., Arteaga, M., Miranda, F. 2014. *Tamandua mexicana*. The IUCN Red List of Threatened Species 2014: e.T21349A47442649 (accessed on September 2nd, 2019).

Paviolo, A., Crawshaw, P., Caso, A., de Oliveira, T., Lopez-Gonzalez, C.A., Kelly, M., de Angelo, C., Payan, E. 2015. *Leopardus pardalis* (errata version published in 2016). The IUCN Red List of Threatened Species 2015: e.T11509A97212355 (accessed on September 2nd, 2019).

Quidley, H., Foster, R., Petracca, L., Payan, E., Salom, R., Harmsen, B. 2017. *Panthera onca* (errata version published in 2018). The IUCN Red List of Threatened Species 2017: e.T15953A123791436 (accessed on September 2nd, 2019).

Roemer, G., Cypher, B., List, R. 2016. *Urocyon cinereoargenteus*. The IUCN Red List of Threatened Species 2016: e.T22780A46178068 (accessed on September 2nd, 2019).

Timm, R., Cuarón, A.D., Reid, F., Helgen, K., González-Maya, J.F. 2016. *Procyon lotor.* The IUCN Red List of Threatened Species 2016: e.T41686A45216638 (accessed on September 2nd, 2019).

Tirira, D.G., Díaz, N.J., Superina, M., Abba, A.M. 2014. *Cabassous centralis*. The IUCN Red List of Threatened Species 2014: e.T3412A47437304. (accessed on September 2nd, 2019).

Table S4. Percentage of change in the structure of landscapes through time (2016-2010), at the largest buffer (1400-m radius from the center of each patch), containing 16 forest patches in the Lacandona rainforest, Mexico. Negative values indicate a decrease in a given landscape metric, whereas positive values indicate the opposite.

Forest patch	Forest cover	Matrix openness	Number of patches	Edge density	Inter-patch distance
FP4	3.75	19.37	-6.67	-17.47	41.96
FP7	28.31	16.41	14.29	-22.50	-7.52
FP8	47.61	-10.12	-2.33	33.14	-1.80
FP10	5.52	16.82	-40.00	-19.92	-14.57
FP11	-27.58	13.65	-22.58	-32.54	-6.80
FP13	24.45	11.95	-11.11	13.64	-45.78
FP14	-15.11	6.76	-41.67	-21.28	-36.56
FP16	40.34	21.07	-19.35	-8.04	-16.89
FP17	-8.47	4.81	22.22	11.52	-17.04
FP18	-6.20	48.04	-41.67	-8.53	-11.84
FP19	0.01	-0.09	-16.67	0.00	0.00
FP20	11.50	21.50	-29.73	1.14	4.95
FP22	14.84	25.50	0.00	-26.66	-4.12
FP23	14.64	10.63	0.00	-19.09	2.50
FP27	37.46	-32.30	-13.64	-14.57	3.98
FP28	0.97	-21.81	100.00	-33.78	-19.38

Table S5. Differences in β-diversity (Δβ-diversity) between 2011 and 2017 for mammal ecological groups, according to Baselga's multisite indices, based on Sorensen indices. Negative values indicate a decrease in dissimilarity (or an increase in similarity) through time. We grouped mammal species according to the following ecological traits (Table A3): body mass = medium (0.5 to 20 kg), large (>20.0 kg); feeding guild = carnivores (carnivores and insectivores), omnivores, and herbivores (herbivores and frugivores); and whether they are forest specialists or not. In parenthesis, we show the number of species included under each category. Significant coefficients are indicated with asterisks (* $P < 0.05$, ** $P < 0.005$).

Ecological trait	**Δβ-SOR (total)**	**Δβ-SIM (turnover)**	**Δβ-SNE (nestedness)**
Body mass			
Medium (n=14)	-0.118*	-0.109*	-0.008
Large (n=7)	-0.072*	-0.319*	0.247*
Diet			
Carnivores (n=9)	-0.106*	-0.224*	0.118*
Herbivores (n=5)	-0.106*	-0.385*	0.279*
Omnivores (n=7)	-0.150*	-0.307*	0.157*
Specialization			
Forest specialists (n=4)	-0.093*	-0.100	0.008
Non-specialists (n=17)	-0.089*	-0.550*	0.460*

Capítulo 6.

Discusión general y conclusiones

Norma P. Arce Peña

Discusión

Esta tesis busca entender cómo responde la comunidad de mamíferos terrestres a los cambios que ocurren en la estructura espacial del paisaje a través del tiempo. Primero, evalúa si la región de estudio está sufriendo un proceso de rodentización debido a la proliferación de roedores pequeños en el interior de los fragmentos de bosque. Después, identifica los cambios temporales en la población de monos aulladores negros (*Alouatta pigra*) y las variables del paisaje que los predicen. Finalmente, evalúa si la región está sufriendo un proceso de defaunación y explora los cambios en diversidad beta y sus causales para identificar si la región está experimentando un proceso de homogenización o de diferenciación biótica. A continuación se discuten los hallazgos más importantes de la presente tesis.

Cambios temporales en la estructura espacial de la selva

El paisaje de la Selva Lacandona está cambiando rápidamente – La Selva Lacandona ha sufrido cambios espaciales importantes a través del tiempo. Esta selva solía cubrir alrededor de 1.4 millones de hectáreas (Dirzo y Miranda 1991). Sin embargo, ha sido fuertemente deforestada y degradada debido a la expansión de actividades humanas como la agricultura y la ganadería (Carabias et al. 2015). Actualmente, queda menos del 50% de su cobertura original. En esta tesis encontramos que la región es altamente dinámica, con cambios notables a través del tiempo en la estructura de los paisajes donde se encuentran los remanentes de bosque. Sin embargo, aún existe un alto grado de conectividad en el paisaje que podría favorecer la conservación de la biodiversidad. Contrario a lo que esperábamos, en la región de estudio se observó un aumento en el porcentaje de cobertura forestal y una disminución en el número de parches de bosque, lo que podría ser explicado por la fusión de algunos parches de bosque. La densidad de borde y la distancia media entre parches también disminuyeron a través del tiempo. Por otro lado, como esperábamos, la calidad de la matriz antrópica disminuyó, es decir, la matriz se hizo más abierta (Fig. 1).

Figura 1. Fotografía aérea de la zona de estudio. En la parte superior se observa la Reserva de la Biósfera Montes Azules, en la parte inferior se observa la región del Marqués de Comillas, altamente deforestada debido al establecimiento de sembradíos (principalmente maíz). Foto: Norma Arce.

Cambios en las comunidades y poblaciones de mamíferos a través del tiempo

No encontramos un proceso de rodentización generalizado – Las alteraciones en el paisaje han tenido un gran efecto sobre los patrones de diversidad de los mamíferos terrestres de la región, los cuales mostraron cambios importantes en sus abundancias a través del tiempo. Los hallazgos indican que, como se esperaba, la abundancia de roedores aumentó. Aunque este resultado podría sugerir que existe un proceso de rodentización, descubrimos que las abundancias observadas en el presente estudio, en general, fueron bajas. Además, las respuestas fueron especie-específicas, es decir, cada especie respondió de manera diferente a los cambios en el paisaje. La abundancia de dos especies aumentó (*Heteromys desmarestianus* y *Oryzomys* sp.), la abundancia de *Peromyscus mexicanus*, especie especialista de bosque, disminuyó, mientras que *Sigmodon toltecus*, especie generalista, se mantuvo sin cambios (Fig. 2). Estos resultados sugieren que no se puede hablar de un proceso generalizado de rodentización en la región, sino que la deforestación podría estar causando el declive en la población de *P. mexicanus* y la proliferación de especies generalistas como *Sigmodon toltecus* y *Oryzomys* sp.

Figura 2. Rata algodonera (*Sigmodon toltecus*) capturada en los muestreos en un sitio de bosque continuo en la Selva Lacandona, Chiapas. Foto: Norma Arce.

Los monos aulladores negros podrían estar en declive **–** Debido a la dependencia forestal de los monos aulladores negros (*Alouatta pigra*; Fig. 3), se esperaba que estos mamíferos arbóreos fueran afectados negativamente por cambios en el paisaje, como la pérdida de bosque y el aumento de áreas abiertas en la matriz antrópica. Sorprendentemente, el número total de individuos aumentó con el tiempo (fue mayor en 2017 que en 2011), pero encontramos una diminución importante en el número de individuos inmaduros por hembra. Además, el número total de individuos y la relación inmaduros/hembras estuvieron fuertemente relacionados con los cambios en el paisaje. Por lo tanto, esta especie de primate podría no ser tan tolerante a los disturbios en el paisaje como generalmente se piensa (e.g. Silver et al. 1998; Rangel-Negrín et al. 2014). Nuestros hallazgos sugieren que sus poblaciones podrían presentar una deuda de extinción, por lo que se esperarían fuertes disminuciones en el futuro.

Figura 3. Mono aullador negro (*Alouatta pigra*) registrado durante los muestreos en un sitio de bosque continuo, en la Selva Lacandona, Chiapas. Foto: Norma Arce.

***La región aun no muestra evidencias de un proceso generalizado de defaunación* –** Debido a que la región ha sufrido importantes alteraciones en el paisaje, se esperaba encontrar un proceso generalizado de defaunación. Sin embargo, se encontraron las mismas especies de mamíferos en 2011 y 2017. Al analizar sus abundancias, algunas especies parecen estar aumentando (e.g. *Pecari tajacu* y *Dasypus novemcinctus*), mientras que otras han disminuido en abundancia (e.g. *Panthera onca* y *Tayassu pecari;* Fig. 4). Estos resultados demuestran que no existe un proceso generalizado de defaunación en la región, sino que las poblaciones de diferentes especies están cambiando en función de sus requerimientos ecológicos. La falta de evidencia de un proceso de defaunación generalizado son buenas noticias para la Selva Lacandona, ya que es el relicto más extenso de bosque tropical húmedo en el país (Dirzo y Miranda 1991). Sin embargo, hay que tener en cuenta que la respuesta a los disturbios no siempre se observan de manera inmediata (Metzger et al. 2009, Hanski 2013). Por tanto, continuar con el monitoreo a largo plazo de estos animales es fundamental para detectar a tiempo los cambios en las poblaciones de las especies más vulnerables y así desarrollar estrategias para su conservación.

Figura 4. Tapir (*Tapirus bairdii*; a) y jaguar (*Panthera onca*; b) en un parche de bosque muestreado en la Selva Lacandona, Chiapas. Foto cámaras trampa: Norma Arce.

***La región podría estar sufriendo un proceso de homogenización biótica* –** El análisis de la diversidad beta de la comunidad de mamíferos terrestres reveló que ésta disminuyó a través del tiempo. Este resultado sugiere que la región está experimentando un proceso de homogenización biótica (Baeten et al. 2012), y no de diferenciación, como esperábamos con base en el modelo propuesto por Socolar et al. (2015). Nuestros hallazgos son similares a los de otros estudios (insectos: Solar et al. 2015; aves: Karp et al. 2012; mamíferos: Spear y Chown 2008, Beca et al. 2017, Longman et al. 2018), lo que demuestra que el proceso de homogenización biótica puede afectar diferentes grupos taxonómicos en varias regiones del planeta.

Los cambios en diversidad beta se asociaron mayormente a variaciones en el recambio de especies. El componente de anidamiento fue muy bajo, sin embargo, aumentó al triple a través del tiempo. Al evaluar la composición de especies entre años se encontró una distribución menos restringida de las especies en el 2017 que en el 2011 y no se observaron invasiones ni extinciones entre años. Esto sugiere que el proceso de homogenización podría deberse a un aumento de la capacidad de las especies para dispersarse entre los sitios y no a la invasión y/o extinción de especies, como se ha reportado en otros estudios (Baeten et al. 2012). Futuras modificaciones en el paisaje podrían resultar en la pérdida de algunas especies de mamíferos más sensibles a la perturbación de su hábitat; esto podría promover un proceso de defaunación y un descenso en la diversidad beta en la región, exacerbando el proceso de homogenización biótica en este importante hotspot de biodiversidad.

Importancia de la estructura del paisaje para los mamíferos

***La pérdida de cobertura forestal es de las mayores amenazas para los mamíferos tropicales* –** Los patrones de diversidad de mamíferos estuvieron fuertemente asociados con cambios en diferentes atributos del paisaje. Como se esperaba, los cambios en el porcentaje de cobertura forestal estuvieron fuertemente asociados con los cambios en la abundancia de la mayoría de las especies. Los sitios que sufrieron mayores pérdidas de cobertura forestal mostraron una disminución en la abundancia de especies como el roedor *Peromyscus mexicanus* y el primate *Alouatta pigra*, ambas especies dependientes de bosque. Por otro lado, se encontró que el componente de recambio de la diversidad beta de las comunidades de mamíferos disminuyó en sitios de bosque en los que disminuyó la cobertura forestal. En conjunto, estos hallazgos son consistentes con otros estudios. Por ejemplo, en su meta-análisis global, Watling et al. (2020) encuentran que la diversidad de diferentes grupos taxonómicos es mayor en paisajes con mayor cobertura forestal. De igual manera, Wearn et al. (2017) encontraron efectos positivos de la cobertura forestal en el paisaje sobre la abundancia de 57 especies de mamíferos en bosques tropicales en Borneo. El incremento en la cobertura forestal puede promover la conectividad del paisaje, favoreciendo la dispersión de individuos y la disponibilidad de recursos (Fahrig 2013), lo que puede contribuir al mantenimiento de la diversidad de especies (Newbold et al. 2016). Por lo tanto, esta tesis se suma a la creciente evidencia que confirma que la pérdida de cobertura forestal es una de las mayores amenazas para la biodiversidad, especialmente para aquellas especies dependientes de bosque.

El incremento de la calidad de la matriz puede prevenir la pérdida de especies – Los cambios en la calidad de la matriz a través del tiempo también promueven cambios en las comunidades de mamíferos. Por ejemplo, las poblaciones de los roedores *Peromyscus mexicanus* y *Heteromys desmarestianus* aumentaron en sitios en los que la cobertura vegetal de la matriz era más abierta. Sin embargo, esto no significa que las poblaciones sean beneficiadas por la matriz antrópica, sino que los individuos de estas especies dependientes del bosque se ven obligados a desplazarse y buscar refugio en los sitios remanentes de bosque cuando habitan paisajes deforestados y dominados por matrices desprovistas de árboles (i.e. "crowding effect"; Debinski y Holt 2000). Por tanto, el aumento en la apertura de la matriz que está ocurriendo en la región de estudio podría tener efectos negativos importantes sobre las especies dependientes de bosque a mediano y largo plazo.

La fragmentación per se suele tener efectos positivos sobre las especies – En relación al efecto de la fragmentación, la presente tesis demuestra que, como se esperaba, las poblaciones de monos aulladores (*Alouatta pigra*) fueron beneficiadas por un aumento en el número de parches en el paisaje. Estos resultados concuerdan con la revisión global realizada por Fahrig (2017), la cual demuestra que, cuando son significativos, los efectos de la fragmentación *per se* son usualmente positivos. Los resultados también son consistentes con una revisión reciente realizada con primates (Galán-Acedo et al. 2019). Diferentes mecanismos no exclusivos pueden explicar dicha respuesta positiva (revisado por Fahrig 2019). Por ejemplo, el incremento en el número de parches en el paisaje se asocia con menores distancias entre parches, lo que puede facilitar el movimiento de los individuos y la obtención de recursos en el paisaje (Fahrig 2017). Además, cuanto mayor es el número de fragmentos, mayor es el número de poblaciones, lo que puede facilitar la persistencia de las metapoblaciones (Hanski 1999). Por tanto, contrario a lo que generalmente se piensa (e.g. Fletcher et al. 2018), tener un mayor número de fragmentos en el paisaje puede tener muchas ventajas para la biodiversidad.

Los bordes pueden tener efectos diferentes sobre las especies – Los cambios en la densidad de borde pueden tener distintos efectos sobre las especies de mamíferos a través del tiempo. De hecho, pueden llegar a tener efectos contrastantes en individuos de la misma especie pero de diferente edad. Por ejemplo, en esta tesis se encontró que un aumento en la densidad de borde podría tener un efecto positivo en la abundancia de hembras de monos aulladores (*Alouatta pigra*). Esto podría deberse a que los sitios con mayor densidad de borde pueden estar mejor conectados a otros parches y facilitar la dispersión de los individuos entre los parches restantes (Ewers y Didham 2006). Adicionalmente, paisajes con mayor cantidad de borde pueden favorecer la disponibilidad de recursos a través de dinámicas de suplementación del paisaje, ya que los bordes incrementan el área de contacto bosque-matriz, facilitando el acceso a recursos suplementarios presentes en la matriz (Dunning et al. 1992). Sin embargo, contrario a lo que se esperaba, se observó un efecto negativo sobre el número de monos inmaduros y sobre la abundancia de tres especies de roedores (*Oryzomys* sp., *Heteromys desmarestianus* y *Peromyscus mexicanus*). Los impactos negativos podrían deberse a que el aumento en la proporción de bordes expone el interior de los parches a la influencia de factores externos, aumentando la vulnerabilidad de los individuos ante depredadores. Por lo tanto, es importante controlar la densidad de bordes para evitar efectos negativos en especies especialistas de bosque.

Figura 5. Foto aérea del sitio de estudio. Del lado derecho se observa el bosque continuo, dentro de la Reserva de la Biósfera de Montes Azúles, mientras que a la izquierda se ve el paisaje antropogénico, formado por diferentes tipos de uso de suelo (cultivos anuales y arbóreos, sitios de pastoreo, carreteras y bosques secundarios). Foto: Norma Arce.

Aportaciones teóricas de la tesis

1. **Losers' vs. 'Winers'** (McKinney y Lockwood 1999). La presente tesis aporta información valiosa sobre la dinámica de especies perdedoras y ganadoras. En particular, parece que perturbaciones en el paisaje tienen efectos diferentes sobre las especies. Algunas especies 'ganadoras' pueden verse beneficiadas por los cambios en el paisaje, aumentando en abundancia, rango de distribución y/u ocupación a través del tiempo (Tabarelli et al. 2012, McGill et al. 2015). En contraste, otras especies 'perdedoras' pueden disminuir en abundancia, rango de distribución y/ ocupación, o incluso llegar a desaparecer, debido a los impactos negativos de los cambios en el paisaje (Tabarelli et al. 2012, McGill et al. 2015). De acuerdo con lo anterior, la tesis muestra que algunas especies tienden a ser más afectadas por los cambios en el paisaje y podrían llegar a desaparecer si el cambio de uso de suelo continúa. Ejemplos de especies 'perdedoras' son *Peromyscus mexicanus, Heteromys desmarestianus, Alouatta Pigra, Tapirus bairdii, Tayassu pecari, Mazama temama* y

Panthera onca. Por otro lado, especies como *Sigmodon toltecus, Oryzomys* sp., *Pecari tajacu, Dasypus novemcinctus* y *Cuniculus paca*, parecen ser buenas candidatas de especies ‘ganadoras’. Este recambio de especies ‘ganadoras’ por especies ‘perdedoras’ puede desencadenar diferentes procesos ecológicos en paisajes antrópicos como la defaunación, la rodentización, la homogenización y la diferenciación biótica. Es importante realizar estudios futuros, a lo largo de un periodo más largo de tiempo, que permitan comprobar los patrones observados en esta tesis.

2. **Rodentización** (Galetti et al. 2015, Mendes 2015). La ausencia de competidores o depredadores y/o el aumento en la disponibilidad de recursos en paisajes antrópicos pueden ocasionar un aumento en la densidad de roedores (Galetti et al. 2015, Mendes 2015, Young et al. 2016). Sin embargo, a pesar de que encontramos un aumento general en la abundancia de roedores a través del tiempo – lo que podría evidenciar un proceso de rodentización – las abundancias registradas fueron muy bajas. Adicionalmente, cada especie respondió de manera diferente. Estos resultados sugieren que no se puede hablar de un proceso generalizado de rodentización para esta región. Sin embargo, si las tasas de cambio de uso de suelo se mantienen, se podría predecir el declive de especies especialistas y la proliferación de especies generalistas.

3. **Defaunación** (Dirzo et al. 2014). La defaunación se refiere a la reducción o pérdida de poblaciones animales en paisajes degradados (Dirzo et al. 2014). Este proceso ha sido mayormente documentado para mamíferos de gran tamaño, con dietas especializadas y/o con grandes ámbitos hogareños (Ewers y Didham 2006, Dirzo et al. 2014). Los resultados de esta tesis demuestran que no existe un proceso generalizado de defaunación en la región de estudio, si no que cada especie tiene respuestas diferentes a los disturbios en el paisaje. Sin embargo, aunque no registramos extinciones, es necesario evaluar los cambios en las abundancias de cada especie en un mayor lapso de tiempo para poder evaluar con mayor precisión el proceso de defaunación, y determinar qué especies podrían estar en vías de extinción.

4. **Homogenización y diferenciación biótica (**Solar et al. 2015). Los disturbios en el paisaje pueden ocasionar el aumento o la disminución en la diversidad beta de las comunidades remanentes, causando la diferenciación o la homogenización biótica, respectivamente. Según Socolar et al. (2015), en las etapas iniciales de disturbio, la heterogeneidad ambiental en la región puede

aumentar, ocasionando un aumento en la diversidad beta (diferenciación biótica). Sin embargo, nuestros resultados sugieren un aumento en la homogeneidad ambiental a través del tiempo (e.g. aumento de la cobertura forestal y de la apertura de la matriz), que se relacionó con una disminución de la diversidad beta, reflejando un posible proceso de homogenización biótica. Otros estudios que han encontrado evidencias de un proceso de homogenización biótica atribuyen el aumento de diversidad beta a un proceso de invasiones y/o extinciones de especies (Baiser et al. 2012, Solar et al. 2015, Spear y Chown 2008, Beca et al. 2017, Longman et al. 2018). Sin embargo, nuestros resultados sugieren que la diminución de la diversidad beta podría ser ocasionada por un aumento en la dispersión de las especies a través del paisaje.

5. **Debate fragmentación vs. pérdida de hábitat** (Fahrig 2003, 2017). El efecto de la pérdida de hábitat es generalmente negativo para diferentes grupos taxonómicos (Fahrig 2003). Por otro lado, el efecto de la fragmentación *per se* es generalmente débil. Fahrig (2017) reporta efectos mayormente positivos de la fragmentación *per se*. De manera consistente con estos hallazgos, encontramos que los cambios en las poblaciones de roedores y monos aulladores estuvieron fuertemente asociados a los cambios en la cobertura forestal en el paisaje. Por otro lado, el efecto de la fragmentación *per se* fue menor, pero positivo. El mantenimiento y aumento de la cantidad de hábitat es de gran importancia para la conservación de los mamíferos tropicales, especialmente de las especies dependientes de bosque.

6. **Matriz antrópica, 'crowding effect' (Debinski y Holt 2000) y dinámicas de 'suplementación y complementación del paisaje' (Dunning et al. 1992)**. La naturaleza de la matriz tiene un gran impacto sobre la dinámica de poblaciones dentro de los paisajes antrópicos (Tscharntke et al. 2012). Sin embargo, la respuesta las especies difiere y depende en gran medida de la composición de la matriz, es decir, del grado de similitud con el hábitat original de las especies. Algunas especies pueden tolerar y hasta beneficiarse de la matriz, que puede ofrecer recursos complementarios y/o suplementarios (Dunning et al. 1992, Tscharntke et al. 2012, Galán-Acedo et al. 2019). Por ejemplo, los monos aulladores utilizan las matrices arboladas para moverse a través del paisaje, refugiarse y obtener alimentos. Las matrices antrópicas más abiertas, con coberturas muy diferentes al hábitat original (e.g. pastizales, cultivos anuales, asentamientos humanos), pueden afectar negativamente a las especies dependientes de bosque. El incremento en

la apertura de la matriz puede ocasionar el 'hacinamiento' de los individuos o un incremento en las densidades poblacionales de algunas especies en los sitios remanentes (i.e. 'crowding effect'; Debinski y Holt 2000). Por ejemplo, en esta tesis encontramos que las poblaciones de roedores y de monos aulladores podrían estar siendo forzadas a refugiarse en los sitios de bosque remanentes, ocasionando un aumento temporal en las abundancias y densidades poblacionales.

Líneas futuras

La presente tesis muestra la importancia que tienen los estudios longitudinales y multiescalares para entender el efecto de los cambios en el paisaje sobre las poblaciones y comunidades de mamíferos. Sin embargo, dado el continuo cambio de uso de suelo en las regiones tropicales, necesitamos realizar estudios a más largo plazo. Esto es particularmente importante en organismos de vida larga, como la mayoría de los mamíferos medianos y grandes, ya que este rasgo de vida puede generar retrasos importantes en las respuestas a la perturbación, lo que puede limitar nuestra capacidad para detectar procesos de extinción de especies.

Adicionalmente, es de gran importancia continuar con el monitoreo de los cambios en el paisaje en la región, y su efecto sobre las especies de mamíferos, por un periodo más largo de tiempo, ya que la región está siendo continuamente deforestada. Al finalizar este estudio, al menos dos parches de bosque habían sido transformados a cultivos, y otros disminuyeron significativamente de tamaño. Estos estudios podrían ayudar a detectar si las tendencias observadas en esta tesis se mantienen o acentúan a lo largo del tiempo. Además, podrían compararse con regiones que presenten características diferentes, como regiones con un mayor tiempo de perturbación – para probar la hipótesis de la deuda de extinción (Metzger et al. 2009) – o regiones con una menor cobertura remanente – que permita probar la hipótesis del umbral de fragmentación (Pardini et al. 2010). Esto permitirá tener un mejor entendimiento sobre los procesos que tienen un mayor efecto sobre los mamíferos de bosques tropicales dentro de paisajes antrópicos y diseñar estrategias efectivas de manejo y conservación.

Una limitación importante de esta tesis es que únicamente se realizaron los muestreos de mamíferos dentro de sitios de bosque, lo que no permite evaluar el efecto de otros tipos de coberturas antrópicas sobre las especies. Futuros estudios deberían de realizar los muestreos en diferentes coberturas del paisaje, como en cultivos anuales, bosques secundarios, cultivos forestales, asentamientos humanos, etc., para poder determinar qué tipo de coberturas son más amigables con la biodiversidad. Por otro lado, sería importante evaluar y controlar el efecto de la cacería, ya que es una de las principales causas de la pérdida de mamíferos en la región, principalmente afectando a los mamíferos grandes y medianos. Por último, en esta tesis no se determinaron las abundancias o densidades de forma precisa, lo que podría estar limitando la capacidad de observar fluctuaciones de las poblaciones a través del tiempo y, por lo tanto, detectar una posible defaunación en la región. Futuros estudios deberán calcular patrones de abundancia, tomando en cuenta las diferentes probabilidades de detección de las especies, para poder establecer estrategias de conservación adecuadas.

Implicaciones de conservación

La presente tesis aporta información valiosa para diseñar paisajes amigables para la biodiversidad. Por ejemplo, parece que incrementar la cantidad de cobertura forestal en el paisaje es la estrategia más importante para mantener y mejorar la calidad del paisaje. La pérdida de cobertura forestal puede tener grandes impactos negativos, especialmente sobre las especies especialistas. Por esto, la prevención de la pérdida y degradación forestal, así como el mantenimiento y aumento de la cobertura forestal (mediante acciones de restauración) es vital para la conservación de las comunidades de mamíferos tropicales y deberá ser priorizado en los planes de manejo y conservación. En un artículo reciente se determinó que el mantenimiento de al menos 40% de la cobertura forestal podría asegurar la persistencia de la mayoría de las especies de bosque (Arroyo-Rodríguez et al. 2020). Además, es necesario mejorar la calidad de la matriz antrópica, disminuyendo la cantidad de áreas abiertas (sin árboles) y promoviendo matrices más similares al hábitat original, como por ejemplo con sistemas agroforestales, cultivos arbóreos (e.g. hule, árboles frutales), zonas de manejo forestal sostenible, corredores arbolados, etc. De manera adicional, es importante mantener y aumentar el número de parches en el paisaje (sin ocasionar la pérdida de cobertura forestal) y mantener la conectividad del paisaje. Algunas acciones para mantener y aumentar la conectividad y promover el movimiento entre parches son el establecimiento de corredores biológicos (Rosenberg et al. 1995, Fischer y Lindemayer 2007), la restauración de la vegetación, o el mantenimiento de una matriz similar a la vegetación original (Fischer y Lindemayer 2007). Todas estas acciones contribuirán al aumento en la disponibilidad de recursos y la conectividad del paisaje, beneficiando a las diferentes especies de mamíferos presentes en los bosques tropicales. Sin embargo, se deben realizar estudios que permitan diseñar estrategias diferenciadas de conservación y manejo, acordes al contexto particular de cada sitio.

Además de las acciones directas de manejo y conservación, es fundamental atender las causas subyacentes de la deforestación para poder lograr la conservación de los mamíferos tropicales y de la biodiversidad a nivel global. Una de la principales causas de la deforestación es el establecimiento de pastizales y la siembra de cultivos para alimento de ganado. Por esto, modificar los patrones de consumo y alimentación de la sociedad en general puede ayudar a evitar o disminuir la pérdida forestal. Por otro lado, las comunidades en la región tienen un alto nivel de pobreza, bajos niveles de educación y una falta de servicios básicos de salud. Esto representa una gran problemática para los bosques tropicales y su biodiversidad, ya que las comunidades buscan atender sus necesidades en los paisajes en los que viven, promoviendo la deforestación, la caza y la extracción de recursos forestales. Por lo tanto, es vital establecer estrategias de manejo que incluyan a las comunidades locales, junto con programas efectivos de educación ambiental, que contribuyan a la creación de una conciencia ambiental que favorezca la conservación de la biodiversidad.

Referencias

Arroyo-Rodríguez, V., Fahrig, L., Tabarelli, M., Watling, J.I., Tischendorf, L., Benchimol, M., Cazetta, E., Faria, D., Leal, I.R., Melo, F.P.L, Morante-Filho, J.C., Santos, B.A., Arasa-Gisbert, R., Arce-Peña, N., Cervantes-López, M.J., Cudney-Valenzuela, S., Galán-Acedo, C., San-José, M., Vieira, I.C.G., Slik, J.W.F., Nowakowski, J., Tscharntke, T. 2020. Designing optimal human-modified landscapes for forest biodiversity conservation. Ecology Letters 23: 1404–1420.

Baeten, L., Vangansbeke, P., Hermy, M., Peterken, G., Vanhuyse, K., Verheyen, K. 2012. Distinguishing between turnover and nestedness in the quantification of biotic homogenization. Biodiversity and Conservation 21: 1399–1409.

Baiser, B., Olden, J.D., Record, S., Lockwood, J.L., McKinney, M.L. 2012. Pattern and process of biotic homogenization in the New Pangaea. Proceedings of the Royal Society B 279: 4772–4777.

Beca, G., Vancine, M.H., Carvalho, C.S., Pedrosa, F., Alvez, R.S.C., Buscariol, D., Peres, C.A., Ribeiro, M.C., Galetti, M. 2017. High mammal species turnover in forest patches immersed in biofuel plantations. Biological Conservation 210: 352–359.

Carabias, J., de la Maza, J., Cadena, R. 2015. Conservación y desarrollo sustentable en la Selva Lacandona. 25 años de actividades y experiencias. Natura y Ecosistemas Mexicanos, México.

Debinski, D.M., Holt, R.D. 2000. A survey and overview of habitat fragmentation experiments. Conservation Biology 14: 342–355.

Dirzo, R., Miranda, A. 1991. Altered patterns of herbivory and diversity in the forest understory: a case study of the possible consequences of contemporary defaunation. In: Plant-animal interactions: evolutionary ecology in tropical and temperate regions. Prince, P.W., Lewinsohn, T.M., Fernandes, G. W., Benson, W.W. (Eds.) John Wiley & Sons, Inc., pp 273–288.

Dirzo, R., Young, H.S., Galetti, M., Ceballos, G., Isaac, N.J.B., Collen, B. 2014. Defaunation in the Anthropocene. Science 345: 401–406.

Dunning J.B., Danielson, B.J., Pulliam, H.R. 1992. Ecological processes that affect populations in complex landscapes. Oikos 65: 169–175.

Ewers R.M., Didham, R.K., 2006. Confounding factors in the detection of species responses to habitat fragmentation. Biol. Rev. 81: 117–142.

Fahrig, L. 2003. Effects of habitat fragmentation on biodiversity. Annual Review of Ecology, Evolution, and Systematics 34: 487–515.

Fahrig, L. 2013. Rethinking patch size and isolation effects: the habitat amount hypothesis. Journal of Biogeography 40: 1649–1663.

Fahrig, L. 2017. Ecological responses to habitat fragmentation *per se*. Annual Reviews of Ecology, Evolution and Systematics 48: 1–23.

Fahrig, L. 2019. Habitat fragmentation: a long and tangled tale. Global Ecology and Biogeography 28: 33–41.

Fischer, J., Lindemayer, D.B. 2007. Landscape modification and habitat fragmentation: a synthesis. Global Ecology and Biogeography 16: 265–280.

Fletcher, R.J., Didham, R.K., Banks-Leite, C., Barlow, J., Ewers, R.M., Rosindell, J., et al. 2018. Is habitat fragmentation good for biodiversity? Biological Conservation 226: 9–15.

Galán-Acedo, C., Arroyo-Rodríguez, V., Andresen, E., Arregoitia, L.V., Vega, E., Peres, C.A., Ewers, R.M. 2019. The conservation value of human-modified landscapes for the world's primates. Nature Communications 10: 152.

Galetti, M., Bovendorp, R., Guevara, R. 2015. Defaunation of large mammals leads to an increase in seed predation in the Atlantic forests. Global Ecology and Conservation 3: 824–830.

Hanski, I. 1999. Habitat connectivity, habitat continuity, and metapopulations in dynamic landscapes. Oikos 87: 209–219.

Hanski, I. 2013. Extinction debt at different spatial scales. Animal Conservation 16: 12–13.

Karp, D.S., Rominger, A.J., Zook, J., Ranganathan, J., Ehrlich, P.R., Daily, G.C. 2010. Intensive agriculture erodes β-diversity at large scales. Ecology Letters 15: 963–970.

Longman, E.K., Rosenblad, K., Sax, D.F. 2018. Extreme homogenization: the past, present and future of mammal assemblages on islands. Ecology and Biogeography 27: 77–95.

McGill, B.J., Dornelas, M., Gotelli, N.J., Magurran, A.E. 2015. Fifteen forms of biodiversity trend in the Anthropocene. Trends in Ecology & Evolution 30: 104–113.

McKinney, M.L., Lockwood, J.L. 1999. Biotic homogenization: a few winners replacing many losers in the next mass extinction. Trends in Ecology and Evolution 14: 450–453.

Mendes, C., Ribeiro, M.C., Galetti, M. 2015. Patch size, shape and edge distance influence seed predation on a palm species in the Atlantic forest. Ecography 38: 1–11.

Metzger, J.P., Camargo, A.M., Dixo, M., Bernacci, L.C., Ribeiro, M.C, Godoy, A.M.T., Pardini, R. 2009. Time-lag in biological responses to landscape changes in a highly dynamic Atlantic forest region. Biological Conservation 142: 1166–1177.

Newbold, T., Hudson, L.N., Arnell, A.P., Contu, S., de Palma, A., Ferrier, S., Hill, S.L.L., Hoskins, A.J., Lysenko, I., Phillips, H.R.P., Burton, V.J., Chng, C.W.T., Emerson, S., Gao, D., Pask-Hale, G., Hutton, J., Jung, M., Sanchez-Ortiz, K., Simmons, B.I., Whitmee, S., Zhang, H., Scharlemann, J.P.W., Purvis, A. 2016. Has land use pushed terrestrial biodiversity beyond the planetary boundary? A global assessment. Science 353: 288–291.

Pardini, R., Bueno, A.A., Gardner, T.A., Prado, P.I., Metzger, J.P. 2010. Beyond the fragmentation threshold hypothesis: regime shifts in biodiversity across fragmented landscapes. PLoS ONE 5: e13666.

Rangel-Negrín, A., Coyohua-Fuentes, A., Canales-Espinosa, D., Dias, P.A.D. 2014. Mammal assemblages in forest fragments and landscapes occupied by black howler monkeys. Primates 55: 345–352.

Rosenberg, D.K., Noon, B.R., Meslow, E.C. 1995. Towards a definition of biological corridor. In: Integrating people and wildlife for a sustainable future. Bissonette, J.A., Krausman, P.R. (Eds). International Wildlife Management Congress, pp 436–439.

Silver, S.C., Ostro, L.E.T., Yeager, C.P., Horwich, R. 1998. Feeding ecology of the black howler monkey (*Alouatta pigra*) in Northern Belize. American Journal of Primatology 45: 262–279.

Socolar, J.B., Gilroy, J.J., Kunin, W.E., Edwards, D.P. 2016. How should beta-diversity inform biodiversity conservation? Trends in Ecology and Evolution 31: 67–80.

Solar, R.R.D., Barlow, J., Ferreira, J., Berenguer, E., Lees, A.C., Thomson, J.R., Louzada, J., Maués, M., Moura, N.G., Oliveira, V.H.F., Chaul, J.C.M., Schroeder, J.H., Vieira, I.C.G., Mac Nally, R., Gardner, T.A. 2015. How pervasive is biotic homogenization in human-modified tropical forest landscapes? Ecology Letters 18: 1108–1118.

Spear, D., Chown, S.L. 2008. Taxonomic homogenization in ungulates: patterns and mechanisms at local and global scales. Journal of Biogeography 35: 1962–1975.

Tabarelli, M., Peres, C.A., Melo, F.P. 2012. The 'few winners and many losers' paradigm revisited: emerging prospects for tropical forest biodiversity. Biological Conservation 155: 136–140.

Tscharntke, T., Tylianakis, J.M., Rand, T.A., Didhma, R.K., Fahrig, L., Batáry, P., Bengtsson, J., et al. 2012. Landscape moderation of biodiversity patterns and processes – eight hypotheses. Biological Reviews 87: 661–685.

Young, H.S., McCauley, D.J., Galetti, M., Dirzo, R. 2016. Patterns, causes, and consequences of Anthropocene defaunation. Annual Review of Ecology, Evolution, and Systematics 47: 333–358.

Watling J.I., Arroyo-Rodríguez, V., Pfeifer, M., Baeten, L., Banks-Leite, C., Cisneros, L.M., Fang, R., Hamel-Leigue, A.C., Lachat, T., Leal, I.R., Lens, L., Possingham, H.P., Raheem, D.C., Ribeiro, D.B., Slade, E.M., Urbina-Cardona, J.N., Wood, E.M., Fahrig, L. 2020. Support for the habitat amount hypothesis from a global synthesis of species density studies. Ecology Letters 23: 674–681.

Wearn, O.R., Rowcliffe, J.M., Carbone, C., Pfeifer, M., Bernard, H., Ewers, R.M. 2017. Mammalian species abundance across a gradient of tropical land-use intensity: a hierarchical multispecies modelling approach. Biological Conservation 212: 162–171.