# UNIVERSIDAD NACIONAL AUTÓNOMA DE MÉXICO

**DOCTORADO EN CIENCIAS BIOMÉDICAS**

INSTITUTO DE ECOLOGÍA

# IMPORTANCIA DE LA CONFIGURACIÓN DEL PAISAJE SOBRE LAS COMUNIDADES DE PLÁNTULAS Y MAMÍFEROS DE UN BOSQUE TROPICAL HIPER FRAGMENTADO

## TESIS

QUE PARA OPTAR POR EL GRADO DE:

**DOCTOR EN CIENCIAS**

PRESENTA:

**SERGIO NICASIO ARZETA**

**DIRECTORA DE TESIS:**

**Dra. Julieta Benítez Malvido**

INSTITUTO DE INVESTIGACIONES EN ECOSISTEMAS Y SUSTENTABILIDAD, UNAM

**COMITÉ TUTOR**

**Dr. Miguel Martínez Ramos**

INSTITUTO DE INVESTIGACIONES EN ECOSISTEMAS Y SUSTENTABILIDAD, UNAM

**Dr. Enrique Martínez Meyer**

INSTITUTO DE BIOLOGÍA, UNAM

CIUDAD DE MÉXICO, ENERO DE 2023

## Agradecimientos institucionales

Al programa de Doctorado en Ciencias Biomédicas de La Universidad Nacional Autónoma de México por aceptarme como estudiante y por todo el apoyo recibido durante la realización de mis estudios

Al Consejo Nacional de Ciencia y Tecnología por la beca de doctorado (CONACyT-317569)

A los proyectos IN14014, IN202117 e IN201620 del Programa de Apoyo a Proyectos de Investigación e Innovación Tecnológica (PAPIIT), así como a los proyectos CB-2005-C01-51043, CB2006-56799 y CB2007-7912 de CONACyT.

Al apoyo técnico y logístico proporcionado por el técnico Juan Manuel Lobato García durante el trabajo de campo.

A la Dra. Julieta Benítez Malvido, quien fue directora de esta tesis y tutora principal durante mis estudios de posgrado.

Al Dr. Miguel Martínez Ramos y al Dr. Enrique Martínez Meyer, integrantes de mi comité tutor, por su asesoría y apoyo académico durante el desarrollo de mi tesis doctoral

## Agradecimientos personales

Este proceso ha sido uno de los más largos, retadores y aleccionadores que he tenido en mi vida personal y académica. El resultado de este trabajo fue posible gracias a la extensa red de apoyo con la que he contado en todos estos años.

En primera a mi madre Guadalupe, quien nunca dejó de apoyarme incondicionalmente y animarme a seguir adelante a pesar de las dificultades. Me brindaste muchas lecciones y nunca dejaste de creer en mis capacidades. Gracias por las palabras, los recursos, los abrazos y la mensajería de mis recetas. Aunque ya no puedas leer estas palabras ni decirme lo feliz que estás, sé que identificarás mi cara de felicidad en este momento, ¡por fin lo logré! A mi padre Amado por su apoyo a distancia y en la cercanía. Nuestra poco ortodoxa relación padre-hijo es la mejor que aprendimos a construir y nos une cada vez más con el paso de los años. Gracias por estar conmigo a pesar de las diferencias, de las largas que te daba y de ser tu hijo más distraído y temperamental. A mi familia cercana, mi hermana Mireille, mi prima Candelaria y mi carnala Paulina.

A todos los habitantes del ejido Quiringüicharo, Chiapas, particularmente a Don José Quintana y a Don Guillermo Velasco, quienes me abrieron sus puertas y me hicieron sentir en familia durante mi trabajo de campo. A Gilberto Jamangapé y Rafa Lombera por compartir sus vastos conocimientos de botánica e historia natural de la selva y ser grandes amigos en toda vicisitud que me ocurría en campo. A Julia Carabias y a Natura y Ecosistemas Mexicanos A.C. por el apoyo logístico, las estancias en la estación Chajul y por permitirme conocer y enamorarme de la selva desde mi servicio social. Por último, mi estadía en Marqués de Comillas también fue posible gracias al Arca de Noé.

Hago un agradecimiento particular a mi asesora, la Dra. Julieta Benítez. Gracias por recibirme en tu laboratorio, darme absoluta libertad académica y creativa en la planeación y ejecución de este proyecto, por confiar en mis conocimientos y capacidades y por la enorme e infinita paciencia que me tuviste durante varias circunstancias que ocurrieron en estos años. A los investigadores que me dieron buenos consejos y la oportunidad de crecer académicamente a través de participaciones en proyectos, artículos y de permitirme trabajar como docente, particularmente a Miguel Martínez, Víctor Arroyo, Antonio González, Yessica Rico, Diego Pérez, Jean Francois Mas, Fernando Pineda, Rodrigo Macip, Hernando Rodríguez y Cynthia Armendáriz.

Buena parte de este proceso lo logré gracias a mi familia moreliana a lo largo de distintas temporadas. Mis amigas y hermanas Miriam y Mariana, con quienes encontré un hogar cálido y seguro donde aprendí a arreglar desperfectos y encontré los consejos académicos y de vida que redireccionaron muchas de mis acciones. Gracias por no dejarme caer, sobre todo durante "Quirinwitz" y "Nickalypsis". Junto a ustedes construí lazos que van más allá de la amistad con Mayitza, Jimmy y Calleros. Siempre recordaré las pláticas, las amanecidas de la ilegalidad yendo con rumbo desconocido, la casita de Riviera y que nunca nos vamos a ir. En esta familia también se encuentran Pili, Aurora, Nadia, La Lau, Andrea, Clarissa y Karla; gracias por su amistad incondicional y por cuidar de mamá mientras escribía esta tesis o cuando tenía que salir a trabajar por varios días. Por último, agradezco la confidencia, empatía, inspiración, porras y momentos de catarsis por parte de mi gran amiga Liz.

Agradezco a la comuna moreliana donde encontré cariño, apoyo y a muchos de los grandes amigos que tengo hoy en día, como Adriana Garmendia, Julio César, Aline, Salo, Daniela, Angy, Kari, Dainiz, Ana Paola, Ángela, Pilar, Alejandro, Chino, Katya, Gaby, Tamandua, Leonel, Gonzalo, Oscar, Luz, Aleida, Flor, Carmen, Tulio, Isela, Moy, Erika, Juan Luis, Ana María, Rebeca, Germán, Merel y Leonardo del IIES. En mi paso por el CIGA también encontré amigos muy preciados, como Rafa, Richard, Gemma, Nico, Rita, Piña, Anita, Diana Laura, Gaby, José Luis, Pedrito, Irene, Espe y Dani. Finalmente, en la ENES tuve la fortuna de ampliar esta comunidad con Ori, Jovis, Isis, Ale, Alexandra, Javier Piña, Mafer, Fabi y Rox. Quiero hacer una mención especial a las dos mujeres que me enseñaron desde como presentar una candidatura hasta como escribir un artículo, así como inspirarme e impulsarme dentro de la docencia y a no claudicar cuando me sentía desolado, las doctoras Beatriz Fuentealba y Susana Maza.

Mi círculo no Moreliano siempre estuvo para escucharme, animarme y decirme que contaba con las capacidades para salir de peores. Gracias compadre Hugo, Celeste, Diana Victoria y Paos. También a aquellas personas que en su momento creyeron en mí y me inspiraron a crecer mientras coincidimos: Netzi, Lupita, Adi y Lucero.

Hago un agradecimiento especial a Juls por el amor, la paciencia y la inmensa ayuda que me has dado. No habría logrado este paso final sin ti. Eres una increíble pareja, familia y equipo. Gracias por confiar en mí, creer en mis metas profesionales, confiarme las tuyas y por el amor que le tienes a Petra.

# ÍNDICE

# RESUMEN

La deforestación y cambio de uso de suelo en los bosques tropicales húmedos son la principal amenaza para la biodiversidad a nivel global al transformar coberturas continuas de bosque en paisajes tropicales modificados por el hombre. Estos paisajes consisten en fragmentos de bosque inmersos en una matriz heterogénea de usos de suelo y vegetación en distintos estados de sucesión. Esto genera una compleja estructura en estos paisajes, tanto en su composición de coberturas, como en la configuración espacial de los remanentes de bosque, los cuales ejercen una fuerte influencia sobre las especies remanentes dentro de los fragmentos. A su vez, esta flora y fauna remanentes dependen de la calidad de hábitat y disponibilidad de recursos dentro de los fragmentos, los cuales están asociados con la estructura y diversidad de la comunidad de árboles. Por lo tanto, preservar la regeneración del bosque dentro de fragmentos es crucial para la conservación de la biodiversidad en estos paisajes en el mediano y largo plazo. La regeneración de los bosques tropicales húmedos está directamente regulada por los patrones de diversidad de la comunidad de plántulas que se desarrollan dentro de ellos. Sin embargo, esta comunidad es influenciada por factores a escala local y de paisaje que modifican la llegada de especies nuevas, las fluctuaciones en las abundancias de especies con distintos atributos funcionales y la llegada de los mamíferos terrestres que promueven su diversidad. No obstante, se conoce muy poco sobre como estos factores influyen directa o indirectamente en la abundancia de plántulas demandantes de luz/tolerantes a la sombra, y en la diversidad alfa y beta, así como en la presencia de mamíferos terrestres. En este trabajo analizamos los efectos directos y en cascada de factores a escalas de fragmento y de paisaje sobre la abundancia y diversidad de plántulas, así como el papel de la estructura del paisaje y las funciones de la matriz sobre la ocupación de mamíferos terrestres en un bosque tropical hiper fragmentado. Encontramos que el disturbio por fuego tiene un efecto en cascada positivo sobre las abundancias de plántulas demandantes de luz al reducir el área basal de la vegetación arbórea. A su vez, el incremento en la abundancia de estas plántulas redujo la diversidad beta de especies típicas y dominantes. Por otro lado, la agregación de fragmentos tuvo un efecto en cascada positivo sobre la riqueza de plántulas al incrementar la abundancia de especies tolerantes a la sombra. También encontramos efectos directos del paisaje sobre la diversidad de plántulas, siendo la configuración del paisaje la que influyó de manera significativa en la diversidad beta, particularmente en paisajes con una alta densidad de fragmentos y un bajo contraste de borde. Finalmente, paisajes con una alta densidad de fragmentos y una matriz que proporciona un mayor porcentaje de hábitat complementario a pequeñas escalas y una menor resistencia al movimiento a grandes escalas incrementó la ocupación de mamíferos terrestres. Estos resultados nos indican que la configuración del paisaje juega un papel muy importante en la diversidad de plántulas y en facilitar la llegada de mamíferos en paisajes hiper fragmentados. Es urgente promover patrones configuracionales que incrementen la diversidad de la comunidad de plántulas dentro de planes de manejo y restauración de estos paisajes modificados por el hombre.

# ABSTRACT

Deforestation and land-use change in tropical rainforests are the major threat for global biodiversity by transforming continuous tracts of undisturbed forest into human-modified tropical landscapes. These landscapes consist in forest patches embedded in a heterogeneous matrix of a variety of land uses and secondary forests. This creates a complex landscape structure, whether in the composition of land covers or in the spatial configuration of forest patches, which strongly influence the remnant species within patches. At the same time, the remaining vegetation and fauna are dependent on the habitat quality and resources availability provided by the structure and diversity of the tree forest community. Thus, sustaining forest regeneration within patches is critical for biodiversity conservation at long term. Tropical forest regeneration is mostly driven by the diversity patterns of tree seedling community. However, seedlings are also affected by local- and landscape-scale factors that alter species arrival, abundance fluctuations of species with contrasting functional traits and the arrival of terrestrial mammals that shape seedling diversity. Nonetheless, the factors that have direct or cascading effects on seedling abundance and diversity, and mammal persistence are poorly understood. We assessed the direct and cascading effects of patch- and landscape-scale factors on seedling abundance and diversity, as well as the role of landscape structure and matrix functionality on mammal occupancy in a hyper-fragmented tropical rainforest. We found that fire disturbance had positive cascading effects on the abundance of light-demanding seedlings, which in turn reduced beta diversity of typical and dominant seedling species. These effects were mediated by forest basal area, which was reduced in patches with previous fire events. Contrarily, patch aggregation had positive cascading effects on seedling richness by increasing the abundance of shade-tolerant species. We also found direct effects of landscape structure on seedling diversity, particularly by landscape configuration on beta diversity in landscapes with a high patch density and a low edge contrast. Finally, a high patch density and matrices that increased habitat availability at smaller scales while reduced resistance to movement at larger scales promoted patch occupancy of terrestrial mammals. These findings indicated that landscape configuration played a key role on seedling diversity and mammal occupancy within patches. Promoting configurational patterns that sustain seedling diversity is crucial in management and restoration actions in these human-modified tropical landscapes.

# CAPÍTULO I. INTRODUCCIÓN GENERAL

# Fragmentación de los bosques tropicales húmedos y sus efectos sobre la comunidad de plántulas

## *Paisajes modificados por el hombre*

La extensión, biodiversidad e integridad ecosistémica de los bosques a nivel mundial están fuertemente amenazadas por la deforestación y cambio de uso de suelo (Grantham et al., 2020; Song et al., 2018). Actualmente solo el 40% de los bosques remanentes presentan una alta integridad ecosistémica (Grantham et al., 2020), mientras que el resto ha sido transformado en paisajes modificados por el hombre (PMH). Los PMH están constituidos por fragmentos de bosque inmersos dentro de un mosaico de coberturas de uso de suelo de origen antropogénico (DeClerck et al., 2010; Perring & Ellis, 2013) y se caracterizan por presentar un ensamble de especies y funciones ecológicas alteradas (DeClerck et al., 2010; Richard J. Hobbs et al., 2013; Western, 2001). Esto limita tanto sus servicios ecosistémicos como su resiliencia a eventos de perturbación a múltiples escalas espaciales y temporales (Watson et al., 2018; Wurtzebach & Schultz, 2016). No obstante, los PMH tienen un alto valor de conservación y sus servicios ecosistémicos son fundamentales para la provisión de alimento, regulación climática y mitigación del disturbio antropogénico al ser una fuente de propágulos para la regeneración del bosque (Cumming & Peterson, 2005; Kennedy et al., 2013; Perring & Ellis, 2013). Mantener estas capacidades requiere de un manejo adaptativo del paisaje que permitan conservar la biodiversidad remanente o manejar los nuevos ensambles de especies y sus funciones asociadas (Hulvey et al., 2013).

Estos PMH son más frecuentes en los bosques tropicales húmedos, donde el 10% de los bosques remanentes persisten como fragmentos menores a las 10,000 ha, inmersos dentro de coberturas agrícolas, pastizales ganaderos, plantaciones agroindustriales (ej., cultivos extensivos de soya y palma de aceite) y bosques secundarios en distintos estadios sucesionales (Arroyo-Rodríguez et al., 2017, 2020; DeClerck et al., 2010). Solamente en América, se estima que existen 55.5 millones de fragmentos con un tamaño promedio de 17 ha y cuyo número se espera que aumente en un factor de 20-33 durante los próximos 30 años, trayendo consigo efectos negativos sobre la biodiversidad que habita en ellos, sus funciones ecológicas y la integridad ecosistémica de los PMH tropicales (Grantham et al., 2020; Haddad et al., 2015; Taubert et al., 2018). Conservar las especies y funciones de los PMH tropicales es fundamental debido a que estos bosques albergan más de la mitad de las especies conocidas en el planeta y juegan un papel importante en procesos como el ciclo de carbono y la regulación del clima a múltiples escalas (Le Quéré et al., 2018; Wright, 2005).

Los fragmentos de bosque tropical son críticos para la preservación de especies de plantas y animales en PMH tropicales (Bueno & Peres, 2019; Laurance et al., 2011; Pfeifer et al., 2014), mantienen la conectividad del paisaje (Jesus et al., 2012) y representan la principal fuente de propágulos para la regeneración de bosques secundarios (Chazdon, 2003; Martínez-Ramos et al., 2016). Estas funciones están fuertemente vinculadas a la vegetación arbórea de los fragmentos, siendo indicadores de calidad de hábitat, disponibilidad de recursos y funciones ecológicas (Cudney-Valenzuela et al., 2021; San-José et al., 2014; Wies et al., 2021). Por lo tanto, para preservar la integridad ecosistémica de los PMH en el trópico es fundamental mantener la regeneración de la comunidad arbórea dentro de los fragmentos.

### *Comunidades de plántulas dentro de fragmentos*

La regeneración de los bosques tropicales húmedos es principalmente a través de la comunidad de plántulas de árboles, la cual representa la principal fuente de propágulos y su diversidad y composición determinan la estructura y diversidad de los bosques futuros (Comita et al., 2007; Nicotra et al., 1999; Wills et al., 2006). Entonces, comprender los factores y procesos que determinan y moldean la comunidad de plántulas de árboles dentro de los fragmentos nos permitirá comprender como preservar la regeneración de fragmentos dentro de PHM tropicales (Benítez-Malvido et al., 2018; Santo-Silva et al., 2013). Estudios a escala de fragmento han encontrado que la comunidad de plántulas es influenciada por el tamaño y la forma del fragmento (Benitez-Malvido, 1998; Benítez-Malvido et al., 2018), los cuales afectan la abundancia y riqueza de plántulas (Benítez-Malvido et al., 2018; Benitez-Malvido & Martinez-Ramos, 2003; Santo-Silva et al., 2013). En PMH tropicales hiper fragmentados, los efectos de borde promueven la abundancia de plántulas pertenecientes a especies generalistas y demandantes de luz (especies dominantes en bosques secundarios) que limitan el establecimiento de plántulas pertenecientes a especies especialistas tolerantes a la sombra (especies dominantes en bosques no perturbados), trayendo consigo una reducción en la riqueza de especies (diversidad α) y una homogenización biótica que consiste en la pérdida de la heterogeneidad espacial de las especies de plántulas (diversidad β) dentro y entre los fragmentos (Tabarelli et al., 2010, 2012).

Asimismo, la diversidad α y β de las plántulas de árboles tropicales también es modificada por la depredación de semillas y plántulas por parte de la comunidad de mamíferos terrestres (Dirzo & Miranda, 1990; Villar et al., 2019; Young et al., 2016). La pérdida de estos mamíferos trae consigo modificaciones tanto en la depredación y dispersión secundaria de semillas de árboles (Galetti et al., 2015; Orrock et al., 2006; Wright et al., 2000), como en la herbivoría de plántulas (Villar et al., 2019), resultando en patrones de regeneración alterados debido a la formación de comunidades de plántulas con una alta abundancia de individuos, con una menor riqueza, dominadas por pocas especies y una baja diversidad β (Camargo-Sanabria et al., 2014; Galetti & Dirzo, 2013; Villar et al., 2019). La deforestación y fragmentación afecta severamente la persistencia de mamíferos terrestres, particularmente aquellos cuyo tamaño, dieta y patrones de forrajeo proveen las funciones ecológicas que promueven la diversidad de plántulas (Magioli et al., 2021; Young et al., 2016). En el caso de los fragmentos de selva, el tamaño tiene un papel importante en explicar la presencia de mamíferos terrestres de talla mediana y grande, mientras que aquellos fragmentos de menor tamaño pueden ser usados de manera temporal como sitios de paso (Magioli et al., 2021; Prugh et al., 2008; Thornton et al., 2011).

Como consecuencia, los bosques resultantes de estos fragmentos presentan una estructura y diversidad semejante a la de bosques secundarios, comprometiendo la integridad ecosistémica de los PMH tropicales al reducirse la calidad del hábitat para plantas y animales de hábitos especialistas y pauperizando sus funciones ecológicas y servicios ecosistémicos (Laurance, Nascimento, Laurance, Andrade, Fearnside, et al., 2006; Laurance, Nascimento, Laurance, Andrade, Ribeiro, et al., 2006; Tabarelli et al., 2012). El resultado de los trabajos a escala de fragmento sugiere que las actividades de conservación y manejo deben orientarse a detener la deforestación de estos fragmentos y promover su restauración activa a lo largo de sus bordes para aminorar los efectos que tienen sobre la comunidad de plántulas, promoviendo así su diversidad a largo plazo.

No obstante, existen otros factores que afectan a la comunidad de plántulas que van más allá del tamaño y forma de los fragmentos. La composición de especies de plántulas y árboles está fuertemente influenciada por la estructura de la vegetación arbórea (Nicotra et al., 1999; Rose, 2000), el tipo de matriz adyacente (Benítez-Malvido & Martínez-Ramos, 2006; Laurance et al., 2007), la heterogeneidad de hábitats entre distintos fragmentos (Arroyo-Rodríguez et al., 2013; Sánchez-Gallen et al., 2010) y la persistencia de mamíferos a través de la conectividad entre fragmentos (Cassano et al., 2012; Magioli et al., 2016; Umetsu & Pardini, 2007).

## Efectos de la estructura del paisaje y la escala sobre la biodiversidad

La biodiversidad es significativamente influenciada por la estructura del paisaje (Fahrig, 2003), la cual está constituida por la composición (número y extensión) y la configuración (formas, distribución y arreglo espacial) de las coberturas de vegetación y uso de suelo (Fletcher & Fortin, 2018; McGarigal et al., 2012). En hábitats fragmentados, los efectos de la composición del paisaje están asociados a la pérdida del hábitat (ej., reducción del porcentaje de hábitat original), mientras que los efectos de la configuración se encuentran relacionados con los efectos de la fragmentación *per se* (Fahrig, 2003). Estos factores tienen un poder explicativo más alto que el tamaño y forma del fragmento sobre la abundancia y diversidad de especies, particularmente la pérdida de hábitat, que suele tener un efecto significativamente mayor (Fahrig, 2003). No obstante, en regiones hiper fragmentadas (cobertura de hábitat < 30%), los efectos de la fragmentación *per se* pueden ser mayores (Andren, 1994), teniendo efectos positivos o negativos sobre las especies remanentes, dependiendo de la interacción que cada una tenga con el paisaje (Fahrig, 2017, 2019).

Además, la escala del efecto que tiene la estructura del paisaje sobre las especies varía entre respuestas biológicas y niveles de disturbio (Jackson & Fahrig, 2012, 2015; Miguet et al., 2016). Por un lado, se espera que respuestas biológicas afectadas por procesos de natalidad/mortalidad, tales como la abundancia, serán afectadas por factores locales o a escalas menores que aquellas respuestas controladas por eventos de colonización/extinción, como la riqueza (Miguet et al., 2016; Moraga et al., 2019). Por otro lado, se ha hipotetizado una escala de efecto menor en paisajes altamente deforestados, donde la dispersión es baja y los efectos son determinados por factores locales (Andren, 1994; Miguet et al., 2016). Determinar las escalas del efecto entre la miríada de escalas, respuestas biológicas y métricas de composición y configuración del paisaje requieren de análisis multiescalares que determinen la escala del efecto de cada métrica para cada respuesta y posteriormente la importancia relativa que tendrá respecto a otras métricas (Jackson & Fahrig, 2012, 2015; Martin, 2018; Miguet et al., 2016).

## Posibles efectos de la estructura del paisaje sobre la comunidad de plántulas

### *Abundancia*

La comunidad regenerativa de los bosques tropicales húmedos no está exenta de la influencia de la estructura del paisaje y la escala a la que son afectados los distintos atributos de la comunidad. Se presume que la abundancia de plántulas podría estar afectada por la estructura del paisaje a través de efectos en cascada. En los Tutlxas, Veracruz, se encontró que la densidad de tallos de plantas del sotobosque se incrementa al reducirse la abundancia de una palma altamente competidora, la cual es negativamente afectada por la proporción de matrices abiertas y el grado de fragmentación de la cobertura de bosque primario (Hernández-Ruedas et al., 2018). Las abundancias de plántulas están influenciadas por la abundancia y diversidad de árboles reproductivos (Comita et al., 2007; Wandrag et al., 2017), la disponibilidad de luz regulada por la estructura de la comunidad arbórea (J S Denslow, 1987; Julie S. Denslow & Guzman G., 2000; Nicotra et al., 1999) y por factores densodependientes entre especies conespecíficas (Comita et al., 2010; Harms et al., 2000). A su vez, los PMH tropicales la estructura y diversidad de árboles es afectada por el porcentaje de bosque remanente, la exposición a bordes y el tipo y manejo de las matrices adyacentes (Laurance et al., 2007; Oliveira et al., 2008; Tenius Ribeiro et al., 2019). Además, las abundancias de plántulas también están sujetas a la extensión, duración y frecuencia del disturbio asociados al manejo agrícola y ganadero de la región, así como a la historia de uso de suelo (Zermeño-Hernández et al., 2015, 2016). Por lo tanto, es posible que la abundancia de plántulas este influenciada por factores locales asociados con atributos estructurales del fragmento, tales como el área basal y la diversidad de los árboles que a su vez son influenciados por la estructura del paisaje, en particular la exposición a bordes y la composición de la matriz adyacente.

### *Diversidad*

Por otro lado, estudios de paisaje han señalado que la diversidad α de plántulas es directamente afectada por la estructura del paisaje. Tanto la diversidad α, como la proporción de especies tolerantes a la sombra de semillas y brinzales están asociadas a la composición del paisaje, en particular a los porcentajes de bosque primario a escalas grandes y de matrices desprovistas de vegetación arbórea a escalas pequeñas (Arasa-Gisbert et al., 2021; San-José et al., 2019; San-José et al., 2019). Estas variables también afectan la abundancia y diversidad de aves frugívoras y primates arborícolas (Carrara et al., 2015; Galán-Acedo et al., 2019; Kormann et al., 2018), los cuales son los principales dispersores de semillas de árboles en los trópicos (Jordano, 2000). Lo anterior sugiere que la reducción de la cobertura de bosque primario y la dominancia de coberturas uso de suelo abiertas pueden limitar la diversidad α de plántulas al restringir la llegada de nuevas especies a través de la dispersión de semillas provenientes de otros fragmentos.

En el caso de la diversidad β, se desconoce si la estructura del paisaje influye o no en su variación. No obstante, evidencia de trabajos a escala de fragmento indican que esta diversidad se encuentra fuertemente influenciada por los efectos de borde y las fluctuaciones de abundancias entre plántulas demandantes de luz y tolerantes a la sombra por los factores locales mencionados anteriormente (Krishnadas et al., 2019, 2020; Tabarelli et al., 2012). Lo anterior a través de procesos de exclusión competitiva y una mayor heterogeneidad ambiental de los bordes que promueve el recambio de especies (Krishnadas et al., 2019; Laurance et al., 2007; McKinney & Lockwood, 1999). Asimismo, trabajos con comunidades arbóreas indican que la diversidad β es promovida en paisajes fragmentados, donde la heterogeneidad espacial entre fragmentos promueve el establecimiento de comunidades arbóreas distintas entre ellos (Arroyo-Rodríguez et al., 2013). Por lo tanto, se sugiere que factores locales como la estructura de la vegetación y la configuración del paisaje relativa al contraste de borde y la fragmentación de los bosques primarios pueden jugar un papel importante sobre la diversidad β de las plántulas. Sin embargo, aún no existen estudios que nos permitan responder estas preguntas.

Finalmente, la estructura del paisaje también tiene una fuerte influencia sobre la persistencia de fauna dentro de fragmentos. Una mayor cobertura de matrices arboladas y la presencia de una mayor cantidad de fragmentos a lo largo del paisaje promueven la riqueza de mamíferos terrestres, siendo la complementación de recursos o la conectividad que provee el paisaje las posibles explicaciones (Arce-Peña et al., 2022; Garmendia et al., 2013; Thornton et al., 2011). Lo anterior indica que la matriz juega un papel importante en la persistencia de mamíferos terrestres en los PMH tropicales. Sin embargo, se carece de estudios que identifiquen el papel de la matriz para facilitar la presencia de mamíferos dentro de fragmentos (complementación/conectividad) y a que escalas están operando. Comprender las funciones que desempeña la matriz permitirá establecer que criterios de manejo se deben implementar ya sea para aumentar su capacidad de complementación de recursos o para aumentar su permeabilidad para el movimiento entre fragmentos (Blaum & Wichmann, 2007; Fischer & Lindenmayer, 2006; Franklin & Lindenmayer, 2009).

Esclarecer lo anterior es primordial para elaborar estrategias que mantengan la diversidad de plántulas en selvas hiper fragmentadas, ya sea a través de mejorar la calidad de hábitat dentro de los fragmentos y/o promover patrones de composición y configuración en el paisaje que aminoren los efectos de la pérdida de hábitat, reduzcan los efectos de borde y faciliten la presencia de mamíferos terrestres. Por lo tanto, es necesario elaborar estudios que evalúen la contribución que tiene la estructura del paisaje sobre los factores que afectan la abundancia y diversidad de plántulas de árboles dentro de fragmentos e identifiquen las coberturas de matriz y los patrones configuracionales prioritarios de conservación y/o manejo en PTH tropicales.

## Objetivos

### *General*

Esta tesis tiene como objetivo evaluar la respuesta de la comunidad de plántulas de árboles tropicales a la estructura del paisaje en una selva hiper fragmentada.

### *Particulares*

1. Identificar los efectos directos e indirectos de los factores a escala de fragmento que afectan la abundancia y diversidad α y β de las plántulas de árboles tropicales (capítulo II)
2. Evaluar la el efecto de la estructura del paisaje y sus escalas de efecto sobre la diversidad α y β de las plántulas de árboles tropicales (capítulo III)
3. Analizar la contribución que los efectos de la matriz (complementación y conectividad) y la fragmentación *per se* tienen sobre la presencia de mamíferos terrestres dentro de fragmentos a distintas escalas espaciales (capítulo IV)
4. Discutir las implicaciones de los resultados obtenidos en la regeneración de fragmentos (capítulo V)

La información generada por este trabajo permitirá identificar aquellos factores a escala de fragmento y de paisaje que moldean la comunidad de plántulas dentro de PMH tropicales, los cuáles serán la cobertura dominante de los bosques tropicales húmedos en el mediano y largo plazo. Favorecer y preservar la regeneración de fragmentos a través del manejo integral de estos paisajes será fundamental tanto para la conservación de la biodiversidad de los bosques tropicales húmedos y sus servicios ecosistémicos, como para aumentar la resiliencia de estos nuevos ecosistemas a los efectos del cambio global.

## Hipótesis

A partir de la evidencia revisada anteriormente y de acuerdo con la hipótesis del umbral de fragmentación de Andren (1994), se plantea que la comunidad de plántulas y los mamíferos terrestres que la afectan, responderán a tanto a factores a escala de fragmento, como a elementos de la estructura del paisaje relacionados con la composición y efectos de la matriz circundante y con los patrones configuracionales asociados a la densidad, aislamiento y agregación de fragmentos.

En el caso de la comunidad de plántulas, la abundancia de especies demandantes de luz será limitada en fragmentos con una mayor área basal y diversidad de la vegetación arbórea, y un menor disturbio asociado al manejo ganadero, que es la actividad productiva dominante en la región (Berget et al., 2021; Lohbeck et al., 2022). Para la diversidad α, se espera que aumente dentro de paisajes dominados por matrices arbóreas (i.e., porcentaje de bosques secundaros) y donde los patrones de configuración reduzcan el aislamiento entre fragmentos, ya sea una mayor densidad, una menor distancia o una mayor agregación de fragmentos en el paisaje. Por su parte, la diversidad β será afectada por factores directos e indirectos, siendo directamente promovida en paisajes con un bajo contraste de borde con la matriz adyacente y una mayor densidad de fragmentos e indirectamente beneficiada tanto por el área basal del fragmento (a través de la fluctuación de abundancias de plántulas). A su vez, la escala de los efectos de la estructura del paisaje sobre la diversidad α y β de las plántulas variará dependiendo de la abundancia de las especies evaluadas, siendo mayor para especies con bajas abundancias y menor para especies dominantes.

Por último, esperamos que la presencia de los mamíferos terrestres que influencian a la comunidad de plántulas sea favorecida por la matriz circundante, la cual tendrá funciones de complementación del paisaje a escalas pequeñas y de conectividad funcional a escalas grandes.

## Literatura citada

Andren, H. (1994). Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. *Oikos*, *71*, 355–366. https://doi.org/10.2307/3545823

Arasa-Gisbert, R., Arroyo-Rodríguez, V., Galán-Acedo, C., Meave, J. A., & Martínez-Ramos, M. (2021). Tree recruitment failure in old-growth forest patches across human-modified rainforests. *Journal of Ecology*, *March*, 1–13. https://doi.org/10.1111/1365-2745.13643

Arce-Peña, N. P., Arroyo-Rodríguez, V., Avila-Cabadilla, L. D., Moreno, C. E., & Andresen, E. (2022). Homogenization of terrestrial mammals in fragmented rainforests: the loss of species turnover and its landscape drivers. *Ecological Applications*, *32*(1). https://doi.org/10.1002/eap.2476

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., … Tscharntke, T. (2020). Designing optimal human-modified landscapes for forest biodiversity conservation. *Ecology Letters*. https://doi.org/10.1111/ele.13535

Arroyo-Rodríguez, V., Melo, F. P. L., Martínez-Ramos, M., Bongers, F., Chazdon, R. L., Meave, J. A., Norden, N., Santos, B. A., Leal, I. R., & Tabarelli, M. (2017). Multiple successional pathways in human-modified tropical landscapes: new insights from forest succession, forest fragmentation and landscape ecology research. *Biological Reviews*, *92*(1), 326–340. https://doi.org/10.1111/brv.12231

Arroyo-Rodríguez, V., Rös, M., Escobar, F., Melo, F. P. L., Santos, B. A., Tabarelli, M., & Chazdon, R. (2013). Plant β-diversity in fragmented rain forests: Testing floristic homogenization and differentiation hypotheses. *Journal of Ecology*, *101*(6), 1449–1458. https://doi.org/10.1111/1365-2745.12153

Benitez-Malvido, J. (1998). Impact of forest fragmentation on seedling abundance in a tropical rain forest. *Conservation Biology*, *12*(2), 380–389. https://doi.org/10.1046/j.1523-1739.1998.96295.x

Benítez-Malvido, J., Lázaro, A., & Ferraz, I. D. K. (2018). Effect of distance to edge and edge interaction on seedling regeneration and biotic damage in tropical rainforest fragments: A long-term experiment. *Journal of Ecology*, *106*(6), 2204–2217. https://doi.org/10.1111/1365-2745.13003

Benitez-Malvido, J., & Martinez-Ramos, M. (2003). Influence of Edge Exposure on Tree Seedling Species Recruitment in Tropical Rain Forest Fragments1. *Biotropica*, *35*(4), 530–541. https://doi.org/10.1111/j.1744-7429.2003.tb00609.x

Benítez-Malvido, J., & Martínez-Ramos, M. (2006). Influence of Edge Exposure on Tree Seedling Species Recruitment in Tropical Rain Forest Fragments1. *BIOTROPICA*, *35*(4), 530. https://doi.org/10.1646/02161

Berget, C., Verschoor, G., García-Frapolli, E., Mondragón-Vázquez, E., & Bongers, F. (2021). Landscapes on the move: Land-use change history in a mexican agroforest frontier. *Land*, *10*(10). https://doi.org/10.3390/land10101066

Blaum, N., & Wichmann, M. C. (2007). Short-term transformation of matrix into hospitable habitat facilitates gene flow and mitigates fragmentation. *Journal of Animal Ecology*, *76*(6), 1116–1127. https://doi.org/10.1111/j.1365-2656.2007.01283.x

Bueno, A. S., & Peres, C. A. (2019). Patch-scale biodiversity retention in fragmented landscapes: Reconciling the habitat amount hypothesis with the island biogeography theory. *Journal of Biogeography*, *46*(3), 621–632. https://doi.org/10.1111/jbi.13499

Camargo-Sanabria, A. A., Mendoza, E., Guevara, R., Martínez-Rmos, M., & Dirzo, R. (2014). Experimental defaunation of terrestrial mammalian herbivores alters tropical rainforest understorey diversity. *Proceedings of the Royal Society B: Biological Sciences*, *282*(1800). https://doi.org/10.1098/rspb.2014.2580

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 Conservation*, *184*, 117–126. https://doi.org/10.1016/j.biocon.2015.01.014

Cassano, C. R., Barlow, J., & Pardini, R. (2012). Large Mammals in an Agroforestry Mosaic in the Brazilian Atlantic Forest. *Biotropica*, *44*(6), 818–825. https://doi.org/10.1111/j.1744-7429.2012.00870.x

Chazdon, R. L. (2003). Tropical forest recovery: Legacies of human impact and natural disturbances. *Perspectives in Plant Ecology, Evolution and Systematics*, *6*(1–2), 51–71. https://doi.org/10.1078/1433-8319-00042

Comita, L. S., Aguilar, S., Pérez, R., Lao, S., & Hubbell, S. P. (2007). Patterns of woody plant species abundance and diversity in the seedling layer of a tropical forest. *Journal of Vegetation Science*, *18*(2), 163. https://doi.org/10.1658/1100-9233(2007)18[163:powpsa]2.0.co;2

Comita, L. S., Muller-Landau, H. C., Aguilar, S., & Hubbell, S. P. (2010). Asymmetrie density dependence shapes species abundances in a tropical tree community. *Science*, *329*(5989), 330–332. https://doi.org/10.1126/science.1190772

Cudney-Valenzuela, S. J., Arroyo-Rodríguez, V., Andresen, E., Toledo-Aceves, T., Mora-Ardila, F., Andrade-Ponce, G., & Mandujano, S. (2021). Does patch quality drive arboreal mammal assemblages in fragmented rainforests? *Perspectives in Ecology and Conservation*, *19*(1), 61–68. https://doi.org/10.1016/j.pecon.2020.12.004

Cumming, G., & Peterson, G. (2005). Ecology in Global Scenarios. In R. Hassan, R. Scholes, & N. Ash (Eds.), *Ecosystems and Human Well-being: Current State and Trends* (pp. 45–70). Island Press.

DeClerck, F. A. J., Chazdon, R., Holl, K. D., Milder, J. C., Finegan, B., Martinez-Salinas, A., Imbach, P., Canet, L., & Ramos, Z. (2010). Biodiversity conservation in human-modified landscapes of Mesoamerica: Past, present and future. *Biological Conservation*, *143*(10), 2301–2313. https://doi.org/10.1016/j.biocon.2010.03.026

Denslow, J S. (1987). Tropical Rainforest Gaps and Tree Species Diversity. *Annual Review of Ecology and Systematics*, *18*(1), 431–451. https://doi.org/10.1146/annurev.es.18.110187.002243

Denslow, Julie S., & Guzman G., S. (2000). Variation in stand structure, light and seedling abundance across a tropical moist forest chronosequence, Panama. *Journal of Vegetation Science*, *11*(2), 201–212. https://doi.org/10.2307/3236800

Dirzo, R., & Miranda, A. (1990). Contemporary Neotropical Defaunation and Forest Structure, Function, and Diversity-A Sequel to John Terborgh*. *Conservation Biology*, *4*(4), 444–447. https://doi.org/10.1111/j.1523-1739.1990.tb00320.x

Fahrig, L. (2003). Effects of Habitat Fragmentation on Biodiversity. *Annual Review of Ecology, Evolution, and Systematics*, *34*(1), 487–515. https://doi.org/10.1146/annurev.ecolsys.34.011802.132419

Fahrig, L. (2017). Ecological Responses to Habitat Fragmentation Per Se. *Annual Review of Ecology, Evolution, and Systematics*, *48*(1), 1–23. https://doi.org/10.1146/annurev-ecolsys-110316-022612

Fahrig, L. (2019). Habitat fragmentation: A long and tangled tale. *Global Ecology and Biogeography*, *28*(1), 33–41. https://doi.org/10.1111/geb.12839

Fischer, J., & Lindenmayer, D. B. (2006). Beyond fragmentation: the continuum model for fauna research and conservation in human-modified landscapes. *Oikos*, *112*(2), 473–480.

Fletcher, R. J., & Fortin, M.-J. (2018). *Spatial Ecology and Conservation Modeling* (Vol. 14). Springer Nature Switzerland AG. https://doi.org/10.1016/j.ecoinf.2013.01.002

Franklin, J. F., & Lindenmayer, D. B. (2009). Importance of matrix habitats in maintaining biological diversity. *Proceedings of the National Academy of Sciences*, *106*(2), 349–350. https://doi.org/10.1073/pnas.0812016105

Galán-Acedo, C., Arroyo-Rodríguez, V., Estrada, A., & Ramos-Fernández, G. (2019). Forest cover and matrix functionality drive the abundance and reproductive success of an endangered primate in two fragmented rainforests. *Landscape Ecology*, *34*(1), 147–158. https://doi.org/10.1007/s10980-018-0753-6

Galetti, M., Bovendorp, R. S., & 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. https://doi.org/10.1016/j.gecco.2015.04.008

Galetti, M., & Dirzo, R. (2013). Ecological and evolutionary consequences of living in a defaunated world. *Biological Conservation*, *163*, 1–6. https://doi.org/10.1016/j.biocon.2013.04.020

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*(4), 331–344. https://doi.org/10.1017/S0266467413000370

Grantham, H. S., Duncan, A., Evans, T. D., Jones, K. R., Beyer, H. L., Schuster, R., Walston, J., Ray, J. C., Robinson, J. G., Callow, M., Clements, T., Costa, H. M., DeGemmis, A., Elsen, P. R., Ervin, J., Franco, P., Goldman, E., Goetz, S., Hansen, A., … Watson, J. E. M. (2020). Anthropogenic modification of forests means only 40% of remaining forests have high ecosystem integrity. *Nature Communications*, *11*(1). https://doi.org/10.1038/s41467-020-19493-3

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., King, A. J., Laurance, W. F., Levey, D. J., Margules, C. R., … Townshend, J. R. (2015). Habitat fragmentation and its lasting impact on Earth’s ecosystems. *Science Advances*, *1*(2), e1500052. https://doi.org/10.1126/sciadv.1500052

Harms, K. E. E., Wright, S. J. J., Calderón, O., Hernández, A., & Herre, E. A. a. (2000). Pervasive density-dependent recruitment enhances seedling diversity in a tropical forest. *Nature*, *404*(6777), 493–495. https://doi.org/10.1038/35006630

Hernández-Ruedas, M. A., Arroyo-Rodríguez, V., Morante-Filho, J. C., Meave, J. A., & Martínez-Ramos, M. (2018). Fragmentation and matrix contrast favor understory plants through negative cascading effects on a strong competitor palm. *Ecological Applications*, *28*(6), 1546–1553. https://doi.org/10.1002/eap.1740

Hobbs, Richard J., Higgs, E. S., & Hall, C. M. (Eds.). (2013). *Novel ecosystems: intervening in the new ecological world order*. Wiley-Blackwell.

Hulvey, K. B., Standish, R. J., Hallett, L. M., Starzomski, B. M., Murphy, S. D., Nelson, C. R., Gardener, M. R., Kennedy, P. L., Seastedt, T. R., & Suding, K. N. (2013). Incorporating Novel Ecosystems into Management Frameworks. In *Novel Ecosystems: Intervening in the New Ecological World Order* (pp. 157–171). John Wiley & Sons, Ltd. https://doi.org/10.1002/9781118354186.ch18

Jackson, H. B., & Fahrig, L. (2012). What size is a biologically relevant landscape? *Landscape Ecology*, *27*(7), 929–941. https://doi.org/10.1007/s10980-012-9757-9

Jackson, H. B., & Fahrig, L. (2015). Are ecologists conducting research at the optimal scale? *Global Ecology and Biogeography*, *24*(1), 52–63. https://doi.org/10.1111/geb.12233

Jesus, F. M., Pivello, V. R., Meirelles, S. T., Franco, G. A. D. C., & Metzger, J. P. (2012). The importance of landscape structure for seed dispersal in rain forest fragments. *Journal of Vegetation Science*, *23*(6), 1126–1136. https://doi.org/10.1111/j.1654-1103.2012.01418.x

Jordano, P. (2000). Fruits and frugivory. In M. Fenner (Ed.), *Seeds: the ecology of regeneration in plant communities* (2nd ed., pp. 125–166). CABI Publishing.

Kennedy, P. L., Lach, L., Lugo, A. E., & Hobbs, R. J. (2013). Fauna and novel ecosystems. In R.J. Hobbs, E. S. Higgs, & C. M. Hall (Eds.), *Novel Ecosystems: Intervening in the New Ecological World Order* (1st ed., pp. 127–141). John Wiley & Sons, Ltd.

Kormann, U. G., Hadley, A. S., Tscharntke, T., Betts, M. G., Robinson, W. D., & Scherber, C. (2018). Primary rainforest amount at the landscape scale mitigates bird biodiversity loss and biotic homogenization. *Journal of Applied Ecology*, *55*(3), 1288–1298. https://doi.org/10.1111/1365-2664.13084

Krishnadas, M., Agarwal, K., & Comita, L. S. (2020). Edge effects alter the role of fungi and insects in mediating functional composition and diversity of seedling recruits in a fragmented tropical forest. *Annals of Botany*, *126*(7), 1181–1191. https://doi.org/10.1093/aob/mcaa138

Krishnadas, M., Kumar, A. N., & Comita, L. S. (2019). Edge effects reduce α-diversity but not β-diversity during community assembly in a human-modified tropical forest. *Ecological Applications*, *29*(8), 1–10. https://doi.org/10.1002/eap.1996

Laurance, W. F., Camargo, J. L. C., Luizão, R. C. C., Laurance, S. G., Pimm, S. L., Bruna, E. M., Stouffer, P. C., Bruce Williamson, G., Benítez-Malvido, J., Vasconcelos, H. L., Van Houtan, K. S., Zartman, C. E., Boyle, S. A., Didham, R. K., Andrade, A., & Lovejoy, T. E. (2011). The fate of Amazonian forest fragments: A 32-year investigation. *Biological Conservation*, *144*(1), 56–67. https://doi.org/10.1016/j.biocon.2010.09.021

Laurance, W. F., Nascimento, H. E. M., Laurance, S. G., Andrade, A. C., Fearnside, P. M., Ribeiro, J. E. L., & Capretz, R. L. (2006). Rain forest fragmentation and the proliferation of successional trees. *Ecology*, *87*(2), 469–482. https://doi.org/10.1890/05-0064

Laurance, W. F., Nascimento, H. E. M., Laurance, S. G., Andrade, A., Ribeiro, J. E. L. S., Giraldo, J. P., Lovejoy, T. E., Condit, R., Chave, J., Harms, K. E., & D'Angelo, S. (2006). Rapid decay of tree-community composition in Amazonian forest fragments. *Proceedings of the National Academy of Sciences of the United States of America*, *103*(50), 19010–19014. https://doi.org/10.1073/pnas.0609048103

Laurance, W. F., Nascimento, H. E. M. M., Laurance, S. G., Andrade, A., Ewers, R. M., Harms, K. E., Luizão, R. C. C. C., & Ribeiro, J. E. (2007). Habitat fragmentation, variable edge effects, and the landscape-divergence hypothesis. *PLoS ONE*, *2*(10), e1017. https://doi.org/10.1371/journal.pone.0001017

Le Quéré, C., Andrew, R. M., Friedlingstein, P., Sitch, S., Pongratz, J., Manning, A. C., Korsbakken, J. I., Peters, G. P., Canadell, J. G., Jackson, R. B., Boden, T. A., Tans, P. P., Andrews, O. D., Arora, V. K., Bakker, D. C. E., Barbero, L., Becker, M., Betts, R. A., Bopp, L., … Zhu, D. (2018). Global Carbon Budget 2018 (pre-print). *Earth System Science Data Discussions*, *pre print*(November), 1–54.

Lohbeck, M., DeVries, B., Bongers, F., Martínez-Ramos, M., Navarrete-Segueda, A., Nicasio-Arzeta, S., Siebe, C., Pingarroni, A., Wies, G., & Decuyper, M. (2022). Mexican agricultural frontier communities differ in forest dynamics with consequences for conservation and restoration. *Remote Sensing in Ecology and Conservation*, *37*(2), 10–14.

https://doi.org/10.1002/RSE2.262

Magioli, M., Ferraz, K. M. P. M. de B., Chiarello, A. G., Galetti, M., Setz, E. Z. F., Paglia, A. P., Abrego, N., Ribeiro, M. C., & Ovaskainen, O. (2021). Land-use changes lead to functional loss of terrestrial mammals in a Neotropical rainforest. *Perspectives in Ecology and Conservation*, *19*(2), 161–170. https://doi.org/10.1016/j.pecon.2021.02.006

Magioli, M., Ferraz, K. M. P. M. de B., Setz, E. Z. F., Percequillo, A. R., Rondon, M. V. de S. S., Kuhnen, V. V., Canhoto, M. C. da S., dos Santos, K. E. A., Kanda, C. Z., Fregonezi, G. de L., do Prado, H. A., Ferreira, M. K., Ribeiro, M. C., Villela, P. M. S., Coutinho, L. L., & Rodrigues, M. G. (2016). Connectivity maintain mammal assemblages functional diversity within agricultural and fragmented landscapes. *European Journal of Wildlife Research*, *62*(4), 431–446. https://doi.org/10.1007/s10344-016-1017-x

Martin, A. E. (2018). The spatial scale of a species' response to the landscape context depends on which biological response you measure. *Current Landscape Ecology Reports*, *3*(1), 23–33. https://doi.org/10.1007/s40823-018-0030-z

Martínez-Ramos, M., Pingarroni, A., Rodríguez-Velázquez, J., Toledo-Chelala, L., Zermeño-Hernández, I., & Bongers, F. (2016). Natural forest regeneration and ecological restoration in human-modified tropical landscapes. *Biotropica*, *48*(6), 745–757. https://doi.org/10.1111/btp.12382

McGarigal, K., Cushman, S. A., & Ene, E. (2012). *FRAGSTATS v4: Spatial Pattern Analysis Program for Categorical and Continuous Maps* (4th ed.).

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*(11), 450–453. https://doi.org/10.1016/S0169-5347(99)01679-1

Miguet, P., Jackson, H. B., Jackson, N. D., Martin, A. E., & Fahrig, L. (2016). What determines the spatial extent of landscape effects on species? *Landscape Ecology*, *31*(6), 1177–1194. https://doi.org/10.1007/s10980-015-0314-1

Moraga, A. D., Martin, A. E., & Fahrig, L. (2019). The scale of effect of landscape context varies with the species' response variable measured. *Landscape Ecology*, *34*, 703–715. https://doi.org/10.1007/s10980-019-00808-9

Nicotra, A. B., Chazdon, R. L., & Iriarte, S. V. B. (1999). Spatial heterogeneity of light and woody seedling regeneration in tropical wet forests. *Ecology*, *80*(6), 1908–1926. https://doi.org/10.1890/0012-9658(1999)080[1908:SHOLAW]2.0.CO;2

Oliveira, M. A., Santos, A. M. M., & Tabarelli, M. (2008). Profound impoverishment of the large-tree stand in a hyper-fragmented landscape of the Atlantic forest. *Forest Ecology and Management*, *256*(11), 1910–1917. https://doi.org/10.1016/j.foreco.2008.07.014

Orrock, J. L., Levey, D. J., Danielson, B. J., & Damschen, E. I. (2006). Seed predation, not seed dispersal, explains the landscape-level abundance of an early-successional plant. *Journal of Ecology*, *94*(4), 838–845. https://doi.org/10.1111/j.1365-2745.2006.01125.x

Perring, M. P., & Ellis, E. C. (2013). The Extent of Novel Ecosystems: Long in Time and Broad in Space. In *Novel Ecosystems: Intervening in the New Ecological World Order* (pp. 66–80). John Wiley & Sons, Ltd. https://doi.org/10.1002/9781118354186.ch8

Pfeifer, M., Lefebvre, V., Gardner, T. A., Arroyo-Rodriguez, V., Baeten, L., Banks-Leite, C., Barlow, J., Betts, M. G., Brunet, J., Cerezo, A., Cisneros, L. M., Collard, S., D'Cruze, N., da

Silva Motta, C., Duguay, S., Eggermont, H., Eigenbrod, F., Hadley, A. S., Hanson, T. R., … Ewers, R. M. (2014). BIOFRAG – a new database for analyzing BIOdiversity responses to forest FRAGmentation. *Ecology and Evolution*, *4*(9), 1524–1537. https://doi.org/10.1002/ece3.1036

Prugh, L. R., Hodges, K. E., Sinclair, A. R. E., & Brashares, J. S. (2008). Effect of habitat area and isolation on fragmented animal populations. *Proceedings of the National Academy of Sciences*, *105*(52), 20770–20775. https://doi.org/10.1073/pnas.0806080105

Rose, S. (2000). Seeds, seedlings, and gaps - size matters. a study in the tropical rain forest of Guyana. In T.-G. Programme & S. Rose (Eds.), *Trobenpos-Guyana Series 9* (pp. 1–184). Trobenpos-Guyana Programme.

San-José, M., Arroyo-Rodríguez, V., Jordano, P., Meave, J. A., & Martínez-Ramos, M. (2019). The scale of landscape effect on seed dispersal depends on both response variables and landscape predictor. *Landscape Ecology*, 1–12. https://doi.org/10.1007/s10980-019-00821-y

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*(3), 413–432. https://doi.org/10.1177/194008291400700304

San-José, M., Arroyo-Rodríguez, V., & Meave, J. A. (2019). Regional context and dispersal mode drive the impact of landscape structure on seed dispersal. *Ecological Applications*, *0*(0), eap.2033. https://doi.org/10.1002/eap.2033

Sánchez-Gallen, I., Álvarez-Sánchez, F. J., & Benítez-Malvido, J. (2010). Structure of the advanced regeneration community in tropical rain forest fragments of Los Tuxtlas, Mexico. *Biological Conservation*, *143*(9), 2111–2118. https://doi.org/10.1016/j.biocon.2010.05.021

Santo-Silva, E. E., Almeida, W. R., Melo, F. P. L., Zickel, C. S., & Tabarelli, M. (2013). The nature of seedling assemblages in a fragmented tropical landscape: Implications for forest regeneration. *Biotropica*, *45*(3), 386–394. https://doi.org/10.1111/btp.12013

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*(7720), 639–643. https://doi.org/10.1038/s41586-018-0411-9

Tabarelli, M., Aguiar, A. V., Ribeiro, M. C., Metzger, J. P., & Peres, C. a. (2010). Prospects for biodiversity conservation in the Atlantic Forest: Lessons from aging human-modified landscapes. *Biological Conservation*, *143*(10), 2328–2340. https://doi.org/10.1016/j.biocon.2010.02.005

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. https://doi.org/10.1016/j.biocon.2012.06.020

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*(7693), 519–522. https://doi.org/10.1038/nature25508

Tenius Ribeiro, J. C., Nunes-Freitas, A. F., Fidalgo, E. C. C., & Uzêda, M. C. (2019). Forest fragmentation and impacts of intensive agriculture: Responses from different tree functional groups. *PLoS ONE*, *14*(8). https://doi.org/10.1371/journal.pone.0212725

Thornton, D. H., Branch, L. C., & Sunquist, M. E. (2011). The relative influence of habitat loss and fragmentation: Do tropical mammals meet the temperate paradigm? *Ecological Applications*, *21*(6), 2324–2333. https://doi.org/10.1890/10-2124.1

Umetsu, F., & Pardini, R. (2007). Small mammals in a mosaic of forest remnants and anthropogenic habitats - Evaluating matrix quality in an Atlantic forest landscape. *Landscape Ecology*, *22*(4), 517–530. https://doi.org/10.1007/s10980-006-9041-y

Villar, N., Siqueira, T., Zipparro, V. B., Farah, F., Schmaedecke, G., Hortenci, L., Brocardo, C. R., Jordano, P., & Galetti, M. (2019). The cryptic regulation of diversity by functionally complementary large tropical forest herbivores. *Journal of Ecology*, 1365-2745.13257. https://doi.org/10.1111/1365-2745.13257

Wandrag, E. M., Dunham, A. E., Duncan, R. P., & Rogers, H. S. (2017). Seed dispersal increases local species richness and reduces spatial turnover of tropical tree seedlings. *Proceedings of the National Academy of Sciences of the United States of America*, *114*(40), 10689–10694. https://doi.org/10.1073/pnas.1709584114

Watson, J. E. M., Evans, T., Venter, O., Williams, B., Tulloch, A., Stewart, C., Thompson, I., Ray, J. C., Murray, K., Salazar, A., McAlpine, C., Potapov, P., Walston, J., Robinson, J. G., Painter, M., Wilkie, D., Filardi, C., Laurance, W. F., Houghton, R. A., … Lindenmayer, D. (2018). The exceptional value of intact forest ecosystems. *Nature Ecology and Evolution*, *2*(4), 599–610. https://doi.org/10.1038/s41559-018-0490-x

Western, D. (2001). Human-modified ecosystems and future evolution. *Proceedings of the National Academy of Sciences*, *98*(10), 5458–5465. https://doi.org/10.1073/pnas.101093598

Wies, G., Nicasio Arzeta, S., & Martinez Ramos, M. (2021). Critical ecological thresholds for conservation of tropical rainforest in Human Modified Landscapes. *Biological Conservation*, *255*, 109023. https://doi.org/10.1016/j.biocon.2021.109023

Wills, C., Harms, K. E., Condit, R., King, D., Thompson, J., He, F., Muller-Landau, H. C., Ashton, P., Losos, E., Comita, L., Hubbell, S., LaFrankie, J., Bunyavejchewin, S., Dattaraja, H. S., Davies, S., Esufali, S., Foster, R., Gunatilleke, N., Gunatilleke, S., … Zimmerman, J. (2006). Nonrandom processes maintain diversity in tropical forests. *Science*, *311*(5760), 527–531. https://doi.org/10.1126/science.1117715

Wright, S. J. (2005). Tropical forests in a changing environment. *Trends in Ecology & Evolution*, *20*(10), 553–560. https://doi.org/10.1016/J.TREE.2005.07.009

Wright, S. J., Zeballos, H., Dominguez, I., Gallardo, M. M., Moreno, M. C., & Ibáñez, R. (2000). Poachers alter mammal abundance, seed dispersal, and seed predation in a neotropical forest. *Conservation Biology*, *14*(1), 227–239. https://doi.org/10.1046/j.1523-1739.2000.98333.x

Wurtzebach, Z., & Schultz, C. (2016). Measuring Ecological Integrity: History, Practical Applications, and Research Opportunities. *BioScience*, *66*(6), 446–457. https://doi.org/10.1093/biosci/biw037

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*(1), 333–358. https://doi.org/10.1146/annurev-ecolsys-112414-054142

Zermeño-Hernández, I., Méndez-Toribio, M., Siebe, C., Benítez-Malvido, J., & Martínez-Ramos,

M. (2015). Ecological disturbance regimes caused by agricultural land uses and their effects on tropical forest regeneration. *Applied Vegetation Science*, *18*(3), 443–455. https://doi.org/10.1111/avsc.12161

Zermeño-Hernández, I., Pingarroni, A., & Martínez-Ramos, M. (2016). Agricultural land-use diversity and forest regeneration potential in human- modified tropical landscapes. *Agriculture, Ecosystems and Environment*, *230*, 210–220. https://doi.org/10.1016/j.agee.2016.06.007

# CAPÍTULO II. CASCADING EFFECTS OF FIRE DISTURBANCE AND LANDSCAPE CONFIGURATION ON SEEDLING DIVERSITY WITHIN RAINFOREST PATCHES

# Cascading effects of fire disturbance and landscape configuration on seedling diversity within rainforest patches

Sergio Nicasio-Arzeta[1,2*], Susana Maza-Villalobos[3], Aline Pingarroni[1], Isela Zermeño-Hernández[4*] and Julieta Benítez-Malvido[2]

[1]Programa de Doctorado en Ciencias Biomédicas, Universidad Nacional Autónoma de México, Unidad de Posgrado, Circuito de Posgrados s/n, Ciudad Universitaria, C.P. 04510, Ciudad de México, México ORCID: https://orcid.org/0000-0002-1481-5660

[2]Instituto de Investigaciones en Ecosistemas y Sustentabilidad, Universidad Nacional Autónoma de México, Campus Morelia, Antigua Carretera a Pátzcuaro #8701, Col. Ex-Hacienda de San José de la Huerta, C.P. 58190, Morelia, Michoacán, México

[3]CONACYT-El Colegio de la Frontera Sur, Unidad Tapachula, Carretera Antiguo Aeropuerto Km 2.5 s/n, Col. Centro, C.P. 30700, Tapachula, Chiapas, México ORCID: https://orcid.org/0000-0002-0123-9756

[4]Instituto de Investigaciones sobre los Recursos Naturales, Universidad Michoacana de San Nicolás de Hidalgo, Av. San Juanito Itzícuaro s/n, Col. Ampliación Río Florido, C.P. 58330, Morelia, Michoacán, México ORCID: https://orcid.org/0000-0002-3180-4138.

Corresponding author:

Sergio Nicasio-Arzeta[1]

Antigua Carretera a Pátzcuaro no. 8701, Morelia, Michoacán, 58190, México

Isela Zermeño-Hernández[4]

Av. San Juanito Itzícuaro s/n, Col. Ampliación Río Florido, C.P. 58330, Morelia, Michoacán, México

Email address: izermeno@gmail.com sergio.nicasio@gmail.com

## Abstract

Seedling community drives forest regeneration in fragmented rainforests. In these novel ecosystems, seedlings are influenced by the structure of patches (i.e., size, shape, vegetation structure and disturbance) and the surrounding landscape (i.e., composition and configuration). However, the attributes of seedling community respond differently to patch and landscape structure, whose direct or cascading effects on seedling composition and diversity are unknown. Given the hierarchical relationship among landscapes, patches and seedlings, we assessed the direct and cascading effects of patch and landscape structure on seedling community within 16 forest patches of a hyper-fragmented rainforest in southeastern Mexico. We used a multi-scale approach to determine the effects of landscape composition/configuration on patch structure. Then, we used piecewise structural equation models to assess the direct and cascading effects of patch and landscape structure on seedling abundance, composition and α- and β-diversity. Our results showed that seedling composition and β-diversity were affected by fire disturbance, whereas seedling richness was influenced by landscape configuration. On one hand, fire disturbance had cascading negative effects on seedling composition and β-diversity through positive effects on the abundance of light-demanding seedlings (i.e., promoting early-successional species). On the other hand, the aggregation of patches had cascading positive effects on seedling richness through positive effects on the abundance of shade-tolerant seedlings (i.e., sustaining seed dispersal). These findings support that patch-scale and landscape configuration effects are greater in hyper-fragmented landscapes, as well as the positive effects of fragmentation on biodiversity.

**Keywords.** abundance, alpha-diversity, beta-diversity, structural equation models, fragmentation, landscape structure

## Introduction

Deforestation has reduced 10% of the remaining rainforests in small-sized patches (< 20 ha), which will dominate tropical landscapes in the next decades (Taubert et al., 2018). Nonetheless, these patches preserve forest species, ecological processes (i.e., pollination and seed dispersal/predation), and landscape connectivity (Laurance et al., 2011; Hernández-Ruedas et al., 2014; Cudney-Valenzuela et al., 2021), urging to promote their natural regeneration to sustain their biodiversity (Crouzeilles et al., 2016; Brancalion et al., 2019). In this sense, it is decisive to understand the abundance and diversity patterns of tree seedlings within patches, since the regeneration, structure and diversity of rainforests is largely determined by the tree seedling community (Brokaw & Scheiner, 1989; Whitmore, 1989; Dalling, Hubbell & Silvera, 1998; Brokaw & Busing, 2000).

The abundance, richness (α-diversity) and spatial heterogeneity (β-diversity) of forest seedling species are shaped by seed production and dispersal, as well as seedling mortality by density-dependence and predation/trampling of herbivorous mammals (Nathan & Muller-Landau, 2000; Harms et al., 2000; Comita et al., 2007; Young et al., 2016). Following forest fragmentation, the size and shape of patches drive the extent and magnitude of edge effects (Haddad et al., 2015), favoring the abundance of light-demanding seedlings – tree species with acquisitive traits commonly found in forest gaps and early-successional stages –, reduce the abundance of shade-tolerant seedlings – tree species with conservative traits dominant in undisturbed forests and late-successional stages – (Benitez-Malvido, 1998; Santo-Silva et al., 2013; Benítez-Malvido, Lázaro & Ferraz, 2018) and impoverish α- and β-diversity (Tabarelli, Peres & Melo, 2012; Krishnadas, Kumar & Comita, 2019; Liu et al., 2019; Krishnadas, Agarwal & Comita, 2020). Nonetheless, seedlings can also be affected by components of patch structure aside from its size and shape.

Tree basal area plays a key role on light availability, microclimate regulation, nutrient cycling and seed production (Hardwick et al., 2015; Lohbeck et al., 2015; Minor & Kobe, 2019; Wies, Nicasio Arzeta & Martinez Ramos, 2021), conditions that regulate the abundance of light-demanding seedlings and shade-tolerant seedlings (Whitmore, 1989; Denslow & Guzman G., 2000). Also, patches with a high basal area harbor a greater diversity of forest-dependent birds and mammals that favor seedling α- and β-diversity (Zurita & Bellocq, 2010; Wearn et al., 2017; Cudney-Valenzuela et al., 2021). Additionally, seedling abundance and composition can be influenced by tree diversity (Terborgh et al., 2001; Comita et al., 2007), particularly where seed input is limited to the surrounding adult trees (Wandrag et al., 2017). Furthermore, disturbance regimes by agricultural land uses affect forest regeneration in the tropics (Guariguata & Ostertag, 2001; Fontúrbel et al., 2015). The size, duration and severity of disturbance by agricultural and cattle management can limit seed rain, reduce soil fertility, and increase temperature and water deficit, leading to a reduced abundance and diversity of seedlings (Zermeño-Hernández et al., 2015). Such effects are higher in landscapes dominated by pastures (Zermeño-Hernández, Pingarroni & Martínez-Ramos, 2016), where cattle grazing and trampling limit seedling establishment. Moreover, these areas are subject to recurrent fires, which not only decrease soil fertility, but also reduce the diversity and basal area of the remaining forest (Barlow, Haugaasen & Peres, 2002).

Additionally, it is well documented that composition (i.e., proportion of primary forest and matrix covers in the landscape) and configuration (i.e., number/aggregation of patches and edge contrast between patches and matrix) of landscape structure have significant effects on seedling communities. Landscape structure can influence seedling abundance, composition and diversity whether by sustaining seed dispersal in landscapes where forest cover and patch density/aggregation are high (Jesus et al., 2012; San-José, Arroyo-Rodríguez & Meave, 2019), or by alleviating edge effects and facilitating the arrival of seed/seedling predators in landscapes with low edge contrast (Arasa-Gisbert et al., 2021; Nicasio-Arzeta et al., 2021). It is noteworthy that landscape fragmentation (modulated by landscape configuration) have stronger effects on understory vegetation, and tree seedlings/saplings than habitat loss (modulated by landscape composition) in highly deforested rainforests (Nicasio-Arzeta et al., 2021; Arasa-Gisbert et al., 2022). Their findings support the "fragmentation threshold hypothesis", which stipulates that patch-scale and landscape configuration have stronger effects on biodiversity within landscapes with < 30% of forest cover (Andren, 1994). Thus, the composition and diversity of tree seedlings from hyper-fragmented rainforests might be driven by the synergistic effect of patch structure and landscape configuration.

However, seedling community and patch structure are expected to be influenced by landscape structure at multiple spatial scales, since the scale of effect vary among biological variables (i.e., structure, abundance, composition, richness), habitat specialization (i.e., light-demanding/shade-tolerant) and disturbance extent (Miguet et al., 2016; Martin, 2018; Suárez-Castro et al., 2018). The latter suggests that landscape structure might have cascading effects on seedling communities, a process observed elsewhere (Hernández-Ruedas et al., 2018). These cascading effects are possible operating through patch-structural attributes. The proportion of forest cover in the landscape is directly related to patch size (Fahrig, 2013; Hernando et al., 2017) and tree basal area/diversity (Laurance et al., 2000; Wies, Nicasio Arzeta & Martinez Ramos, 2021; Brindis-Badillo et al., 2022). Alternatively, tree diversity is affected by the surrounding secondary forests and the aggregation of forest patches (Nascimento et al., 2006; Laurance et al., 2007; Jesus et al., 2012). Forest disturbance by fires and management intensity can also be modulated by edge contrast, forest cover and patch density. On one hand, edge exposure increases fuel availability and fire ignition (Román-Cuesta & Martínez-Vilalta, 2006; Avila-Flores et al., 2010; Farfán Gutiérrez et al., 2018). On the other hand, cattle presence is limited where forest cover or patch number are high, since they increase the occurrence of large predators (Trolle, 2003; Desbiez, Bodmer & Aparecida, 2009; de Souza et al., 2018). Although patch and landscape structure can potentially have direct and/or cascading effects on seedling community, their evaluation remains unexplored.

We aimed to identify the direct and cascading effects of patch and landscape structure on seedling abundance, composition and diversity in a fragmented rainforest. We hypothesized that patch structure and landscape configuration are exerting direct or cascading effects on seedling composition and diversity. We expect that seedling composition and β-diversity are more influenced by patch structure, since these community attributes are sensitive to abundance fluctuations of species with contrasting life-history traits (Comita et al., 2007; Santo-Silva et al., 2015). Hence, we expect a similar composition of a set of species and greater β-diversity within patches with lower abundances of light-demanding seedlings and higher abundances of shade-tolerant seedlings, fluctuations favored in large-sized, highly-diverse and low-disturbed patches. Additionally, we expect that seedling α-diversity will be favored in landscapes with high forest cover or high density/aggregation of patches, since species richness is strongly associated to large-scale processes that sustain seed dispersal (San-José et al., 2019; Arasa-Gisbert et al., 2022). These effects can occur whether by cascading effects of landscape structure by influencing patch structure (Fig 1, hypothetical pathway 1), or by cascading effects of patch structure by mediating abundance fluctuations (Fig 1, hypothetical pathway 2). We employed structural equation models to assess the direct and indirect effects of patch components (Fig S1).

## Material and methods

### *Study site.*

We conducted the study at the Marqués de Comillas region in the Lacandona rainforest in southeastern Mexico (Fig 2a). The majority of cleared areas in the study site are employed to raise cattle (Carabias, De la Maza & Cadena, 2015; Berget et al., 2021), and use of forest patches to provide shade for cattle is a common practice. The latter implies that some landowners slash the understory vegetation in forerst fragments to facilitate the movement of cows and people along patches. Land clearing by fire is another practice in the area, and sometimes, mismanaged fires expand into patches, partially burning tree vegetation. Another disturbance factor in the study area is the periodic flooding of patches nearby the Lacantún river during rainy season.

We selected 16 forest patches (Fig 2b). Land tenure of Marqués de Comillas is private, and land property is distributed among the inhabitants (Carabias, De la Maza & Cadena, 2015; Kolb & Galicia, 2018; Berget et al., 2021). Therefore, we conducted our study only in patches where permission was granted beforehand by the owners. Patches were distributed over alluvial terraces, so diversity and composition of tree assemblages, soil type and abiotic factors remain relatively constant (Navarrete-Segueda et al., 2018; Lohbeck et al., 2022).

### *Seedling sampling.*

Patches were sampled in 1-ha blocks placed at the center of each forest patch from February to June of 2014. Each block contained ten 1-m$^2$ plots randomly arranged in groups of two or three plots along five equidistant transects (20 m apart; Fig 2d). For 1-ha forest patches, we never positioned plots at the edge in order to have a 20-m buffer zone of vegetation that protect them from strong edge effects as much as possible (Fig 2d). Within each 1-m$^2$ plot we counted and identified all tree seedlings (10-100 cm height) to the lowest possible taxonomic level with the help of a local parataxonomist and field guides (Martínez, Ramos-A. & Chiang, 1994; Sousa, 2009). When field identification was not possible, we took samples for identification at several herbariums (MEXU, ECO-SC-H). This study did not involve the extraction or damage of endangered species. Plant nomenclature followed the Missouri Botanical Garden database Tropicos (Missouri Botanical Garden, 2019). Once identified, seedlings species were classified by dispersal syndrome (Ibarra-Manríquez, Martínez Ramos & Oyama, 2001; Ibarra-Manríquez & Cornejo-Tenorio, 2010) and light requirements for establishment and growth: light-demanding species, shade-tolerant species and intermediate species (Nicotra, Chazdon & Iriarte, 1999; Rose, 2000; Comita et al., 2007; Kitajima, Cordero & Wright, 2013).

### *Seedling community.*

We assessed the sampling completeness with the sample coverage estimator of Chao and Shen (Chao et al., 2016). We combined the data of the 10 sampling plots within each patch and then we estimated the proportion of the total number of individuals that belong to the species represented in the sample (Chao & Lee, 1992). The sample coverage among patches was of 91.07 ± 7.47%, indicating that our sampling effort was adequate to estimate diversity (Chao & Jost, 2012).

We summed the seedlings of the 10 1-m$^2$ plots to obtain the abundance of light-demanding and shade-tolerant seedlings for each patch (seedlings · 10 m$^{-2}$). Additionally, we employed a Nonmetric Multidimensional Scaling (NMDS) to estimate species compositional similarity among patches (Laurance et al., 2007; Santo-Silva et al., 2015; Liu et al., 2019). We used the *metaMDS* function based on the Bray-Curtis dissimilarity index of the *vegan* package (Oksanen et al., 2019) and the whole seedling dataset. We used the NMDS scores of the first two axes as response variables.

We used the diversity decomposition of effective numbers of species or the Hill numbers (Jost, 2006, 2007). Hill numbers ($^qD$) are expressed in units of species, which permits to characterize the distribution of species abundances and provide complete information about the community diversity (Jost, 2006; Chao, Chiu & Hsieh, 2012). We calculated Hill numbers of all species (species richness or $^0D$), typical species (the exponential of Shannon's entropy index or $^1D$), and dominant species (the inverse of Simpson's index or $^2D$). The $^0D$ is not sensitive to individual abundances  (Jost, 2007; Tuomisto, 2010), permitting to include rare species in assessments, while $^1D$ and $^2D$ give a high weight to the equally abundant and the most abundant species, respectively (Jost, 2007, 2010; Chao, Chiu & Hsieh, 2012).

We followed Jost (2007) and Tuomisto (2010) procedure to calculate the gamma (γ), alpha (α) and beta (β) diversity (Fig S2c and Table S2). The α-diversity values are expressed in species · $m^{-2}$, whereas β-diversity is the effective number of completely distinct assemblages, ranging between one (when the assemblages of all 1-$m^2$ plots are identical) and 10 (when the assemblages of the 10 1-$m^2$ plots are completely different from each other; Table 1). We used the package *vegan* in R for the entire procedure (Oksanen et al., 2019).

### *Patch structure.*

We employed a multispectral SPOT-5 satellite image of 10 × 10 m pixel resolution recorded in March 2013 to carry out a supervised classification using the GRASS GIS software

(GRASS Development Team, 2017). We elaborated a forest/non-forest classification and used sampling points to assess classification accuracy. The overall classification accuracy was 79%. We exported the resulting raster file into a shapefile to calculate patch perimeter in meters (m) and patch area in $m^2$ using the *rgeos* package (Bivand & Rundel, 2019). We employed these data to measure patch size in hectares and patch shape as a limitless index that measures patch complexity compared to a square of the same size (Patton, 1975). For patch shape, we controlled for patch size effects by using the residuals of a linear model between patch shape and size ($R^2 = 0.63$; $F_{1,14} = 26.32$; $P = 0.0001$).

Within each patch, we sampled tree community by recording the diameter at breast height (dbh, 130 cm above the ground) of all trees with dbh ≥ 10 cm within ten 50 × 2 m transects (Gentry, 1982). When possible, we minimized the forest diversity and structural biases derived from edge effects by locating all transects at least 20 m from patch edges (Laurance et al., 2007). Within each transect, we counted, measured the diameter and the identified each tree to species level (Martínez, Ramos-A. & Chiang, 1994; Missouri Botanical Garden, 2019). Then, we calculated tree abundance (trees $\cdot$ 0.1 $ha^{-1}$), basal area ($m^2 \cdot ha^{-1}$), and richness, exponential of Shannon's entropy index and the inverse of Simpson's index (species $\cdot$ 0.1 $ha^{-1}$).

Additionally, we gathered information regarding disturbance factors within patches through a questionary applied to landowners and field observations throughout the study period. We used the questionary results to elaborate a binary database of the following disturbance factors of patches (Table S3): flooding during rainy season, fire events during the last 10 years, presence of cattle, slashing of understory vegetation and the predominant land use in the adjacent matrix. Then, we employed a logistic PCA (Landgraf & Lee, 2020) to construct disturbance indices from binary data. We previously estimated the number of dimensions ($k$) and the tunning parameter ($m$) through a cross-validation of the negative Log-likelihood, and obtained $k = 3$ and $m = 3$ to perform the analysis (Fig S2). We final model contained the 77.8%

of deviance explained. We used the *logisticPCA* package for the entire procedure (Landgraf & Lee, 2015). According to Spearman correlation between disturbance factors and PCA components, the slash of understory vegetation, the adjacent land use and the presence of cattle were strongly associated to the first component, whereas flooding and fire events were associated to the second component (Table S4). Accordingly, we used the first component as the management disturbance index ($D_M$) and the second component as the fire disturbance index ($D_F$).

### *Landscape structure*

We calculated five landscape metrics (Table S5) known to influence patch size, vegetation, and disturbance in the tropics, as well as seedling community. The composition metrics were the proportion of forest cover (FC) and secondary forest (SF), whereas the configuration metrics were patch density (PD), patch aggregation AI and edge contrast (EC). We calculated the EC by assigning quality values to each matrix cover. These values were indicators of matrix cover capacity to alleviate edge effects facilitate the movement of terrestrial mammals. The quality values were the following: 1 (water bodies, with the lowest suitability); 2 (anthropogenic cover); 3 (cattle pasture); 4 (arboreal crops); 5 (floodplains); 6 (secondary forest); and 7 (old-growth forest, representing the highest suitability). To obtain a more robust and realistic representation of landscape structure effects, we estimated the area-weighted mean of the EC index (Li & Archer, 1997).

We measured these landscape metrics within 13 circular buffers (300 to 1500 m radius, at 100 m intervals) from the center of each focal patch (Fig 2c). Radius were based in the dispersal distances of seed dispersers and terrestrial mammals, landscape size to assess seedling community and disturbances, and spatial scales at which landscape structure affects forest diversity and structure in the study region (Zermeño-Hernández, Pingarroni & Martínez-Ramos, 2016; San-José, Arroyo-Rodríguez & Meave, 2019; Wies, Nicasio Arzeta & Martinez Ramos, 2021; Nicasio-Arzeta et al., 2021). Independence among sampling sites, landscape metrics and buffer sizes can be found in Nicasio-Arzeta et al. (2021).

### *Statistical analysis*

We estimated the scale of effect of each landscape metric on patch structure using linear models. We fitted a patch size, shape, basal area, diversity and disturbance by fire and management with a single landscape metric for each buffer and obtained its coefficient of determination ($R^2$). Then, we plotted the resulting 13 $R^2$ values and selected the one with the strongest response as the scale of effect for that landscape metric. We repeated this procedure for each patch variable and landscape metric. Thereafter, we evaluated the effects of landscape metrics and fire disturbance on each patch structure variable through multiple linear models. We only used the landscape metrics at the scale of effect identified in the previous step (Table S6). All models were additive due to our limited sample size of 16 forest patches.

We employed the dredge function of the *MuMIn* package (Barton, 2018) to create all possible combinations of explanatory variables plus the null model (only the intercept) to assess the relative importance and effects of landscape metrics and fire disturbance using an information theory approach and multimodel inference (Burnham & Anderson, 2002). We used the accumulated sum of Akaike weights ($w_i$) of each model to select the subset of models that $\sum w_i \leq 0.95$. Then, we employed the $w_i$ of the model's subset to calculate the relative importance and the model-averaged parameter estimates of each explanatory variable. We considered as influential variable those for which the confidence interval did not include zero in the averaged parameters. We carried out all statistical analysis in the R 3.5.2 statistical computing environment (R Development Core Team, 2018). We selected the significant landscape metrics and disturbance factor for each patch structural variable for further analysis (Table S7).

We analyzed the direct and indirect effects of patch and landscape structure on seedling abundance, composition and diversity through structural equation models (SEM). SEM is a statistical method that test for causal relationships (Fan et al., 2016; Tarka, 2018). We proposed a conceptual model of multiple casualties to explain seedling abundance, diversity and composition in relation to the patch components (size, shape, basal area, tree diversity, and disturbance by fire and management), which served as the exogenous predictors (Fig S1). Indirect paths included the abundance of light-demanding and shade-tolerant seedlings, representing the hypothesis regarding cascading effects mediated by abundance fluctuations. We previously assessed the association among explanatory variables to avoid variance inflation. We found that patch structural variables were strongly correlated (Table S8), and only tree basal area and tree diversity were employed for further analysis.

We fitted the SEM using the *piecewiseSEM* package (Lefcheck, 2016). Multivariate normality of seedling ($\gamma_{1,p} = 217.39$; $P = 0.54$ and $\gamma_{2,p} = -1.95$; $P = 0.052$) and patch data ($\gamma_{1,p} = 67.41$; $P = 0.14$ and $\gamma_{2,p} = -1.03$; $P = 0.30$) was validated. We applied a logarithmic transformation to patch size and abundance of light-demanding seedlings, and a square root transformation to abundance of shade-tolerant seedlings to meet normality assumptions. We performed simple model structures (few variables) due to sample size limitations. Hence, we tested different combinations of patch structure ($D_M$, $T_{BA}$, $T_D$, $P_{SZ}$ and $P_{SI}$) in alternative models instead of all together. We employed the fire disturbance index and the selected landscape metrics ($D_F$, $FC_{1200}$, $PD_{600}$, $PD_{900}$, $AI_{600}$) to explain variation of exogenous variables. Alternative models consisted in combinations of one and two exogenous predictors. This produced 15 alternative models for each diversity order (all species: ${}^0\alpha$, ${}^0\beta$; typical species: ${}^1\alpha$, ${}^1\beta$; dominant species: ${}^2\alpha$, ${}^2\beta$) and composition index (MDS1, MDS2). Model selection procedure consisted in rejecting all models with lack-of-fit ($P < 0.05$), then, we excluded the models that had no significant links to seedling abundance, composition or diversity variables we attempted to explain. Finally, we selected the best-fitting models based on the lowest AICc values.

## Results

We recorded 1378 seedlings belonging to 27 families, 38 genera and 67 species. We only considered animal-dispersed species for further analysis because they comprise up to 90% of the seed rain in rainforests (Jordano, 2000; San-José et al., 2019). The 94.7% of seedlings (1305) were animal-dispersed, represented in 24 families, 30 genera and 56 species. From this subset, we found 668 seedlings (52.72%) from 27 shade-tolerant tree species, followed by 527 seedlings (40.38%) from 18 light-demanding species and 90 seedlings (6.9%) from 11 intermediate or indetermined species (Table S1).

Our candidate models were good-fitted, indicating that the conceptual model adequately described the data (Fig 1). The best-fitted models (those with the lowest AICc; Table S9) included patch size and aggregation for diversity of all species (Fig 3b), whereas tree basal area explained seedling composition (Fig 3a) and diversity of typical and dominant species, and (Fig 3c and d). For the latter models, tree basal area decreased in patches affected by previous fire events ($B = -0.63$), and light-demanding seedling abundance was reduced by tree basal area ($B = -0.54$). The latter indicated that fire disturbance had indirect effects in the increase of light-demanding seedlings ($B = -0.63 \times 0.54 = 0.34$).

Seedling composition model explained 39% of basal area, 30% of light-demanding seedling abundance, 12% of shade-tolerant seedling abundance, and 64% and 56% of the first and second NMDS axis, respectively (Fig 3a). The first axis was negatively influenced by light-demanding seedlings (B = -0.55), whereas the second NMDS axis was negatively affected by the abundance of shade-tolerant-seedlings (B = -0.76). The indirect effect of fire disturbance on the first composition axis was lower (i.e., -0.63 × -0.55 × 0.54 = -0.18) than the indirect effect of basal area (i.e., -0.55 × 0.54 = 0.29). Seedling composition differed between fire-disturbed and non-disturbed patches ($F_{1,14}$ = 2.64; $R^2$ = 0.16; $P$ = 0.01), where the abundance of light-demanding seedlings was higher in fire-disturbed patches than in their non-disturbed counterparts (Fig 4).

The typical species model (Fig 3c) explained 40% of α-diversity, and was positively influenced only by the abundance of shade-tolerant seedlings (B = 0.54), whereas the 68% explained of β-diversity variation was strongly attributed to the negative effect of light-demanding seedlings (B = -1), and indirectly promoted by tree basal area (i.e., -1 × 0.54 = 0.54). This also held true for the dominant species model (Fig 3d), which explained 69% of β-diversity through the negative effects of light-demanding (B = -0.94) and shade-tolerant (B = -0.43) seedling abundances. Tree basal area also had a positive indirect effect on β-diversity of dominant species (i.e., -0.94 × 0.54 = 0.50). Finally, fire disturbance had overall indirect effects on the decline of β-diversity of typical (B = -1 × -0.54 × -0.63 = 0.34) and dominant species (B = -0.94 × -0.54 × -0.63 = 0.32).

Finally, the model for all species explained 40% of patch size, 10% of light-demanding seedlings, 51% of shade-tolerant seedlings, 50% of α-diversity and 17% of β-diversity (Fig 3b). Patch aggregation had direct effects on patch size (B = 0.64) and shade-tolerant seedlings (B = 0.63), which was also affected by light-demanding seedlings (B = -0.58). In turn, shade tolerant seedlings had positive effects on α-diversity (B = 0.56), which was indirectly reduced by the abundance of light-demanding seedlings (B = -0.58 × 0.56 = -0.32). Patch aggregation had cascading effects on the increase of seedling a-diversity (B = -0.63 × 0.54 = 0.34).

## Discussion

Our findings confirm that landscape configuration and disturbance factors within patches, such as fire incidence, defined species composition and α- and β-diversity of typical and dominant species of seedling community. As expected, patches with low disturbance regimes and higher basal area reduced the abundance of light-demanding seedlings, which in turn led to a more diversified and complex regenerative community. Also, landscapes with more aggregated patches increased the abundance of shade-tolerant seedlings with cascading effect that favored α- diversity of species in the regenerative community. Thus, cascading effects of patch disturbance and landscape configuration shaped species composition and α- and β-diversity, respectively.

Disturbance by fire was the main local factor having major cascading effects that modulated the abundance, composition and diversity of the regenerative community.  Fire is an atypical natural disturbance in tropical rainforests where most of their tree species are considered fire-sensitive (Rodriguez Trejo 2008). Nevertheless, land-use changes to pastures and farmlands, forest fragmentation and extreme weather events are increasing fire frequency, severity, and extent (Cochrane & Laurance, 2008). In this study, fire occurrence, which was present in almost 50% of forest patches, significantly reduced the basal area of adult trees leading to an increased abundance of light-demanding species in the understory. This is consistent with other studies where surface fires reduced basal by the loss of medium- and large-sized trees and lianas (Nepstad et al., 1999; Barlow et al., 2003; Cochrane & Laurance, 2008). The consequent canopy openness -which can be four times greater than in unburned forests-, lead to an increased light incidence in the forest floor (Barlow et al., 2003). These microclimate alterations favor the dominance of disturbance-loving tree species in the understory vegetation (Cochrane & Laurance, 2002), as was found here. In turn, the abundance of light-demanding seedlings had direct effects on seedling composition and the turnover of equally common and abundant species. In this sense, patches that had fires during the last 10 years, had a different seedling community from that found in patches without fires, which was dominated mainly by light-demanding species such as *Inga punctata*. Some tropical rain forest tree species are reported to respond well to fire, for example *Swietenia macrophylla* which is promoted by fire species reported for tropical rain forests of southern Mexico. However, the vast majority of tree species in tropical forests are fire-sensitive. Then, the presence of species like *Brosimum alicastrum* and *Ampelocera hottlei*, found exclusively in unburned patches dominated by shade tolerant, could be threatened by the occurrence of fires.

In our study, basal area only affected the abundance of light-demanding seedlings, suggesting that disturbed fragments (lower abundance of large trees) promote the establishment and survival of these species by increasing light availability (Denslow, 1987, 1996). These conditions promote the establishment of a subset of species that are ecologically redundant, that lack phylogenetic relationship and that give rise to impoverished species assemblages dominated by few species with high abundances (Oliveira, Santos & Tabarelli, 2008; Tabarelli, Peres & Melo, 2012). These assemblages indicate a process of biotic homogenization, characterized by low community composition (i.e., less dissimilarity between communities), as well as a reduction in β-diversity (i.e., less species turnover) at local and landscape scales (Olden & Rooney, 2006; Tabarelli, Peres & Melo, 2012; Solar et al., 2015). Basal area influences the abundance and composition of seedlings through fruit production (Chapman et al., 1992), the availability of light, water and nutrients in the soil (Denslow, 1987; Martinez-Ramos & Soto-Castro, 1993; Turner, 2004) and conspecific seedling mortality (Wright, 2002).

This is consistent with our observations, where a greater abundance of light-demanding seedlings reduced both the composition of seedlings and the β-diversity of typical and dominant species, variables that are sensitive to abundance fluctuations (Jost, 2007; Roden et al., 2018). In addition, the absence of direct effects by the landscape structure supports the hypotheses that establish that generalist species and populations with a high density of individuals are mainly affected by factors at small scales (Miguet et al., 2016). This supports the cascading effects of landscape structure on the abundance of a light-competing palm, which represented the local factor that had the greatest impact on biological responses affected at small scales, such as the density of species and individuals (Hernández-Ruedas et al., 2018).

On the contrary, the abundance of shade-tolerant seedlings was mainly explained by the aggregation of fragments in the landscape, which supports the hypotheses of Miguet et al. (2016) mentioned above. Shade-tolerant seedlings have higher habitat specialization than light-demanding species, as well as lower population densities (Denslow, 1996; Turner, 2004). In addition, their abundances are regulated by the conspecific mortality of seedlings and the foraging of fruits, seeds, and seedlings by terrestrial mammals (Dirzo & Miranda, 1990; Comita et al., 2007, 2010; Camargo-Sanabria et al., 2014). This suggests that landscape structure affects the abundance of shade-tolerant seedlings by facilitating or limiting the arrival of seed dispersers and seed/seedling predators.

This assumption is supported by studies that found a significant contribution of the percentage of primary forest in the landscape on the richness and abundance of seed rain and saplings of specialist tree species of biotic dispersal (San-José, Arroyo-Rodríguez & Meave, 2019; Arasa-Gisbert et al., 2021). These studies concluded that the loss of shade-tolerant species is the result of a lack of seed dispersal in landscapes where low forest cover limits the movement of fauna, which disperses 90% of tropical forest tree species (Jordano, 2000). However, the size of the home range of fauna can vary depending on the aggregation of fragments in landscapes with a low percentage of habitat (Radford, Bennett & Cheers, 2005; Hodgson et al., 2012; Gardiner et al., 2019).

In this work, we found that the abundance of shade-tolerant seedlings increased in landscapes with high fragment aggregation, suggesting that this configurational pattern promotes the arrival of seed dispersers and predators of seeds and seedlings. The functions of dispersal and predation, together with the conspecific mortality of seedlings that promote their diversity (Harms et al., 2000; Wright, 2002; Comita et al., 2010), explain the positive effect that the abundance of seedlings tolerant to the shadow has on the α diversity of all seedling species. Interestingly, the abundance of shade-tolerant seedlings was affected by the abundance of light-demanding seedlings, suggesting that the latter exert competitive pressure for resources. Competitive exclusion may play an important role in reducing α diversity within forests with high light availability and low herbivore pressure (Wright, 2002). This supports the indirect effect that the abundance of light-demanding seedlings had on species richness.

## Acknowledgments

We thank to the people of Quiringüicharo for their hospitality and support. We acknowledge the logistical and technical support provided by J. Manuel Lobato-García during the fieldwork. We thank Gilberto Jamangapé and Rafael Lombera for plant identification. Estación Chajul provided logistical assistance and accommodation.

## References

Andren H. 1994. Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. *Oikos*:355–366. DOI: 10.2307/3545823.

Arasa-Gisbert R, Arroyo-Rodríguez V, Galán-Acedo C, Meave JA, Martínez-Ramos M. 2021. Tree recruitment failure in old-growth forest patches across human-modified rainforests. *Journal of Ecology*:1–13. DOI: 10.1111/1365-2745.13643.

Arasa-Gisbert R, Arroyo-Rodríguez V, Meave JA, Martínez-Ramos M, Lohbeck M. 2022. Forest loss and treeless matrices cause the functional impoverishment of sapling communities in old-growth forest patches across tropical regions. *Journal of Applied Ecology* 069. DOI: 10.1111/1365-2664.14197.

Avila-Flores D, Pompa-Garcia M, Antonio-Nemiga X, Rodriguez-Trejo DA, Vargas-Perez E, Santillan-Perez J. 2010. Driving factors for forest fire occurrence in Durango State of Mexico: A geospatial perspective. *Chinese Geographical Science* 20:491–497. DOI: 10.1007/s11769-010-0437-x.

Barlow J, Haugaasen T, Peres CA. 2002. Effects of ground fires on understorey bird assemblages in Amazonian forests. *Biological Conservation* 105:157–169. DOI: 10.1016/S0006-3207(01)00177-X.

Barlow J, Peres CA, Lagan BO, Haugaasen T. 2003. Large tree mortality and the decline of forest biomass following Amazonian wildfires. *Ecology Letters* 6:6–8. DOI: 10.1046/j.1461-0248.2003.00394.x.

Barton K. 2018. MuMIn: Multi-Model Inference. *R package version 1.42.1*.

Benitez-Malvido J. 1998. Impact of forest fragmentation on seedling abundance in a tropical rain forest. *Conservation Biology* 12:380–389. DOI: 10.1046/j.1523-1739.1998.96295.x.

Benítez-Malvido J, Lázaro A, Ferraz IDK. 2018. Effect of distance to edge and edge interaction on seedling regeneration and biotic damage in tropical rainforest fragments: A long-term experiment. *Journal of Ecology* 106:2204–2217. DOI: 10.1111/1365-2745.13003.

Berget C, Verschoor G, García-Frapolli E, Mondragón-Vázquez E, Bongers F. 2021. Landscapes on the move: Land-use change history in a mexican agroforest frontier. *Land* 10. DOI: 10.3390/land10101066.

Bivand R, Rundel C. 2019. rgeos: Interface to Geometry Engine - Open Source ('GEOS’).

Brancalion PHS, Niamir A, Broadbent E, Crouzeilles R, Barros FSM, Almeyda Zambrano AM, Baccini A, Aronson J, Goetz S, Leighton Reid J, Strassburg BBN, Wilson S, Chazdon RL. 2019. Global restoration opportunities in tropical rainforest landscapes. *Science Advances* 5:3223–3226. DOI: 10.1126/sciadv.aav3223.

Brindis-Badillo DA, Arroyo-Rodríguez V, Mendoza E, Wies G, Martínez-Ramos M. 2022. Conserving dominant trees in human-modified landscapes at the Lacandon tropical rainforest. *Biological Conservation* 270:109548. DOI: 10.1016/J.BIOCON.2022.109548.

Brokaw N, Busing RT. 2000. Niche versus chance and tree diversity in forest gaps. *Trends in Ecology and Evolution* 15:183–188. DOI: 10.1016/S0169-5347(00)01822-X.

Brokaw N, Scheiner SM. 1989. Species composition in gaps and structure of a tropical forest. *Ecology* 70:538–541. DOI: 10.2307/1940196.

Burnham KP, Anderson DR. 2002. *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach (2nd ed)*. Springer-Verlag. DOI: 10.1016/j.ecolmodel.2003.11.004.

Camargo-Sanabria AA, Mendoza E, Guevara R, Martínez-Rmos M, Dirzo R. 2014. Experimental defaunation of terrestrial mammalian herbivores alters tropical rainforest understorey diversity. *Proceedings of the Royal Society B: Biological Sciences* 282. DOI: 10.1098/rspb.2014.2580.

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

Chao A, Chiu CH, Hsieh TC. 2012. Proposing a resolution to debates on diversity partitioning. *Ecology* 93:2037–2051. DOI: 10.1890/11-1817.1.

Chao A, Jost L. 2012. Coverage-based rarefaction and extrapolation: Standardizing samples by completeness rather than size. *Ecology* 93:2533–2547. DOI: 10.1890/11-1952.1.

Chao A, Lee SM. 1992. Estimating the number of classes via sample coverage. *Journal of the American Statistical Association* 87:210–217. DOI: 10.1080/01621459.1992.10475194.

Chao A, Ma KH, Hsieh TC, Chiu C-H. 2016. *User's Guide for Online Program SpadeR (Species-richness Prediction And Diversity Estimation in R)*. Taiwan.

Chapman CA, Chapman LJ, Wangham R, Hunt K, Gebo D, Gardner L. 1992. Estimators of Fruit Abundance of Tropical Trees. *Biotropica* 24:527–531. DOI: 10.2307/2389015.

Cochrane MA, Laurance WF. 2002. Fire as a large-scale edge effect in Amazonian forests. *Journal of Tropical Ecology* 18:311–325. DOI: 10.1017/S0266467402002237.

Cochrane MA, Laurance WF. 2008. Synergisms among fire, land use, and climate change in the Amazon. *Ambio* 37:522–527. DOI: 10.1579/0044-7447-37.7.522.

Comita LS, Aguilar S, Pérez R, Lao S, Hubbell SP. 2007. Patterns of woody plant species abundance and diversity in the seedling layer of a tropical forest. *Journal of Vegetation Science* 18:163. DOI: 10.1658/1100-9233(2007)18[163:powpsa]2.0.co;2.

Comita LS, Muller-Landau HC, Aguilar S, Hubbell SP. 2010. Asymmetrie density dependence shapes species abundances in a tropical tree community. *Science* 329:330–332. DOI: 10.1126/science.1190772.

Crouzeilles R, Curran M, Ferreira MS, Lindenmayer DB, Grelle CEV, Rey Benayas JM. 2016. A global meta-Analysis on the ecological drivers of forest restoration success. *Nature Communications* 7:1–8. DOI: 10.1038/ncomms11666.

Cudney-Valenzuela SJ, Arroyo-Rodríguez V, Andresen E, Toledo-Aceves T, Mora-Ardila F, Andrade-Ponce G, Mandujano S. 2021. Does patch quality drive arboreal mammal assemblages in fragmented rainforests? *Perspectives in Ecology and Conservation* 19:61–68. DOI: 10.1016/j.pecon.2020.12.004.

Dalling JW, Hubbell SP, Silvera K. 1998. Seed dispersal, seedling establishment and gap partitioning among tropical pioneer trees. *Journal of Ecology* 86:674–689. DOI:

10.1046/j.1365-2745.1998.00298.x.

Denslow JS. 1987. Tropical Rainforest Gaps and Tree Species Diversity. *Annual Review of Ecology and Systematics* 18:431–451. DOI: 10.1146/annurev.es.18.110187.002243.

Denslow JS. 1996. Functional Group Diversity and Responses to Disturbance. In: *Biodiversity and Ecosystem Processes in Tropical Forests*. Springer, Berlin, Heidelberg, 127–151. DOI: 10.1007/978-3-642-79755-2_7.

Denslow JS, Guzman G. S. 2000. Variation in stand structure, light and seedling abundance across a tropical moist forest chronosequence, Panama. *Journal of Vegetation Science* 11:201–212. DOI: 10.2307/3236800.

Desbiez AL, Bodmer RE, Aparecida S. 2009. Wildlife habitat selection and sustainable resources management in a Neotropical wetland. *International Journal of Biodiversity and Conservation* 1:11–20.

Dirzo R, Miranda A. 1990. Contemporary Neotropical Defaunation and Forest Structure, Function, and Diversity-A Sequel to John Terborgh*. *Conservation Biology* 4:444–447. DOI: 10.1111/j.1523-1739.1990.tb00320.x.

Fahrig L. 2013. Rethinking patch size and isolation effects: The habitat amount hypothesis. *Journal of Biogeography* 40:1649–1663. DOI: 10.1111/jbi.12130.

Fan Y, Chen J, Shirkey G, John R, Wu SR, Park H, Shao C. 2016. Applications of structural equation modeling (SEM) in ecological studies: an updated review. *Ecological Processes* 5:19. DOI: 10.1186/s13717-016-0063-3.

Farfán Gutiérrez M, Pérez-Salicrup DR, Flamenco-Sandoval A, Nicasio-Arzeta S, Mas J-F, Ramírez Ramírez I. 2018. Modeling anthropic factors as drivers of wildfire occurrence at the Monarch Butterfly Biosphere. *Madera y Bosques* 24. DOI: 10.21829/myb.2018.2431591.

Fontúrbel FE, Candia AB, Malebrán J, Salazar DA, González-Browne C, Medel R. 2015. Meta-analysis of anthropogenic habitat disturbance effects on animal-mediated seed dispersal. *Global Change Biology* 21:3951–3960. DOI: 10.1111/gcb.13025.

Gardiner R, Proft K, Comte S, Jones M, Johnson CN. 2019. Home range size scales to habitat amount and increasing fragmentation in a mobile woodland specialist. *Ecology and Evolution* 9:14005–14014. DOI: 10.1002/ece3.5837.

Gentry AH. 1982. Patterns of Neotropical Plant Species Diversity. In: Hecht MK, Wallace B, Prance GT eds. *Evolutionary Biology*. Springer US, 1–84.

GRASS Development Team. 2017.Geographic Resources Analysis Support System (GRASS GIS) Software, Version 7.2. *Available at http://grass.osgeo.org*

Guariguata MR, Ostertag R. 2001. Neotropical secondary forest succession: changes in structural and functional characteristics. *Forest Ecology and Management* 148:185–206. DOI: 10.1016/S0378-1127(00)00535-1.

Haddad NM, Brudvig LA, Clobert J, Davies KF, Gonzalez A, Holt RD, Lovejoy TE, Sexton JO, Austin MP, Collins CD, Cook WM, Damschen EI, Ewers RM, Foster BL, Jenkins CN, King AJ, Laurance WF, Levey DJ, Margules CR, Melbourne BA, Nicholls AO, Orrock JL, Song DX, Townshend JR. 2015. Habitat fragmentation and its lasting impact on Earth’s ecosystems. *Science Advances* 1. DOI: 10.1126/sciadv.1500052.

Hardwick SR, Toumi R, Pfeifer M, Turner EC, Nilus R, Ewers RM. 2015. The relationship between leaf area index and microclimate in tropical forest and oil palm plantation: Forest disturbance drives changes in microclimate. *Agricultural and Forest Meteorology* 201:187–195. DOI: 10.1016/j.agrformet.2014.11.010.

Harms KEE, Wright SJJ, Calderón O, Hernández A, Herre EA a. 2000. Pervasive density-dependent recruitment enhances seedling diversity in a tropical forest. *Nature* 404:493–5. DOI: 10.1038/35006630.

Hernández-Ruedas MA, Arroyo-Rodríguez V, Meave JA, Martínez-Ramos M, Ibarra-Manríquez G, Martínez E, Jamangapé G, Melo FPL, Santos BA. 2014. Conserving tropical tree diversity and forest structure: The value of small rainforest patches in moderately-managed landscapes. *PLoS ONE* 9:e98931. DOI: 10.1371/journal.pone.0098931.

Hernández-Ruedas MA, Arroyo-Rodríguez V, Morante-Filho JC, Meave JA, Martínez-Ramos M. 2018. Fragmentation and matrix contrast favor understory plants through negative cascading effects on a strong competitor palm. *Ecological Applications* 28:1546–1553. DOI: 10.1002/eap.1740.

Hernando A, Velázquez J, Valbuena R, Legrand M, García-Abril A. 2017. Influence of the resolution of forest cover maps in evaluating fragmentation and connectivity to assess habitat conservation status. *Ecological Indicators* 79:295–302. DOI: 10.1016/j.ecolind.2017.04.031.

Hodgson JA, Thomas CD, Dytham C, Travis JMJ, Cornell SJ. 2012. The Speed of Range Shifts in Fragmented Landscapes. *PLOS ONE* 7:e47141. DOI: 10.1371/journal.pone.0047141.

Ibarra-Manríquez G, Cornejo-Tenorio G. 2010. Diversidad de frutos de los árboles del bosque tropical perennifolio De México. *Acta botánica mexicana* 104:51–104.

Ibarra-Manríquez G, Martínez Ramos M, Oyama K. 2001. Seedling functional types in a lowland rain forest in Mexico. *American Journal of Botany* 88:1801–1812. DOI: 10.2307/3558356.

Jesus FM, Pivello VR, Meirelles ST, Franco GADC, Metzger JP. 2012. The importance of landscape structure for seed dispersal in rain forest fragments. *Journal of Vegetation Science* 23:1126–1136. DOI: 10.1111/j.1654-1103.2012.01418.x.

Jordano P. 2000. Fruits and frugivory. In: Fenner M ed. *Seeds: the ecology of regeneration in plant communities*. Wallingford, U.K.: CABI Publishing, 125–166.

Jost L. 2006. Entropy and diversity. *Oikos* 113:363–375. DOI: 10.1111/j.2006.0030-1299.14714.x.

Jost L. 2007. Partitioning diversity into independent alpha and beta components. *Ecology* 88:2427–2439. DOI: 10.1890/06-1736.1.

Jost L. 2010. The relation between evenness and diversity. *Diversity* 2:207–232. DOI: 10.3390/d2020207.

Kitajima K, Cordero RA, Wright SJ. 2013. Leaf life span spectrum of tropical woody seedlings: Effects of light and ontogeny and consequences for survival. *Annals of Botany* 112:685–699. DOI: 10.1093/aob/mct036.

Kolb M, Galicia L. 2018. Scenarios and story lines: drivers of land use change in southern Mexico. *Environment, Development and Sustainability* 20:681–702. DOI: 10.1007/s10668-016-9905-5.

Krishnadas M, Agarwal K, Comita LS. 2020. Edge effects alter the role of fungi and insects in mediating functional composition and diversity of seedling recruits in a fragmented tropical forest. *Annals of Botany* 126:1181–1191. DOI: 10.1093/aob/mcaa138.

Krishnadas M, Kumar AN, Comita LS. 2019. Edge effects reduce α-diversity but not β-diversity during community assembly in a human-modified tropical forest. *Ecological Applications* 29:1–10. DOI: 10.1002/eap.1996.

Landgraf AJ, Lee Y. 2015. *Dimensionality Reduction for Binary Data through the Projection of Natural Parameters*.

Landgraf AJ, Lee Y. 2020. Dimensionality reduction for binary data through the projection of natural parameters. *Journal of Multivariate Analysis* 180. DOI: 10.1016/j.jmva.2020.104668.

Laurance WF, Camargo JLC, Luizão RCC, Laurance SG, Pimm SL, Bruna EM, Stouffer PC, Bruce Williamson G, Benítez-Malvido J, Vasconcelos HL, Van Houtan KS, Zartman CE, Boyle SA, Didham RK, Andrade A, Lovejoy TE. 2011. The fate of Amazonian forest fragments: A 32-year investigation. *Biological Conservation* 144:56–67. DOI: 10.1016/j.biocon.2010.09.021.

Laurance WF, Delamonica P, Laurance SG, Vasconcelos HL, Lovejoy TE. 2000. Rainforest fragmentation kills big trees. *Nature* 404:836. DOI: 10.1038/35009032.

Laurance WF, Nascimento HEMM, Laurance SG, Andrade A, Ewers RM, Harms KE, Luizão RCCC, Ribeiro JE. 2007. Habitat fragmentation, variable edge effects, and the landscape-divergence hypothesis. *PLoS ONE* 2:e1017. DOI: 10.1371/journal.pone.0001017.

Lefcheck JS. 2016. piecewiseSEM: Piecewise structural equation modelling in r for ecology, evolution, and systematics. *Methods in Ecology and Evolution* 7:573–579. DOI: 10.1111/2041-210X.12512.

Li BL, Archer S. 1997. Weighted mean patch size: A robust index for quantifying landscape structure. *Ecological Modelling* 102:353–361. DOI: 10.1016/S0304-3800(97)00071-9.

Liu J, Coomes DA, Hu G, Liu J, Yu J, Luo Y, Yu M. 2019. Larger fragments have more late-successional species of woody plants than smaller fragments after 50 years of secondary succession. *Journal of Ecology* 107:582–594. DOI: 10.1111/1365-2745.13071.

Lohbeck M, DeVries B, Bongers F, Martínez-Ramos M, Navarrete-Segueda A, Nicasio-Arzeta S, Siebe C, Pingarroni A, Wies G, Decuyper M. 2022. Mexican agricultural frontier communities differ in forest dynamics with consequences for conservation and restoration. *Remote Sensing in Ecology and Conservation* 37:10–14. DOI: 10.1002/RSE2.262.

Lohbeck M, Poorter L, Martínez-Ramos M, Bongers F, Martinez-Ramos M, Bongers F, Craft NJB. 2015. Biomass is the main driver of changes in ecosystem process rates during tropical forest succession. *Ecology* 96:1242–1252. DOI: 10.1890/14-0472.1.

Martin AE. 2018. The spatial scale of a species' response to the landscape context depends on which biological response you measure. *Current Landscape Ecology Reports* 3:23–33. DOI: 10.1007/s40823-018-0030-z.

Martinez-Ramos M, Soto-Castro A. 1993. Seed rain and advanced regeneration in a tropical rain forest. *Vegetatio* 107:299–318. DOI: 10.1007/BF00052231.

Martínez E, Ramos-A. CH, Chiang F. 1994. Lista florística de la Lacandona, Chiapas. *Botanical Sciences* 0:99–177. DOI: 10.17129/botsci.1430.

Miguet P, Jackson HB, Jackson ND, Martin AE, Fahrig L. 2016. What determines the spatial extent of landscape effects on species? *Landscape Ecology* 31:1177–1194. DOI: 10.1007/s10980-015-0314-1.

Minor DM, Kobe RK. 2019. Fruit production is influenced by tree size and size-asymmetric crowding in a wet tropical forest. *Ecology and Evolution* 9:1458–1472. DOI: 10.1002/ece3.4867.

Missouri Botanical Garden. 2019.Tropicos.org. *Available at https://www.tropicos.org/* (accessed June 4, 2019).

Nascimento HEM, Andrade ACS, Camargo JLC, Laurance WF, Laurance SG, Ribeiro JEL. 2006. Effects of the Surrounding Matrix on Tree Recruitment in Amazonian Forest Fragments. *Conservation Biology* 20:853–860. DOI: 10.1111/j.1523-1739.2006.00344.x.

Nathan R, Muller-Landau HC. 2000. Spatial patterns of seed dispersal, their determinants and consequences for recruitment. *Trends in Ecology and Evolution* 15:278–285. DOI: 10.1016/S0169-5347(00)01874-7.

Navarrete-Segueda A, Martínez-Ramos M, Ibarra-Manríquez G, Vázquez-Selem L, Siebe C. 2018. Variation of main terrestrial carbon stocks at the landscape-scale are shaped by soil in a tropical rainforest. *Geoderma* 313:57–68. DOI: 10.1016/j.geoderma.2017.10.023.

Nepstad DC, Veríssimo A, Alencar A, Nobre C, Lima E, Lefebvre P, Schlesinger P, Potter C, Moutinho P, Mendoza E, Cochrane M, Brooks V. 1999. Large-scale impoverishment of amazonian forests by logging and fire. *Nature* 398:505–508. DOI: 10.1038/19066.

Nicasio-Arzeta S, Zermeño-Hernández IE, Maza-Villalobos S, Benítez-Malvido J. 2021. Landscape structure shapes the diversity of tree seedlings at multiple spatial scales in a fragmented tropical rainforest. *PLoS ONE* 16:e0253284. DOI: 10.1371/journal.pone.0253284.

Nicotra AB, Chazdon RL, Iriarte SVB. 1999. Spatial heterogeneity of light and woody seedling regeneration in tropical wet forests. *Ecology* 80:1908–1926. DOI: 10.1890/0012-9658(1999)080[1908:SHOLAW]2.0.CO;2.

Oksanen J, Blanchet FG, Friendly M, Kindt R, Legendre P, McGlinn D, Minchin PR, O'Hara RB, Simpson GL, Solymos P, Stevens MHH, Szoecs E, Wagner H. 2019.vegan: Community Ecology Package. *Available at https://cran.r-project.org/web/packages/vegan/index.html*

Olden JD, Rooney TP. 2006. On defining and quantifying biotic homogenization. *Global Ecology and Biogeography* 15:113–120. DOI: 10.1111/j.1466-822X.2006.00214.x.

Oliveira MA, Santos AMM, Tabarelli M. 2008. Profound impoverishment of the large-tree stand in a hyper-fragmented landscape of the Atlantic forest. *Forest Ecology and Management* 256:1910–1917. DOI: 10.1016/j.foreco.2008.07.014.

Patton DR. 1975. A diversity index for quantifying habitat “edge.” *Wildlife Society Bulletin*:171–173.

R Development Core Team. 2018.R: A Language and Environment for Statistical Computing. *Available at https://www.r-project.org/*

Radford JQ, Bennett AF, Cheers GJ. 2005. Landscape-level thresholds of habitat cover for woodland-dependent birds. *Biological Conservation* 124:317–337. DOI: 10.1016/j.biocon.2005.01.039.

Roden VJ, Kocsis ÁT, Zuschin M, Kiessling W. 2018. Reliable estimates of beta diversity with incomplete sampling. *Ecology* 99:1051–1062. DOI: 10.1002/ecy.2201.

Román-Cuesta RM, Martínez-Vilalta J. 2006. Effectiveness of protected areas in mitigating fire within their boundaries: Case study of Chiapas, Mexico. *Conservation Biology* 20:1074–1086. DOI: 10.1111/j.1523-1739.2006.00478.x.

Rose S. 2000. Seeds, seedlings, and gaps - size matters. a study in the tropical rain forest of Guyana. In: Programme T-G, Rose S eds. *Trobenpos-Guyana Series 9*. Georgetown, Guyana: Trobenpos-Guyana Programme, 1–184.

San-José M, Arroyo-Rodríguez V, Jordano P, Meave JA, Martínez-Ramos M. 2019. The scale of landscape effect on seed dispersal depends on both response variables and landscape predictor. *Landscape Ecology*:1–12. DOI: 10.1007/s10980-019-00821-y.

San-José M, Arroyo-Rodríguez V, Meave JA. 2019. Regional context and dispersal mode drive the impact of landscape structure on seed dispersal. *Ecological Applications* 0:eap.2033. DOI: 10.1002/eap.2033.

Santo-Silva EE, Almeida WR, Melo FPL, Zickel CS, Tabarelli M. 2013. The nature of seedling assemblages in a fragmented tropical landscape: Implications for forest regeneration. *Biotropica* 45:386–394. DOI: 10.1111/btp.12013.

Santo-Silva EE, Withey KD, Almeida WR, Mendes G, Lopes A V, Tabarelli M. 2015. Seedling assemblages and the alternative successional pathways experienced by Atlantic forest fragments. *Plant Ecology and Diversity* 8:483–492. DOI: 10.1080/17550874.2015.1048486.

Solar RR, Barlow J, Ferreira J, Berenguer E, Lees AC, Thomson JR, Louzada J, Maués M, Moura NG, Oliveira VHF, Chaul JCM, Schoereder JH, Vieira ICG, Mac Nally R, Gardner TA. 2015. How pervasive is biotic homogenization in human-modified tropical forest landscapes? *Ecology Letters* 18:1108–1118. DOI: 10.1111/ele.12494.

Sousa M. 2009. Adiciones al género Inga para la flora Mesoamericana. *Acta botánica mexicana* 89:25–41.

de Souza JC, da Silva RM, Gonçalves MPR, Jardim RJD, Markwith SH. 2018. Habitat use, ranching, and human-wildlife conflict within a fragmented landscape in the Pantanal, Brazil. *Biological Conservation* 217:349–357. DOI: 10.1016/j.biocon.2017.11.019.

Suárez-Castro AF, Simmonds JS, Mitchell MGE, Maron M, Rhodes JR. 2018. The Scale-Dependent Role of Biological Traits in Landscape Ecology: A Review. *Current Landscape Ecology Reports* 3:12–22. DOI: 10.1007/s40823-018-0031-y.

Tabarelli M, Peres CA, Melo FPL. 2012. The “few winners and many losers” paradigm revisited: Emerging prospects for tropical forest biodiversity. *Biological Conservation* 155:136–140. DOI: 10.1016/j.biocon.2012.06.020.

Tarka P. 2018. An overview of structural equation modeling: its beginnings, historical development, usefulness and controversies in the social sciences. *Quality and Quantity* 52:313–354. DOI: 10.1007/s11135-017-0469-8.

Taubert F, Fischer R, Groeneveld J, Lehmann S, Müller MS, Rödig E, Wiegand T, Huth A. 2018. Global patterns of tropical forest fragmentation. *Nature* 554:519–522. DOI: 10.1038/nature25508.

Terborgh J, Pitman N, Silman MR, Schichter H, Núñez P V. 2001. Maintenance of Tree Diversity in Tropical Forests. In: Levey DJ, Wesley Rodrigues S, Galetti M eds. *Seed Dispersal and Frugivory: Ecology, Evolution and Conservation*. London: CABI Publishing, 1–17.

Trolle M. 2003. Mammal survey in the southeastern Pantanal, Brazil. *Biodiversity and Conservation* 12:823–836. DOI: 10.1023/A:1022489426920.

Tuomisto H. 2010. A diversity of beta diversities: Straightening up a concept gone awry. Part 1. Defining beta diversity as a function of alpha and gamma diversity. *Ecography* 33:2–22. DOI: 10.1111/j.1600-0587.2009.05880.x.

Turner IM. 2004. *The Ecology of Trees in the Tropical Rain Forest*. Singapore: Cambridge University Press.

Wandrag EM, Dunham AE, Duncan RP, Rogers HS. 2017. Seed dispersal increases local species richness and reduces spatial turnover of tropical tree seedlings. *Proceedings of the National Academy of Sciences of the United States of America* 114:10689–10694. DOI: 10.1073/pnas.1709584114.

Wearn OR, Rowcliffe JM, Carbone C, Pfeifer M, Bernard H, Ewers RM. 2017. Mammalian species abundance across a gradient of tropical land-use intensity: A hierarchical multi-species modelling approach. *Biological Conservation* 212:162–171. DOI: 10.1016/j.biocon.2017.05.007.

Whitmore TC. 1989. Canopy gaps and the two major groups of forest. *Ecology* 70:536–538. DOI: 10.2307/1940195.

Wies G, Nicasio Arzeta S, Martinez Ramos M. 2021. Critical ecological thresholds for conservation of tropical rainforest in Human Modified Landscapes. *Biological Conservation* 255:109023. DOI: 10.1016/j.biocon.2021.109023.

Wright SJ. 2002. Plant diversity in tropical forests: A review of mechanisms of species coexistence. *Oecologia* 130:1–14. DOI: 10.1007/s004420100809.

Young HS, McCauley DJ, Galetti M, Dirzo R. 2016. Patterns, Causes, and Consequences of Anthropocene Defaunation. *Annual Review of Ecology, Evolution, and Systematics* 47:333–358. DOI: 10.1146/annurev-ecolsys-112414-054142.

Zermeño-Hernández I, Méndez-Toribio M, Siebe C, Benítez-Malvido J, Martínez-Ramos M. 2015. Ecological disturbance regimes caused by agricultural land uses and their effects on tropical forest regeneration. *Applied Vegetation Science* 18:443–455. DOI: 10.1111/avsc.12161.

Zermeño-Hernández I, Pingarroni A, Martínez-Ramos M. 2016. Agricultural land-use diversity and forest regeneration potential in human- modified tropical landscapes. *Agriculture, Ecosystems and Environment* 230:210–220. DOI: 10.1016/j.agee.2016.06.007.

Zurita GA, Bellocq MI. 2010. Spatial patterns of bird community similarity: Bird responses to landscape composition and configuration in the Atlantic forest. *Landscape Ecology* 25:147–158. DOI: 10.1007/s10980-009-9410-4.

**Table 1. Summary of response and explanatory variables of the study**

| Variable | Component | Name | Range | Label |
|---|---|---|---|---|
| Seedling | Abundance | Light-demanding seedlings | 0 – 109 | $S_{LD}$ |
| | | Shade-tolerant seedlings | 4 – 130 | $S_{ST}$ |
| | Diversity | α-diversity of all species | 1.60 – 4.11 | $^0\alpha$ |
| | | β-diversity of all species | 3.33 – 6.12 | $^0\beta$ |
| | | α-diversity of typical species | 1.45 – 3.60 | $^1\alpha$ |
| | | β-diversity of typical species | 1.25 – 3.90 | $^1\beta$ |
| | | α-diversity of dominant species | 1.34 – 2.98 | $^2\alpha$ |
| | | β-diversity of dominant species | 0.94 – 3.11 | $^2\beta$ |
| Patch | Spatial | Size | 1.96 – 71.13 | $P_{SZ}$ |
| | | Shape | 1.40 – 5.30 | $P_{SI}$ |
| | Vegetation | Tree basal area | 20.04 – 186 | $T_{BA}$ |
| | | Tree abundance | 33 – 74 | $T_A$ |
| | | Number of adult tree species | 10 – 27 | $T_{0D}$ |
| | | Number of typical adult tree species | 6.12 – 20.1 | $T_{1D}$ |
| | | Number of dominant adult tree species | 4.3 – 16.3 | $T_{2D}$ |
| | Disturbance | Fire index | -5.28 – 5.57 | $D_F$ |
| | | Management index | -5.99 – 5.9 | $D_M$ |
| Landscape | Composition | Forest cover (1200 m radius) | 1.83 – 3.49 | $FC_{1200}$ |
| | Configuration | Patch density (600 m radius) | 0.89 – 6.2 | $PD_{600}$ |
| | | Patch density (900 m radius) | 1.97 – 5.9 | $PD_{900}$ |
| | | Patch aggregation (600 m radius) | 89.56 – 97.56 | $AI_{600}$ |

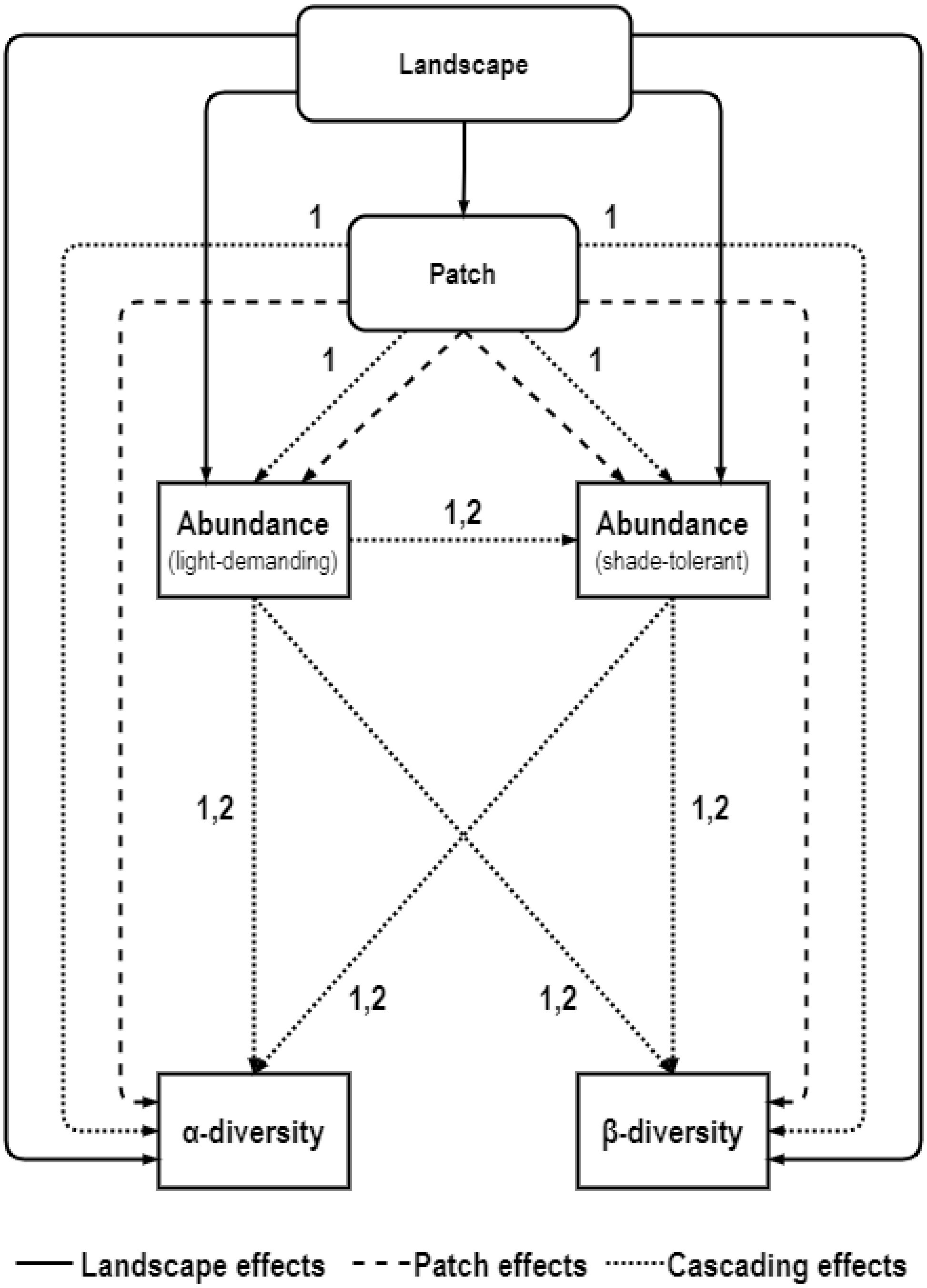


**Fig 1. Conceptual model employed to assess the association among landscape (i.e., composition and configuration) and patch structure (i.e., size, shape, tree basal area, tree diversity, and disturbance), and seedling community (i.e., abundance and diversity)**. The hypothesis evaluated in this study are presented in two hypothetical pathways: direct effects of landscape/patch and cascading effects whether by landscape structure through patches (1) or by patch structure through seedling abundances (2).

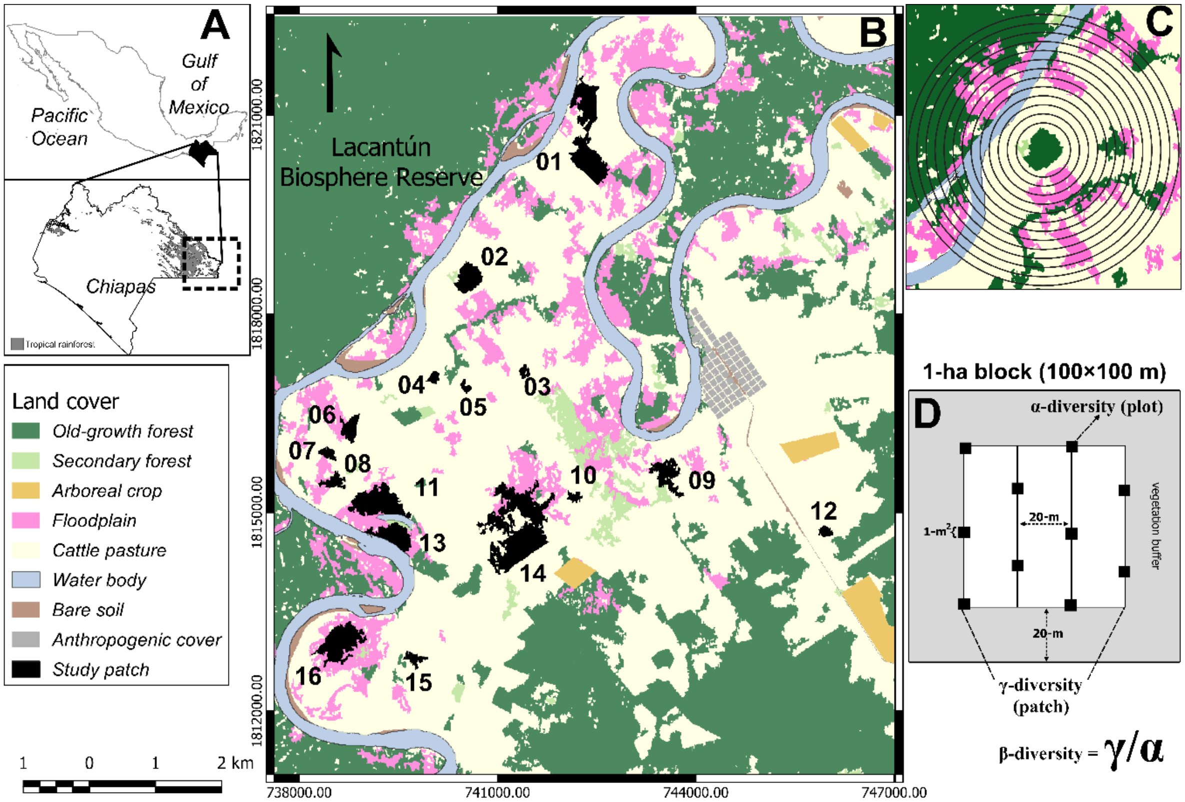
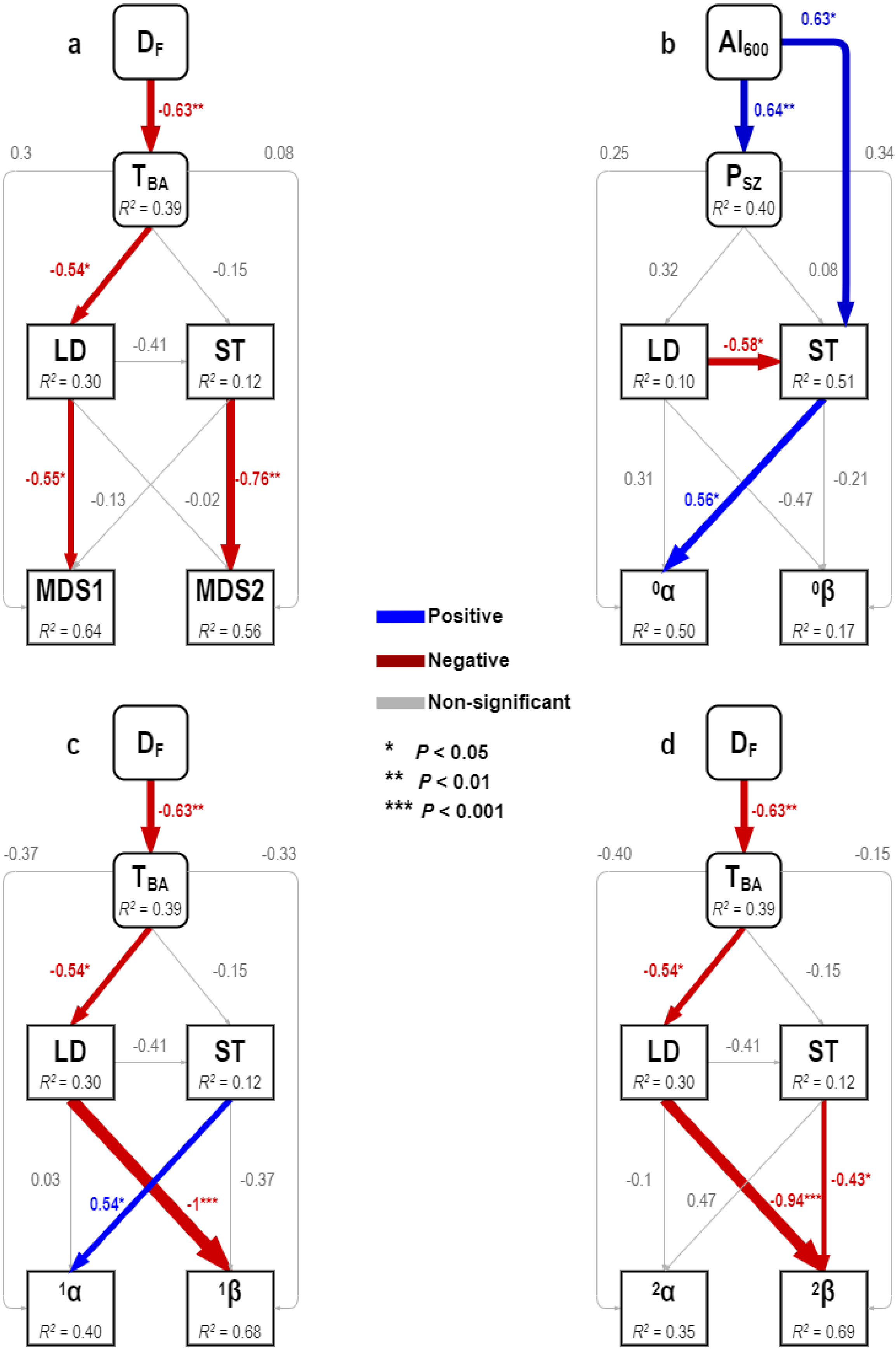


**Fig 2. Location of the study area in the Lacandona rain forest in Chiapas, southeastern Mexico** (a). We show the location of the 16 study forest fragments (black) in the Marqués de Comillas Region (b). The 13 buffer sizes (300-1500ha) around the geographic center of the focal patch (c) and the seedling sampling procedure (d)are also indicated.



a
$D_F$
-0.63**
0.3
0.08
$T_{BA}$ $R^2 = 0.39$
-0.54*
-0.15
LD $R^2 = 0.30$
-0.41
ST $R^2 = 0.12$
-0.55*
-0.13
-0.02
-0.76**
MDS1 $R^2 = 0.64$
MDS2 $R^2 = 0.56$
b
$AI_{600}$
0.63*
0.64**
0.25
0.34
$P_{SZ}$ $R^2 = 0.40$
0.32
0.08
LD $R^2 = 0.10$
-0.58*
ST $R^2 = 0.51$
0.31
0.56*
-0.47
-0.21
$^0\alpha$ $R^2 = 0.50$
$^0\beta$ $R^2 = 0.17$
Positive
Negative
Non-significant
* $P < 0.05$
** $P < 0.01$
*** $P < 0.001$
c
$D_F$
-0.63**
-0.37
-0.33
$T_{BA}$ $R^2 = 0.39$
-0.54*
-0.15
LD $R^2 = 0.30$
-0.41
ST $R^2 = 0.12$
0.03
0.54*
-1***
-0.37
$^1\alpha$ $R^2 = 0.40$
$^1\beta$ $R^2 = 0.68$
d
$D_F$
-0.63**
-0.40
-0.15
$T_{BA}$ $R^2 = 0.39$
-0.54*
-0.15
LD $R^2 = 0.30$
-0.41
ST $R^2 = 0.12$
-0.1
0.47
-0.94***
-0.43*
$^2\alpha$ $R^2 = 0.35$
$^2\beta$ $R^2 = 0.69$

**Fig 3. Best-fitted structural equation models for seedling (a) composition (*df* =12), and α- and β-diversity of (b) all species (*df* =10), (c) typical species (*df* =10) and (d) dominant species (*df* =10) in 16 forest patches in the Lacandona rainforest, southeast Mexico**. Arrow thickness are proportional to the standardized path-coefficient value. The coefficients of determination of linear models ($R^2$) are reported. Patch size ($P_{SZ}$), tree basal area ($T_{BA}$), disturbance by fire ($D_F$), patch aggregation (AI), as well as the abundances of light-demanding (LD), and shade-tolerant seedlings (ST), compositional axes from the NMDS analysis (MDS1 and MDS2), and α- and β-diversity of all species (${}^0\alpha$, ${}^0\beta$) typical species (${}^1\alpha$, ${}^1\beta$) and dominant species (${}^2\alpha$, ${}^2\beta$) are shown.

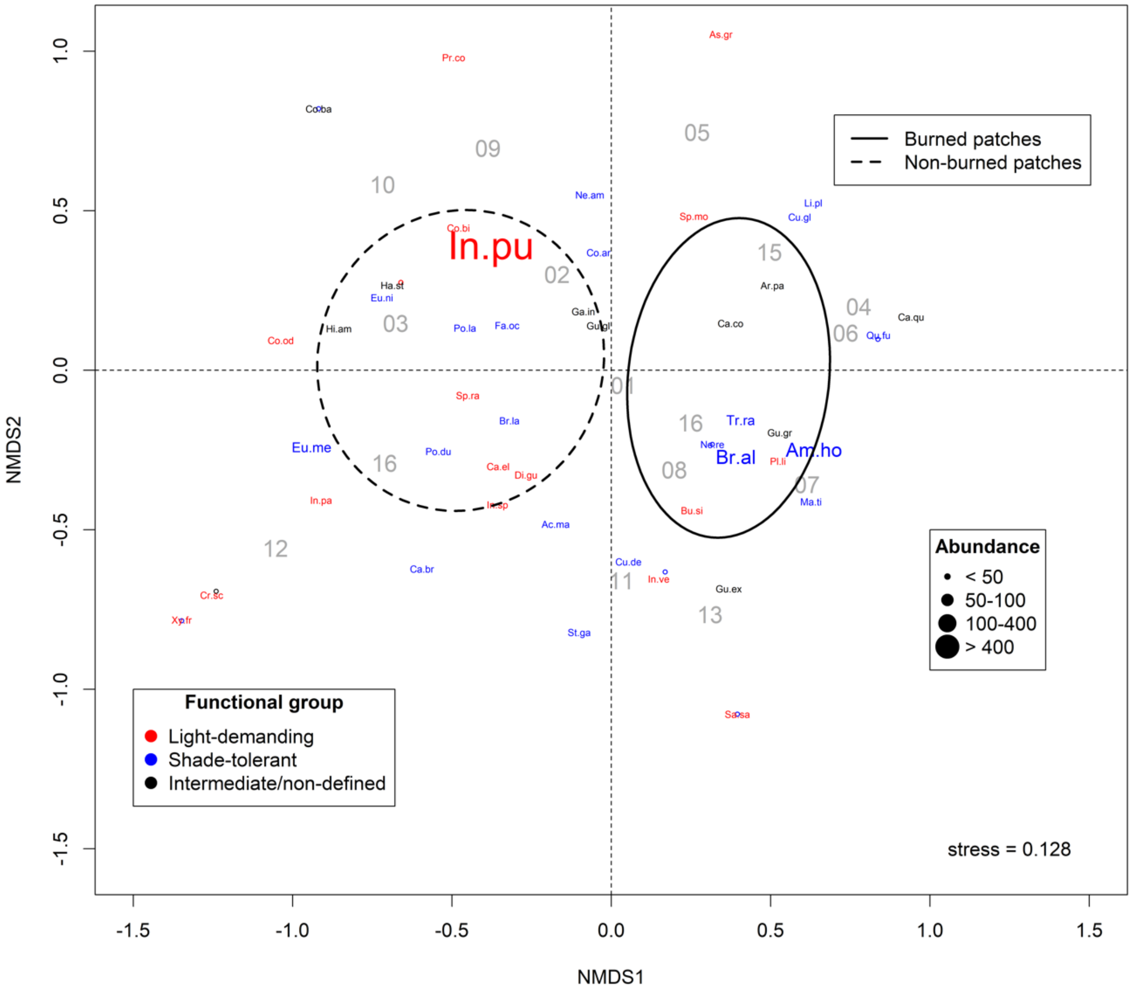


**Fig 4. NMDS ordination of seedling assemblages of 16 forest patches (grey numbers) in the Lacandona rainforest, southeast Mexico**. Abbreviations are seedling species (Table S1).

## Supporting information

Table S1. Seedling species recorded in 16 forest patches in the Lacandona rainforest, southeast Mexico.

| Family | Specie | Abbreviation | Light | Dispersion | Abundance |
|---|---|---|---|---|---|
| ACANTHACEAE | *Bravaisia integerrima* | Br.in | L | A | 29 |
| ANACARDIACEAE | *Astronium graveolens* | As.gr | L | B | 1 |
|  | *Spondias mombin* | Sp.mo | L | B | 7 |
|  | *Spondias radlkoferi* | Sp.ra | L | B | 4 |
| ANNONACEAE | *Annona sp* | An.sp | S | B | 4 |
|  | *Xylopia frutescens* | Xy.fr | L | B | 1 |
| APOCYNACEAE | *Stemmadenia galeottiana* | St.ga | S | B | 2 |
| BIGNONIACEAE | *Tabebuia rosea* | Ta.ro | S | A | 1 |
| BORAGINACEAE | *Cordia bicolor* | Co.bi | L | B | 2 |
|  | *Cordia odorata* | Co.od | L | B | 4 |
| BURSERACEAE | *Bursera simaruba* | Bu.si | L | B | 1 |
|  | *Protium copal* | Pr.co | L | B | 7 |
| CAPPARACEAE | *Capparis quiringuensis* | Ca.qu | I | B | 1 |
| CHRYSOBALANACEAE | *Hirtella americana* | Hi.am | I | B | 15 |
|  | *Licania hypoleuca* | Li.hy | I | B | 8 |
|  | *Licania platypus* | Li.pl | S | B | 1 |
| CLUSIACEAE | *Calophyllum brasilense* | Ca.br | S | B | 10 |
|  | *Garcinia intermedia* | Ga.in | I | B | 4 |
| EUPHORBIACEAE | *Croton schiedeanus* | Cr.sc | L | B | 11 |
| FABACEAE | *Acacia mayana* | Ac.ma | S | B | 12 |
|  | *Albizia leucocalyx* | Al.le | S | A | 5 |
|  | *Andira inermis* | An.in | S | B | 4 |

| | | | | | |
|---|---|---|---|---|---|
| | *Cojoba arboreum* | Co.ar | S | B | 4 |
| | *Dialium guianense* | Di.gu | L | B | 10 |
| | *Inga dulis* | In.du | L | B | 3 |
| | *Inga pavoneana* | In.pa | L | B | 1 |
| | *Inga punctata* | In.pu | L | B | 418 |
| | *Inga sp* | In.sp | L | B | 4 |
| | *Inga vera* | In.ve | L | B | 2 |
| | *Lonchocarpus cruentus* | Lo.cr | L | A | 3 |
| | *Lonchocarpus pubescens* | Lo.pu | L | A | 8 |
| | *Platymiscium yucatanum* | Pl.yu | I | A | 10 |
| | *Pterocarpus hayesii* | Pt.ha | S | A | 1 |
| | *Pterocarpus yucatanum* | Pt.yu | S | A | 1 |
| ICACINACEAE | *Calatola costaricanum* | Ca.co | | B | 3 |
| LASCISTEMATACEAE | *Lacistema agreggatum* | La.ag | S | B | 2 |
| LAURACEAE | *Licaria capitata* | Li.ca | S | B | 8 |
| | *Nectandra ambigiens* | Ne.am | S | B | 17 |
| | *Nectandra reticulata* | Ne.re | S | B | 5 |
| MALVACEAE | *Hampea stipitata* | Ha.st | I | B | 4 |
| | *Luehea seemannii* | Lu.se | L | A | 4 |
| | *Quararibea funebris* | Qu.fu | S | B | 5 |
| MELIACEAE | *Cederela odorata* | Ce.od | L | A | 3 |
| | *Guarea excelsa* | Gu.ex | I | B | 9 |
| | *Guarea glabra* | Gu.gl | I | B | 10 |
| | *Guarea grandifolia* | Gu.gr | I | B | 5 |
| | *Trichilia havanensis* | Tr.ha | S | B | 3 |
| MORACEAE | *Brosimum alicastrum* | Br.al | S | B | 177 |
| | *Brosimum latescens* | Br.la | S | B | 20 |

|  |  |  |  |  |  |
|---|---|---|---|---|---|
|  | *Castilla elastica* | Ca.el | L | B | 32 |
|  | *Maclura tinctoria* | Ma.ti | S | B | 3 |
|  | *Trophis racemosa* | Tr.ra | S | B | 94 |
| MYRTACEAE | *Eugenia edulis* | Eu.ed | S | B | 4 |
|  | *Eugenia mexicana* | Eu.me | S | B | 56 |
|  | *Eugenia nigrita* | Eu.ni | S | B | 5 |
| POLYGONACEAE | *Coccoloba barbadensis* | Co.ba | I | B | 1 |
| PRIMULACEAE | *Ardisia paschalis* | Ar.pa | I | B | 30 |
| RUBIACEAE | *Faramea occidentalis* | Fa.oc | S | B | 20 |
|  | *Posoqueria latifolia* | Po.la | S | B | 18 |
| SALICACEAE | *Pleuranthodendron lindenii* | Pl.li | L | B | 18 |
| SAPINDACEAE | *Cupania dentata* | Cu.de | S | B | 8 |
|  | *Cupania glabra* | Cu.gl | S | B | 15 |
|  | *Sapindus saponaria* | Sa.sa | L | B | 1 |
| SAPOTACEAE | *Chrysophyllum mexicanum* | Ch.me | S | B | 10 |
|  | *Pouteria durlandii* | Po.du | S | B | 5 |
| ULMACEAE | *Ampelocera hottlei* | Am.ho | S | B | 176 |
| VOCHYSIACEAE | *Vochysia guatemalensis* | Vo.gu | S | A | 8 |

Table S2. Formulas employed to estimate Hill numbers of seedling α- and β-diversity in the Lacandona rainforest, southeast Mexico.

| **Diversity** | **Order** | **Formula** |
|---|---|---|
| **Gamma** | ${}^{0}D_{\gamma}$<br>${}^{2}D_{\gamma}$ | $${}^{q}D_{\gamma} = \left(\sum_{i=1}^{S} \bar{p}_i^{q}\right)^{\frac{1}{(1-q)}}$$ |
| | ${}^{1}D_{\gamma}$ | $${}^{1}D_{\gamma} = exp\left(-\sum_{i=1}^{S} \bar{p}_i \log \bar{p}_i\right)$$ |
| **Alpha** | ${}^{0}D_{\alpha}$<br>${}^{2}D_{\alpha}$ | $${}^{q}D_{\alpha} = \left(\frac{1}{N}\sum_{i=1}^{S} p_{i1}^{q} + \frac{1}{N}\sum_{i=1}^{S} p_{i2}^{q} + \cdots\right)^{\frac{1}{(1-q)}}$$ |
| | ${}^{1}D_{\alpha}$ | $${}^{1}D_{\propto} = exp\left\{-\frac{1}{N}\left(\sum_{i=1}^{S}\left(p_{i1}^{q}\ \ln p_{i1}^{q}\right) + \sum_{i=1}^{S}\left(p_{i2}^{q}\ \ln p_{i2}^{q}\right) + \cdots\right)\right\}$$ |
| **Beta** | ${}^{0}D_{\beta}$<br>${}^{1}D_{\beta}$<br>${}^{2}D_{\beta}$ | $${}^{q}D_{\beta} = \frac{{}^{q}D_{\gamma}}{{}^{q}D_{\alpha}}$$ |

where $p_i$ denotes the relative abundance of the *i*th species in each of the *N* 1-m$^2$ plots, $\bar{p}_i$ denotes the mean relative abundance of the *i*th species in the *N* 1-m$^2$ plots and $q$ is a parameter that determines the sensitivity of the measure to the relative abundances (Jost, 2007; Tuomisto, 2010).

References:

Jost, L. (2007). Partitioning diversity into independent alpha and beta components. *Ecology*, *88*(10), 2427–2439. https://doi.org/10.1890/06-1736.1

Tuomisto, H. (2010). A diversity of beta diversities: Straightening up a concept gone awry. Part 1. Defining beta diversity as a function of alpha and gamma diversity. *Ecography*, *33*(1), 2–22. https://doi.org/10.1111/j.1600-0587.2009.05880.x

Table S3. Binary data of disturbance factors of the 16 forest patches in the Lacandona rainforest, southeast Mexico.

| Patch | Flood | Fire | Slash | Cow | Use |
|---|---|---|---|---|---|
| **1** | 0 | 1 | 0 | 0 | 1 |
| **2** | 1 | 0 | 1 | 1 | 1 |
| **3** | 0 | 0 | 1 | 1 | 1 |
| **4** | 1 | 1 | 0 | 1 | 1 |
| **5** | 1 | 1 | 1 | 1 | 1 |
| **6** | 0 | 0 | 1 | 1 | 1 |
| **7** | 1 | 0 | 1 | 1 | 1 |
| **8** | 0 | 0 | 1 | 1 | 0 |
| **9** | 0 | 1 | 0 | 0 | 0 |
| **10** | 1 | 1 | 1 | 0 | 0 |
| **11** | 0 | 0 | 0 | 0 | 0 |
| **12** | 1 | 0 | 0 | 0 | 1 |
| **13** | 0 | 0 | 0 | 0 | 0 |
| **14** | 1 | 0 | 0 | 0 | 0 |
| **15** | 1 | 1 | 0 | 1 | 0 |
| **16** | 1 | 1 | 0 | 1 | 1 |

The disturbance factors are the following: flooding during rainy season (*Flood*: 0 = no; 1 = yes), fire events during the last 10 years (*Fire*: 0 = no; 1 = yes), presence of cattle (*Cow*: 0 = cattle do not enter to the patch; 1 = cattle roams within the patch), understory vegetation (*Slash*: 0 = non-slashed; 1 = slashed) and the predominant land use in the adjacent matrix (*Use*: 0 = temporal agriculture; 1 = cattle pasture)

Table S4. Spearman correlation matrix between disturbance factors and logistic PCA components.

| | Flood | Fire | Slash | Use | Cow | PC1 | PC2 | PC3 |
|---|---|---|---|---|---|---|---|---|
| **Flood** | 1 | | | | | | | |
| **Fire** | 0.27 | 1 | | | | | | |
| **Slash** | 0.016 | -0.27 | 1 | | | | | |
| **Use** | 0.238 | 0.016 | 0.27 | 1 | | | | |
| **Cow** | 0.238 | 0.016 | 0.524* | 0.492 | 1 | | | |
| **PC1** | 0.397 | -0.123 | 0.699** | 0.726** | 0.863*** | 1 | | |
| **PC2** | 0.644** | 0.863*** | -0.425 | 0.151 | 0.014 | -0.027 | 1 | |
| **PC3** | -0.452 | 0.069 | -0.206 | 0.617* | 0.069 | 0.062 | -0.024 | 1 |

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$

Table S5. Abbreviation and description of the landscape metrics employed in the analysis

| Landscape metric | Abbreviation | Formula | Description |
|---|---|---|---|
| Aggregation index | AI | $\mathrm{AI} = 100 \times \left[\frac{g_{ii}}{max \to g_{ii}}\right]$ | Where $g_{ii}$ is the number of joins between pixels of forest patch *i* and *max*→$g_{ii}$ is the maximum number of joins between pixels of forest patch *i* based on the single-count method |
| Edge contrast index | EC | $\mathrm{EC} = 100 \times \left[\frac{\sum_{k=1}^{m} p_{ijk} \cdot d_{ik}}{p_{ij}}\right]$ | Where $p_{ijk}$ is the edge length (m) of patch *ij* adjacent to cover type *k*, $d_{ik}$ is the edge contrast weight between patch *i* and cover *k*, and $p_{ij}$ is the length of perimeter of patch *ij* |
| Forest cover | FC | $\mathrm{FC} = 100 \times \left[\frac{\sum_{j=1}^{n} a_i}{A}\right]$ | Where *a* is the area ($m^2$) of forest patch *i* and *A* the is the total landscape area |
| Secondary forest | SF | $\mathrm{SV} = 100 \times \left[\frac{\sum_{j=1}^{n} a_i}{A}\right]$ | Where *a* is the area ($m^2$) of cover patch *i* and *A* the is the total landscape area |
| Patch density | PD | $\mathrm{PD} = 100 \times \left[\frac{n_i}{A} \times (10{,}000)\right]$ | Where $n_i$ is the total number of patches in the landscape of the land cover *i* and *A* is the total landscape area ($m^2$) |

Table S6. Landscape metrics selected from the multi-scale assessment for each patch structural variable

| Patch structure | Landscape metric | Radius (m) | $R^2$ |
|---|---|---|---|
| **$D_F$** | PD | 600 | 0.23 |
| **$D_M$** | FC | 1200 | 0.59 |
|  | PD | 900 | 0.44 |
| **$T_{BA}$** | EC | 1100 | 0.21 |
| **$T_{1D}$** | FC | 700 | 0.27 |
| **$P_{SZ}$** | PD | 1100 | 0.22 |
|  | AI | 600 | 0.36 |
| **$P_{SI}$** | PD | 900 | 0.23 |

Table S7. Relative importance and significance of disturbance and landscape variables for each patch structural variable

| Patch | Variable | *β* (SE) | $\sum w_i$ |
|---|---|---|---|
| **DF** | **$PD_{600}$** | **-0.532 (0.528)** | **0.754** |
| **$D_M$** | **$FC_{1200}$** | **-0.611 (0.424)** | **1** |
|  | **$PD_{900}$** | **-0.41 (0.38)** | **0.827** |
|  | $P_{SZ}$ | -0.138 (0.381) | 0.127 |
| **$T_{BA}$** | **$D_F$** | **-0.575 (0.494)** | **0.919** |
|  | $EC_{1100}$ | -0.394 (0.493) | 0.552 |
|  | $P_{SZ}$ | -0.032 (0.517) | 0.114 |
| **$T_{1D}$** | $D_F$ | 0.306 (0.551) | 0.248 |
|  | $FC_{700}$ | 0.486 (0.563) | 0.596 |
|  | $P_{SZ}$ | 0.329 (0.661) | 0.222 |

| | | | |
|---|---|---|---|
| **$P_{SZ}$** | **$AI_{600}$** | **0.611 (0.516)** | **0.834** |
| | $D_F$ | 0.223 (0.507) | 0.308 |
| | $PD_{1100}$ | 0.396 (0.653) | 0.202 |
| **$P_{SI}$** | **$D_F$** | **0.541 (0.452)** | **1** |
| | **$PD_{900}$** | **-0.473 (0.435)** | **0.808** |

Table S8. Pearson correlation matrix among explanatory variables

| | **$D_F$** | **$D_M$** | **$T_{BA}$** | **$T_A$** | **$T_{0D}$** | **$T_{1D}$** | **$T_{2D}$** | **$P_{SZ}$** |
|---|---|---|---|---|---|---|---|---|
| **$D_M$** | 0.001 | | | | | | | |
| **$T_{BA}$** | -0.63** | 0.35 | | | | | | |
| **$T_A$** | -0.25 | 0.27 | 0.73** | | | | | |
| **$T_{0D}$** | 0.014 | 0.23 | 0.32 | 0.49 | | | | |
| **$T_{1D}$** | 0.31 | 0.16 | -0.09 | 0.14 | 0.88*** | | | |
| **$T_{2D}$** | 0.46 | 0.06 | -0.31 | -0.05 | 0.72** | 0.95*** | | |
| **$P_{SZ}$** | 0.23 | -0.46 | -0.14 | -0.12 | 0.25 | 0.41 | 0.49 | |
| **$P_{SI}$** | 0.58* | -0.21 | -0.13 | 0.31 | 0.28 | 0.35 | 0.40 | 0 |

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

Table S9. Best-fitted structural equation models for seedling composition and diversity in 16 forest patches in the Lacandona rainforest, southeast Mexico.

| Model | Exogenous variables | $\chi^2$ | *df* | *P* | AIC**c** | *Δ*i |
|---|---|---|---|---|---|---|
| Seedling composition | $T_{BA}$ | 15.78 | 10 | 0.11 | -178.5 | 0 |
| | $D_M$ | 22.6 | 16 | 0.12 | -152.24 | 26.26 |
| | $P_{SZ}$ | 8.54 | 8 | 0.38 | -134.78 | 43.72 |
| | $P_{SZ}$, $P_{SI}$ | 37.27 | 32 | 0.24 | -108.88 | 69.62 |
| | $T_{BA}$, $D_M$ | 41.19 | 30 | 0.08 | -107.94 | 70.56 |
| | $T_{BA}$, $P_{SZ}$ | 25.7 | 22 | 0.26 | -100.55 | 77.95 |
| | $D_M$, $P_{SZ}$ | 32.35 | 30 | 0.35 | -98.51 | 79.99 |
| | $T_{BA}$, $T_{1D}$ | 19.37 | 12 | 0.08 | -97.82 | 80.68 |
| | $D_M$, $P_{SI}$ | 30.33 | 30 | 0.45 | -96.35 | 82.14 |
| | $T_{BA}$, $P_{SI}$ | 20.44 | 20 | 0.43 | -89.65 | 88.85 |
| All-species diversity | $P_{SZ}$ | 9.15 | 8 | 0.33 | -136.39 | 0 |
| | $D_M$ | 11.2 | 16 | 0.8 | -126.17 | 10.23 |
| | $D_M$, $T_{1D}$ | 38.9 | 32 | 0.19 | -110.74 | 25.65 |
| | $D_M$, $P_{SI}$ | 33.53 | 30 | 0.3 | -99.77 | 36.62 |
| | $T_{BA}$, $D_M$ | 29.68 | 30 | 0.48 | -95.66 | 40.73 |
| | $D_M$, $P_{SZ}$ | 25.15 | 30 | 0.72 | -90.83 | 45.56 |
| Typical-species diversity | $T_{BA}$ | 15.35 | 10 | 0.12 | -177.11 | 0 |
| | $D_M$ | 18.56 | 16 | 0.29 | -143 | 34.12 |
| | $P_{SZ}$ | 8.47 | 8 | 0.39 | -134.59 | 42.53 |
| | $D_M$, $T_{1D}$ | 45.67 | 32 | 0.06 | -118.48 | 58.63 |

| | | | | | | |
|---|---|---|---|---|---|---|
| | $D_M$, $P_{SI}$ | 42.3 | 30 | 0.07 | -109.12 | 67.99 |
| | $T_{BA}$, $D_M$ | 34.37 | 30 | 0.27 | -100.66 | 76.45 |
| | $D_M$, $P_{SZ}$ | 29.39 | 30 | 0.5 | -95.35 | 81.76 |
| | $T_{BA}$, $P_{SZ}$ | 20.78 | 22 | 0.53 | -94.5 | 82.62 |
| | $T_{BA}$, $T_{1D}$ | 14.52 | 12 | 0.27 | -91.36 | 85.76 |
| | $T_{BA}$, $P_{SI}$ | 21.52 | 20 | 0.37 | -90.89 | 86.23 |
| Dominant-species diversity | $T_{BA}$ | 13.84 | 10 | 0.18 | -172.29 | 0 |
| | $D_M$ | 16.25 | 16 | 0.44 | -137.71 | 34.59 |
| | $P_{SZ}$ | 6.23 | 8 | 0.62 | -128.62 | 43.67 |
| | $D_M$, $T_{1D}$ | 38.14 | 32 | 0.21 | -109.87 | 62.42 |
| | $P_{SZ}$, $P_{SI}$ | 38.05 | 32 | 0.21 | -109.77 | 62.52 |
| | $D_M$, $P_{SI}$ | 37.03 | 30 | 0.18 | -103.5 | 68.79 |
| | $T_{BA}$, $D_M$ | 31.1 | 30 | 0.41 | -97.17 | 75.12 |
| | $T_{BA}$, $P_{SZ}$ | 18.75 | 22 | 0.66 | -92 | 80.29 |
| | $D_M$, $P_{SZ}$ | 24.83 | 30 | 0.73 | -90.48 | 81.81 |
| | $T_{BA}$, $T_{1D}$ | 12.7 | 12 | 0.39 | -88.94 | 83.35 |

Results of the alternative models that fitted selection criteria for each index of seedling composition and diversity and the exogenous variables included in each model (patch size: $P_{SZ}$, patch shape: $P_{SI}$, tree basal area: $T_{BA}$, tree diversity: $T_{1D}$ and patch disturbance by management: $D_M$). Given are the degrees of freedom (*df*), Fisher's C value statistic ($\chi^2$) and p-value (*P*), Akaike Information Criterion corrected for small samples (AICc), and AICc differences compared to be best-supported model by data ($\Delta$i).

Table S10. Test statistics for the single best model for each index of seedling composition and diversity in 16 forest patches in the Lacandona rainforest, southeast Mexico.

| Seedling variable | Response | Predictor | $\beta_i$ | SE | df | *t* | *P* | $\beta'_i$ |
|---|---|---|---|---|---|---|---|---|
| Composition | $T_{BA}$ | **$D_F$** | **-8.069** | **2.683** | **14** | **-3.007** | **0.009** | **-0.626** |
| | LD | **$T_{BA}$** | **-0.007** | **0.003** | **14** | **-2.426** | **0.029** | **-0.544** |
| | ST | LD | -1.694 | 1.273 | 13 | -1.331 | 0.206 | -0.412 |
| | | $T_{BA}$ | -0.009 | 0.017 | 13 | -0.499 | 0.626 | -0.154 |
| | MDS1 | **LD** | **-0.504** | **0.201** | **12** | **-2.504** | **0.028** | **-0.547** |
| | | ST | 0.028 | 0.041 | 12 | 0.685 | 0.507 | 0.126 |
| | | $T_{BA}$ | 0.004 | 0.002 | 12 | 1.487 | 0.163 | 0.308 |
| | MDS2 | LD | -0.02 | 0.186 | 12 | -0.108 | 0.916 | -0.026 |
| | | **ST** | **-0.141** | **0.038** | **12** | **-3.713** | **0.003** | **-0.758** |
| | | $T_{BA}$ | 0.001 | 0.002 | 12 | 0.341 | 0.739 | 0.078 |
| All-species diversity | $P_{SZ}$ | **$AI_{600}$** | **0.335** | **0.108** | **14** | **3.083** | **0.008** | **0.636** |

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | LD | $P_{SZ}$ | 0.17 | 0.134 | 14 | 1.267 | 0.226 | 0.321 |
| | ST | **LD** | **-2.384** | **0.893** | **12** | **-2.669** | **0.02** | **-0.579** |
| | | $P_{SZ}$ | 0.177 | 0.574 | 12 | 0.308 | 0.763 | 0.081 |
| | | **$AI_{600}$** | **0.726** | **0.306** | **12** | **2.372** | **0.035** | **0.632** |
| | $^{0}\alpha$ | LD | 0.353 | 0.28 | 12 | 1.26 | 0.232 | 0.308 |
| | | **ST** | **0.157** | **0.068** | **12** | **2.326** | **0.038** | **0.564** |
| | | $P_{SZ}$ | 0.154 | 0.147 | 12 | 1.046 | 0.316 | 0.253 |
| | $^{0}\beta$ | LD | -0.514 | 0.346 | 12 | -1.484 | 0.164 | -0.467 |
| | | ST | -0.057 | 0.084 | 12 | -0.688 | 0.505 | -0.214 |
| | | $P_{SZ}$ | 0.198 | 0.182 | 12 | 1.086 | 0.299 | 0.338 |
| Typical-species diversity | $T_{BA}$ | **$D_F$** | **-8.069** | **2.683** | **14** | **-3.007** | **0.009** | **-0.626** |
| | LD | **$T_{BA}$** | **-0.007** | **0.003** | **14** | **-2.426** | **0.029** | **-0.544** |
| | ST | LD | -1.694 | 1.273 | 13 | -1.331 | 0.206 | -0.412 |
| | | $T_{BA}$ | -0.009 | 0.017 | 13 | -0.499 | 0.626 | -0.154 |
| | $^{1}\alpha$ | LD | 0.026 | 0.24 | 12 | 0.107 | 0.917 | 0.03 |
| | | **ST** | **0.111** | **0.049** | **12** | **2.258** | **0.043** | **0.539** |
| | | $T_{BA}$ | -0.004 | 0.003 | 12 | -1.369 | 0.196 | -0.368 |
| | $^{1}\beta$ | **LD** | **-1.339** | **0.277** | **12** | **-4.84** | **0** | **-1.011** |
| | | ST | -0.117 | 0.056 | 12 | -2.069 | 0.061 | -0.364 |
| | | $T_{BA}$ | -0.006 | 0.004 | 12 | -1.681 | 0.119 | -0.333 |
| Dominant-species diversity | $T_{BA}$ | **$D_F$** | **-8.069** | **2.683** | **14** | **-3.007** | **0.009** | **-0.626** |
| | LD | **$T_{BA}$** | **-0.007** | **0.003** | **14** | **-2.426** | **0.029** | **-0.544** |
| | ST | LD | -1.694 | 1.273 | 13 | -1.331 | 0.206 | -0.412 |
| | | $T_{BA}$ | -0.009 | 0.017 | 13 | -0.499 | 0.626 | -0.154 |
| | $^{2}\alpha$ | LD | -0.07 | 0.214 | 12 | -0.325 | 0.751 | -0.096 |
| | | ST | 0.083 | 0.044 | 12 | 1.895 | 0.082 | 0.47 |
| | | $T_{BA}$ | -0.004 | 0.003 | 12 | -1.442 | 0.175 | -0.403 |

|  |  |  |  |  |  |  |
|---|---|---|---|---|---|---|
| $^2\beta$ | **LD** | **-0.987** | **0.214** | **12** | **-4.613** | **0.001** | **-0.944** |
|  | **ST** | **-0.108** | **0.044** | **12** | **-2.479** | **0.029** | **-0.427** |
|  | $T_{BA}$ | -0.002 | 0.003 | 12 | -0.759 | 0.463 | -0.147 |

The response and predictor variables are patch size ($P_{SZ}$), patch shape ($P_{SI}$), tree basal area ($T_{BA}$), patch disturbance by fire ($D_F$), abundance of light-demanding seedlings (LD), abundance of shade-tolerant seedlings (ST), and alpha and beta diversity of all species ($^0\alpha$,$^0\beta$), typical species ($^1\alpha$,$^1\beta$) and dominant species ($^2\alpha$,$^2\beta$). Given are unstandardized path coefficients ($\beta_i$) and associated standard error (SE), degrees of freedom (*df*), t-value (*t*), p-value (*P*) and standardized path coefficients ($\beta'_i$). The significant paths are highlighted in bold.

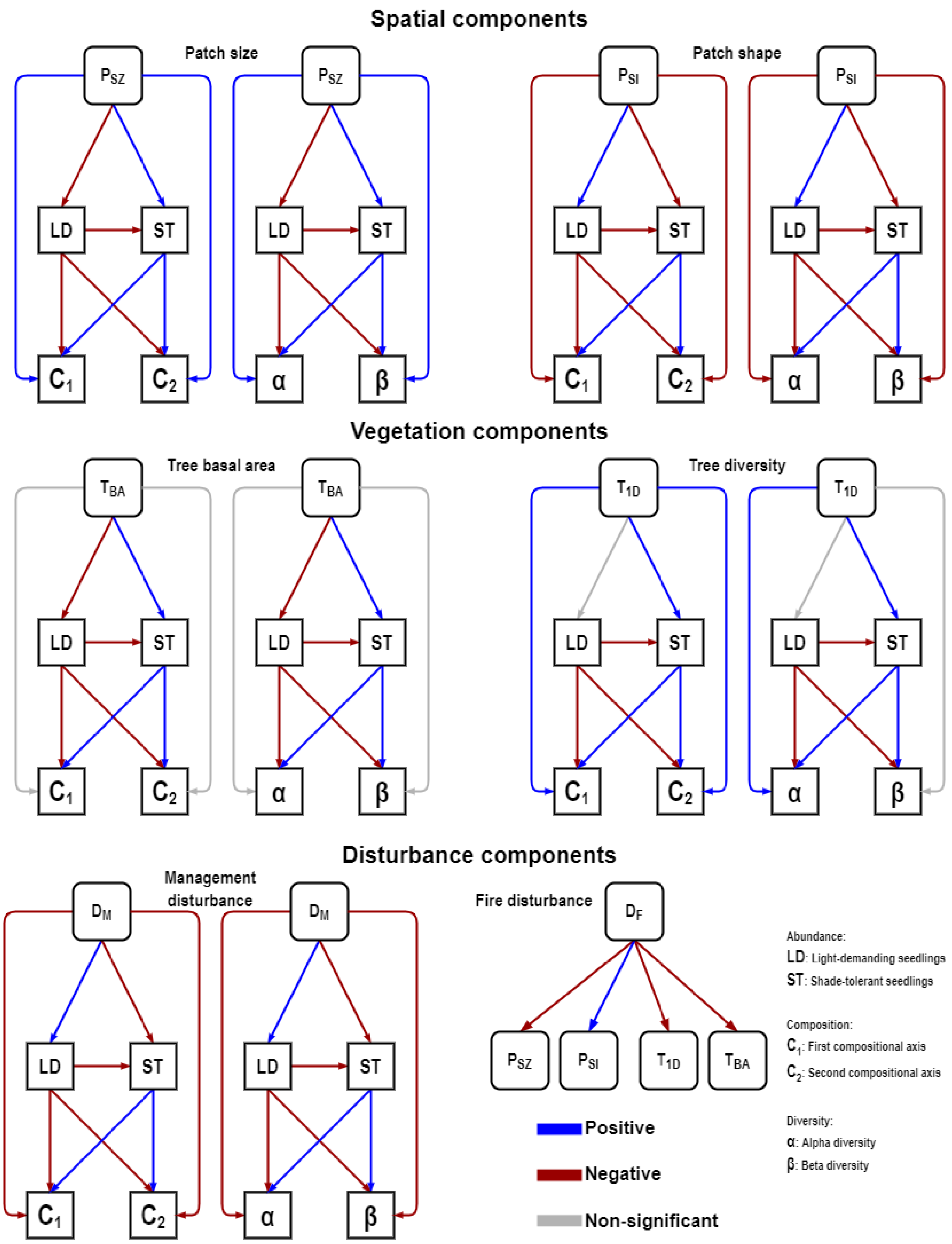


Figure S1. Expected relationships between patch components and seedling community

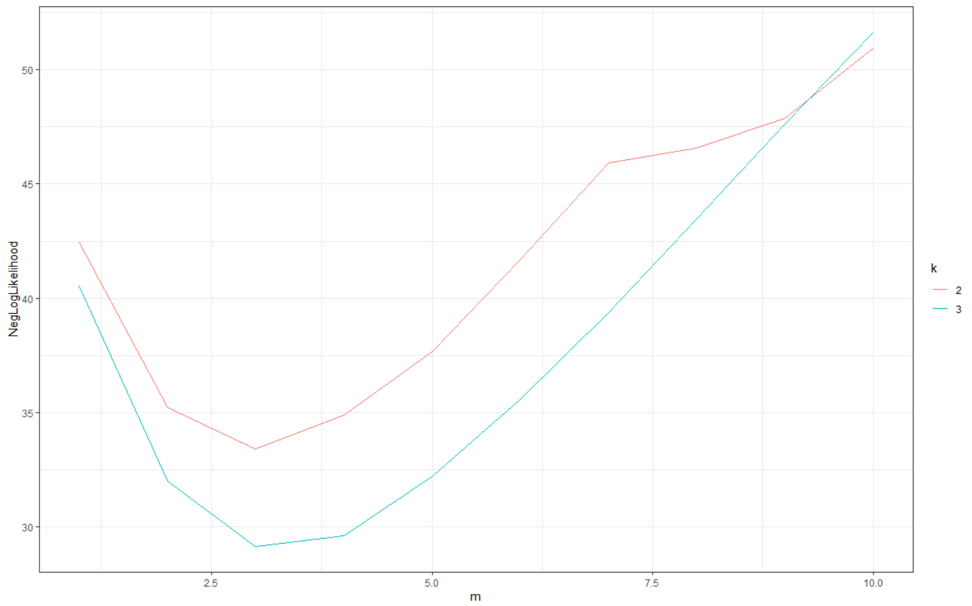


**Figure S2. Association between the tunning parameter (*m*) and the negative Log-likelihood of models with varying *m* values.** The red line represents a logistic PCA of two dimensions and the blue line a PCA of three dimensions.

# CAPÍTULO III. LANDSCAPE STRUCTURE SHAPES THE DIVERSITY OF TREE SEEDLINGS AT MULTIPLE SPATIAL SCALES IN A FRAGMENTED TROPICAL RAINFOREST

PLOS ONE

RESEARCH ARTICLE

# Landscape structure shapes the diversity of tree seedlings at multiple spatial scales in a fragmented tropical rainforest

**Sergio Nicasio-Arzeta**[1,2☯]*, **Isela E. Zermeño-Hernández**[3‡], **Susana Maza-Villalobos**[4‡], **Julieta Benítez-Malvido**[2☯]

**1** Programa de Doctorado en Ciencias Biomédicas, Universidad Nacional Autónoma de México (UNAM), Ciudad de México, Morelia, México, **2** Instituto de Investigaciones en Ecosistemas y Sustentabilidad, Universidad Nacional Autónoma de México, Morelia, Michoacán, México, **3** CONACyT-Universidad Michoacana de San Nicolás de Hidalgo, Morelia, Michoacán, Mexico, **4** CONACyT-El Colegio de la Frontera Sur, Tapachula, Chiapas, México

☯ These authors contributed equally to this work.
‡ These authors also contributed equally to this work.
* sergio.nicasio@iies.unam.mx

## Abstract

The maintenance of seedling diversity of animal-dispersed tree species is fundamental for the structure and function of forest patches in fragmented tropical rainforests. Nonetheless, the effects of landscape structure at different spatial scales on α- and β-diversity of tree seedling communities are recently explored. Using a multi-scale approach, we assessed the relative effect of landscape composition and configuration on α- and β-diversity of animal-dispersed seedlings within 16 forest patches in the Lacandona rainforest, Mexico. We assessed these effects at 13 spatial scales (from 300 to 1500 m radius, at 100 m intervals) for three metrics of effective number of species considering α- and β-diversity. We found that α-diversity was largely affected by landscape composition and β-diversity by landscape configuration. On the one hand, the amount of secondary forest influenced α-diversity. Additionally, species richness increased in landscapes with highly aggregated forest patches. On the other hand, β-diversity was affected positively by forest fragmentation and negatively by the edge contrast of forest patches with the surrounding matrix. Our findings indicate that landscape configuration is a strong driver of seedling diversity in highly deforested rainforests. Promoting forest patches and secondary forests through payment for ecosystem services' programs, favoring matrix quality within land-sharing schemes of smallholder agriculture and secondary forest management, and identifying restoration opportunities for assisted or unassisted natural regeneration are urgently needed for conservation of seedling diversity in human-modified tropical landscapes.

**Citation:** Nicasio-Arzeta S, Zermeño-Hernández IE, Maza-Villalobos S, Benítez-Malvido J (2021) Landscape structure shapes the diversity of tree seedlings at multiple spatial scales in a fragmented tropical rainforest. PLoS ONE 16(7): e0253284. https://doi.org/10.1371/journal.pone.0253284

**Editor:** Juliana Hipólito, Instituto Nacional de Pesquisas da Amazonia, BRAZIL

**Received:** February 25, 2021

**Accepted:** June 1, 2021

**Published:** July 16, 2021

**Peer Review History:** PLOS recognizes the benefits of transparency in the peer review process; therefore, we enable the publication of all of the content of peer review and author responses alongside final, published articles. The editorial history of this article is available here: https://doi.org/10.1371/journal.pone.0253284

**Data Availability Statement:** The data of seedling abundance and landscape metrics have been deposited with the Dryad Data Repository

## Introduction

Tropical rainforests harbor half of known animal and plant species of the planet [1], yet accelerated forest conversion to cattle pastures and large-scale plantations is restraining them to since each response is influenced at different spatial and temporal scales [39,42]. For example, it is hypothesized that biological variables shaped by species colonization and extinction dynamics (i.e. species occurrence) should have larger scales of effect than those affected by local drivers (i.e. species abundance) [43]. Thus, the scale of effect is expected to be larger for lower-density populations (rare species) than for higher-density populations (typical or dominant species) [42]. This is particularly important in tropical rainforests, where a high number of species coexist at very low-density populations, making seedling communities highly α- and β-diverse in space [17,44].

Multi-scale approaches are a hierarchical approach useful to increase the possibility to detect the scale of effect of landscape structure on biological responses [45,46]. In these approaches, it is necessary the use of a wide range of scales, as assessments performed using very few scales within narrow ranges overlook the scale of effect [41,45]. To our knowledge, studies that have employed multi-scale analysis on plant communities in the tropics are scant [30,47], and none of them have assessed the effect of landscape structure on seedling communities in HMTLs (but see [30]). In this study, we employed a multi-scale approach to assess the contribution of landscape composition and configuration on tree seedling α- and β-diversity within rainforest patches. We particularly focused on the following question: Which components of landscape structure are influencing seedling α- and β-diversity and at which spatial scales?

Furthermore, we tested the following predictions: (1) α-diversity will increase in landscapes with high forest cover and β-diversity will increase in fragmented landscapes with low edge contrast; and (2) there should be larger scales of effect for richness-based metrics than for abundance-based metrics of seedling α- and β-diversity (i.e. dominant < typical < all species).

## Material and methods

### Study site

We conducted the study at the Marqués de Comillas region in the Lacandona rainforest in southeastern Mexico (Fig 1A). The monthly temperature oscillates between 24 and 26˚C, and the annual precipitation ranges from 2500 to 3500 mm [48]. This region encompasses the largest rainforest of the Mesoamerican biodiversity hotspot and the Montes Azules and Lacantún Biosphere Reserves, which protect 393,000 ha of old-growth forest [49–51]. Land-cover change to cattle pastures has reduced its forest cover outside the reserve by more than 50% of its original extension [51,52]. Despite deforestation in the last 40 years, large mammals, birds, and primate species are still present in forest patches [6,53,54]. We selected 16 old-growth forest patches, ranging from 1 ha to 63 ha (Fig 1B). We only considered only patches located in floodplains to keep adult tree species composition, soil type and abiotic factors relatively constant. The land tenure of the Marqués de Comillas region is private, and land property is distributed among the inhabitants [51,52]. Therefore, we conducted our study only in those forest patches where permission was granted by the owners.

### Tree seedling sampling

Patches were sampled by 1-ha blocks placed at the center of each forest patch from February to June of 2014 (Fig 1C). Each block contained ten 1-$m^2$ plots randomly arranged in groups of two or three plots along five equidistant transects (20 m apart; Fig 1D). For 1-ha forest patches, we never positioned plots at the edge in order to have a 20-m buffer zone of vegetation that protect them from edge effects as much as possible (Fig 1D) [13,15]. Within each 1-$m^2$ plot we counted and identified all tree seedlings (10–100 cm height) to the lowest possible taxonomic level with the help of a local parataxonomist and field guides [56,57]. When field identification

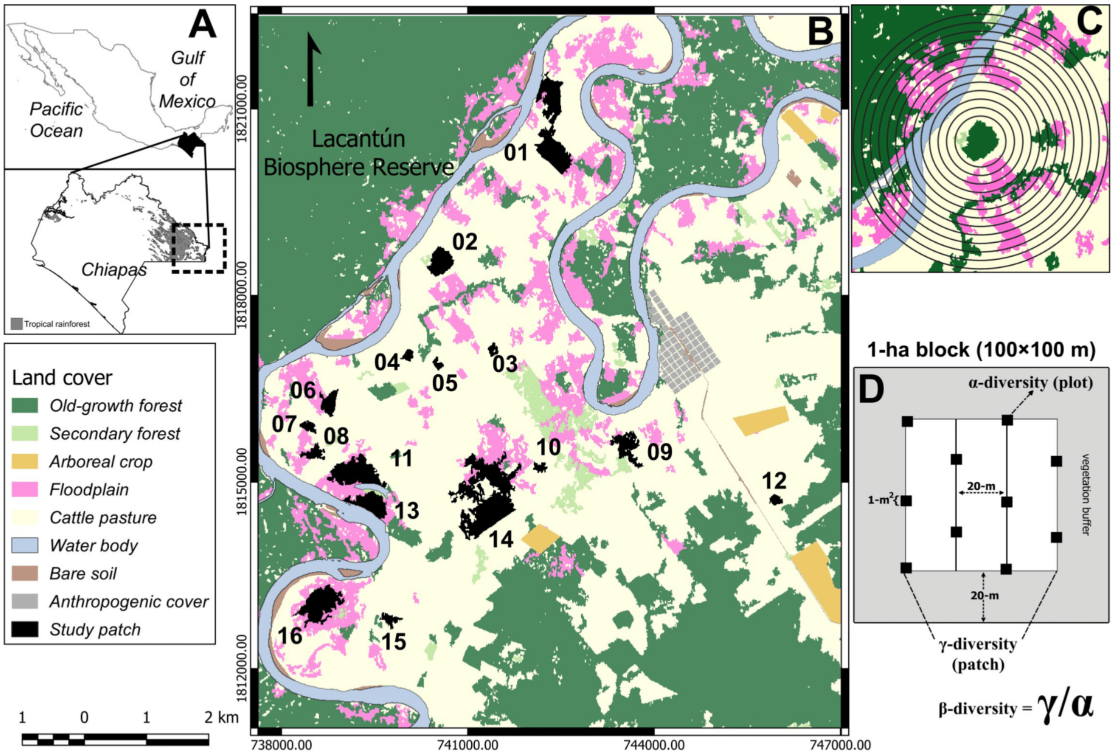


**Fig 1. Study site and sampling design of tree seedlings.** The figure shows the location of the study area (A) and the 16 study patches (black) in the Marqués de Comillas region (B). The 13 buffer sizes around the geographic center of the sampling block (C). Sampling method of tree seedlings (see material and methods), and the source of γ-diversity (species located in the 1-ha block), α-diversity (the average number of species per 1-m2 plot) and β-diversity (the effective number of completely distinct assemblages within each 1-ha block) (D). Reprinted from [55] under a CC BY license, with permission from Sergio Nicasio-Arzeta, original copyright 2019.

https://doi.org/10.1371/journal.pone.0253284.g001

was not possible, we took samples for identification at several herbariums (MEXU, ECO-SC-H). We determined the dispersal syndrome of each species, based on their fruits and seed morphology [58,59]. This study did not involve the extraction or damage of endangered species. We based our analyses on animal-dispersed tree species only because they comprise up to 90% of the seed rain in rainforests [20,60]. In our case, 94% of the seedling species were animal-dispersed (see Results). Plant nomenclature followed the Missouri Botanical Garden database Tropicos [61].

## Diversity estimation

We assessed the sampling completeness with the sample coverage estimator of Chao and Shen [62]. We combined the data of the 10 sampling plots within each patch. Then, we estimated the proportion of the total number of individuals that belong to the species represented in the sample [63]. The sample coverage among patches was high (91.07 ± 7.47%; mean ± SD), indicating that our sampling effort was adequate for estimating seedling species diversity [64]. We then estimated the effective number of species for seedlings using the diversity decomposition of effective numbers of species (the Hill numbers [65,66]). This method assesses the relative importance of species occurrence and abundance on α- and β-diversity [65,67]. Assessing these diversity metrics is important in the tropics because most tree species have small populations, and the scale of effect of landscape structure is expected to differ among species with varying abundances [60,68]. Consequently, diversity metrics that account for species abundance are expected to have smaller scales of effect than those measured by species occurrence only (presence-absence) [42,43]. Hill numbers (${}^{q}D$) are in units of species, which permit the characterization of species abundance distribution of a community and provide complete information about the community diversity [66,67]. We first calculated the patch gamma (γ) diversity of order $q$ as follows:

$$ {}^{q}D_{\gamma} = \left(\sum_{i=1}^{S} \bar{p}_i^{q}\right)^{\frac{1}{(1-q)}} $$

where $\bar{p}_i$ denotes the mean relative abundance of the $i$th species in the $N$ 1-m$^2$ plots [65,69], and $q$ is a parameter that determines the sensitivity of the measure to the relative abundances. Since this measure is undefined for q = 1, the γ-diversity of order one can be estimated with the following formula:

$$ {}^{1}D_{\gamma} = exp\left(-\sum_{i=1}^{S} \bar{p}_i \log \bar{p}_i\right) $$

The ${}^{0}D$ represents the species richness (hereafter called all species), which is not sensitive to individual abundances [65,69]. The ${}^{1}D$ (equivalent to the exponential of Shannon's entropy index) weights each species according to its abundance in the community, and could be interpreted as the number of equally common species which does not favor rare nor abundant species (hereafter called typical species) [65]. Finally, the ${}^{2}D$ (equivalent to the inverse Simpson index) gives a high weight to abundant species and could be understood as the effective number of the most abundant species (hereafter called dominant species) [67,70]. We then considered the 1-m$^2$ plots to calculate the alpha (α) diversity with the formula:

$$ {}^{q}D_{\alpha} = \left(\frac{1}{N}\sum_{i=1}^{S} p_{i1}^{q} + \frac{1}{N}\sum_{i=1}^{S} p_{i2}^{q} + \cdots\right)^{\frac{1}{(1-q)}} $$

Where $p_i$ denotes the relative abundance of the $i$th species in each of the $N$ 1-m$^2$ plots. We estimated α-diversity when q = 1 as:

$$ {}^{1}D_{\alpha} = exp\left\{-\frac{1}{N}\left(\sum_{i=1}^{S}(p_{i1}^{q}\ln p_{i1}^{q}) + \sum_{i=1}^{S}(p_{i2}^{q}\ln p_{i2}^{q}) + \cdots\right)\right\} $$

Afterward, we used the resulting $\alpha_{\text{plot}}$- and $\gamma_{\text{patch}}$-diversity to calculate the "effective number of completely distinct assemblages" within each patch (β-diversity) as follows [65]:

$$ {}^{q}\beta_{plot} = \frac{{}^{q}\gamma_{patch}}{{}^{q}\alpha_{plot}} $$

This β-diversity ranges between one (when the assemblages of all 1-m$^2$ plots are identical) and $N$ (when the assemblages of the $N$ 1-m$^2$ plots are completely different from each other). We used the package *vegan* in R [71].

## Landscape metrics and multi-scale assessment

We employed a multispectral SPOT-5 satellite image of 10 × 10 m pixel resolution recorded in March 2013 to carry out a supervised classification using the GRASS GIS software [72]. We

**Table 1. Description, metric type and ecological relevance of the landscape metrics measured at class level employed in the study.**

| Metric | Description | Metric type | Ecological relevance | References |
|---|---|---|---|---|
| Forest cover (FC) | Percentage of landscape area covered by old-growth forest | Composition | Indicator of the landscape-scale habitat amount. It is positively associated with availability of propagules and seed dispersal | [31,60] |
| Secondary forest (SF) | Percentage of landscape area covered by secondary forest (regrowth of ≤15 years) | Composition | Measurement related to impacts on the dynamics and trajectories of floristic change within forest patches | [32,74] |
| Patch density (PD) | Number of forest patches per landscape area (n/ha) | Configuration | Fragmentation metric associated with increasing edge effects, the number of seed sources in the landscape and with landscape connectivity of seed dispersers in the tropics | [47,75] |
| Aggregation index (AI) | Percentage of like-adjacencies between forest patches. Maximum aggregation indicates a single, compact patch | Configuration | Aggregated patches facilitate the inter-patch movement, promoting dispersal at smaller spatial scales. These conditions allow the persistence of species in highly fragmented landscapes through complementation/supplementation dynamics | [8,76,77] |
| Patch isolation (PI) | Mean distance between forest patches within the landscape | Configuration | Metric employed to estimate connectivity on seed dispersal, altering seed abundance/richness and floristic differentiation among patches | [31,78] |
| Edge contrast index (EC) | Average degree of edge contrast between forest patches and their immediate neighborhoods | Configuration | High percentages of contrasting edges reduce the connectivity of vertebrate seed dispersers and terrestrial mammals in tropical forests | [6,79] |

https://doi.org/10.1371/journal.pone.0253284.t001

used sampling points representing seven land-cover classes, including the following: 1) old-growth forest (undisturbed rainforest), 2) secondary forest (rainforest regrowth), 3) floodplains (swamp forests of bamboo and palm trees subjected to periodic flooding), 4) arboreal crops (oil-palm plantations), 5) cattle pasture (induced grassland for cattle raising), 6) anthropogenic cover (roads and urban settlements), and 7) water bodies (rivers and permanently flooded areas). The overall classification accuracy was 79%.

We then calculated six landscape metrics (Table 1) considered as drivers of seed and seedling community diversity [47,60]. The composition metrics included the percentages of old-growth forest (FC) and secondary forest (SF) covers, whereas the configuration metrics were the number of forest patches per landscape area (patch density; PD), the adjacency among forest patches (aggregation index; AI), the mean distance among forest patches (patch isolation; PI), and the edge contrast index (EC). We calculated the EC using quality values for matrix covers that describe both their capacity to reduce edge effects and the permeability for terrestrial mammals' movement. These values were based on the assumption that edge effects increase and mammals' presence declines along a gradient of habitat loss and relates the percentage of each land-cover type within the landscape matrix to its relative quality [2,6]. We ranked the relative quality of each land-cover type based on the suitability of vegetation structure for regulating edge microclimate and for mammal feeding, movement and/or habitat on a seven-point scale, including the following: 1 (water bodies, with the lowest suitability); 2 (anthropogenic cover); 3 (cattle pasture); 4 (arboreal crops); 5 (floodplains); 6 (secondary forest); and 7 (old-growth forest, representing the highest suitability). To obtain a more robust and realistic representation of landscape structure effects, we estimated the area-weighted mean of the EC index [73].

We neither considered patch size nor patch shape because both variables were highly correlated ($r = 0.81$), and none of them had significant effects on any of the α- and β-diversity metrics (Table A in S1 Text).

We followed the recommendation about the landscape radius that best predicts biological responses, which is 0.3–0.5 times the maximum dispersal distance of seed dispersers and herbivore mammals foraging behavior [41,45]. The maximum dispersal distance of arboreal seed dispersers and terrestrial mammals in the study region ranges between 500 and 4000 m [54,80–82].Thus, we estimated six landscape metrics within 13 circular buffers (300 to 1500 m radius, at 100 m intervals) from the center of each focal patch (Fig 1C). We only found correlations between AI and FC between the 900–1500 m radius (Table C in S1 Text). The distance among sampling sites was of 3602.56 ± 1932.21 m (mean ± standard deviation), and were randomly aggregated (Clark-Evans $R = 1.02$; $p = 0.86$) [83]. The overlapping between buffers of nearby sampling points increased with buffer sizes (Table D in S1 Text). However, we did not find spatial autocorrelation between the distance of sampling sites and the diversity metrics (Table E in S1 Text), nor between the distance of sampling sites and the landscape metrics across the 13 buffer sizes (Table F in S1 Text).

## Statistical analyses

Firstly, we estimated the scale of effect of each landscape metric using linear models. We fitted a diversity metric with a single landscape metric. We repeated this process on each buffer size and obtained 13 linear models of the same landscape metric. We verified variable normality with a Shapiro-Wilk test [84]. Then, we assessed the predictive power of each model using a leave-two-out cross-validation. This analysis splits the dataset in two sections; the first split contains the diversity data from 14 patches as calibration data and fits a linear model which is employed to predict the diversity values of the second split, which contains the two remaining values (validation data). We calculated the sums of squares between the estimated and observed diversity values employed as validation data. We repeated this procedure for each possible split of the data set and calculated the average sum of squares ($\bar{SS}_{cv}$). Next, we employed the $\bar{SS}_{cv}$ to calculate the proportion of the variation that can be predicted by the model using the leave-two-out coefficient of determination ($R^2_{CV}$) as follows:

$$R^2_{CV} = 1 - \frac{\bar{SS}_{cv}}{\frac{1}{n}\sum_{i=1}^{n}(y_i - \bar{y})^2}$$

where $\bar{SS}_{cv}$ is the average sum of squares obtained from the leave-two-out cross-validation, $y_i$ is the diversity value for the $i^{th}$ patch, $\bar{y}$ is the mean value of a given diversity metric, and $n$ is the number of patches. The $R^2_{CV}$ ranges between $-\infty$ (indicating the model has a worse prediction power than the null model) and one (indicating the model predicts the validation data perfectly), and can be used to compare between response variables and scales of measurement [85–87]. Finally, we plotted the resulting 13 $R^2_{CV}$ values and selected the one with the strongest response as the scale of effect for that landscape metric (Figs A and B in S1 Text [45]). We repeated this procedure for each diversity and landscape metric ($N = 468$ models).

Flawed study design, such as selecting a narrow range of spatial extents (smallest to largest) or by establishing wide distances among the analyzed extents, can lead to inaccurate estimations of the scale of effect [41,43]. Therefore, we estimated the uncertainty around the selected scale of effect through bootstrapping [88]. We randomly resampled the data from $n$ patches, with resampling, from the set of 16 patches 1000 times. Then, we estimated the scale of effect for each resampled data set as described above and summed the number of times (out of 1000) that each buffer size was selected as the scale of effect. Although the uncertainty around the selected scale of effect varied among landscape- and diversity-metrics, the most frequently selected scale of effect based on the bootstrapped analysis matched with the scale of effect that we selected based on the highest $R^2_{CV}$ value (Figs C and D in S1 Text). Additionally, we employed the data from the bootstrapped analysis to assess if the scale of effect differed among α- and β-diversity metrics and among landscape metrics. We only employed the data from the selected landscape metrics in the previous step.

Thereafter, we evaluated the effects of landscape metrics on diversity metrics through multiple linear models with a normal distribution. We constructed a global model for each of the

**Table 2. Global model of each diversity metric employed for the model selection assessment.**

| α-diversity | β-diversity |
|---|---|
| $\boldsymbol{\alpha_{all} \sim AI_{600}+PI_{1200}+SF_{600}}$ | $\beta_{all} \sim EC_{800}+PD_{1400}$ |
| $\boldsymbol{\alpha_{typical} \sim AI_{600}+PI_{1200}+SF_{600}}$ | $\beta_{typical} \sim PD_{500}+SF_{1300}$ |
| $\boldsymbol{\alpha_{dominant} \sim AI_{600}+PI_{1200}+SF_{600}}$ | $\beta_{dominant} \sim AI_{500}+PD_{500}$ |

The landscape metrics are the aggregation index (AI), the edge contrast index (EC), patch isolation (PI), and the percentage of secondary forest (SF). The subscript numbers indicate the scale of effect (radius meters) of each landscape metric.

https://doi.org/10.1371/journal.pone.0253284.t002

α- and β-diversity metrics using only the landscape metrics at the scale of effect identified in the previous step (Table 2). All models were additive due to our limited sample size of 16 forest patches.

We did not find spatial autocorrelation between the distance of sampling sites and the model residuals of the selected landscape metrics (Table G in S1 Text). Therefore, we assured samples independency because spatial autocorrelation of model residuals–an indicator of pseudoreplication–is associated with the proximity between sampling sites [89,90]. We estimated the variance inflation factor (VIF) of landscape metrics beforehand with the *car* package [91]. Since we did not find significant collinearity ($VIF \geq 4$) between the explanatory variables [92], we employed the *dredge* function of the *MuMIn* package [93] to create all possible combinations of explanatory variables plus the null model (only the intercept). We ranked the models using the Akaike's information criterion corrected for small samples (AICc) and selected those models with a AICc difference lower than two ($\Delta AICc < 2$) as the best supported by the data [94].

Finally, we assessed the importance and the relative effect of each landscape metric measured at the scale of effect on each diversity value using an information theory approach and multimodel inference [94]. For this, we selected the subset of models that had 95% probability of containing the best model using the summed Akaike weights ($w_i$) of ranked models until $\Sigma w_i \leq 0.95$. We employed the $w_i$ of the model's subset to calculate the relative importance and the model-averaged parameter estimates of each explanatory variable. We considered as influential variable those for which the unconditional standard error (USE) did not include zero in the averaged parameters. We carried out all statistical analysis in the R 3.5.2 statistical computing environment [95].

## Results

We recorded a total of 1334 tree seedlings from 29 families, 51 genera and 72 species in 160 $m^2$ (Table H in S1 Text). Most seedlings were animal-dispersed species (1258 individuals; 94.3%), belonging to 24 families, 42 genera and 58 species. Mean species density of the animal-dispersed seedlings were 11.37 ± 2.96 species/10 $m^2$ (range 6–16 species; mean ± standard error), mean seedling density was 78.62 ± 34.03 individuals/10 $m^2$ (range 10–129 individuals). The most abundant species was *Inga punctata*,—an early successional and disturbance tolerant tree species -, which represented 33% of all individuals sampled, followed by the late-successional tree species *Ampelocera hottlei* (13%) and *Brosimum alicastrum* (11%). Less than half of the species (ca. 31%) were restricted to one patch. We found that α- and β-diversity metrics were significantly higher than the other metrics when species abundances were not considered (Fig E in S1 Text).

### Scale of effect and importance of landscape structure on seedling diversity

We observed that scale of effect of landscape composition and configuration was similar for all α-diversity metrics (Fig 2A–2C). The bootstrapped data showed the scale of effect of α-

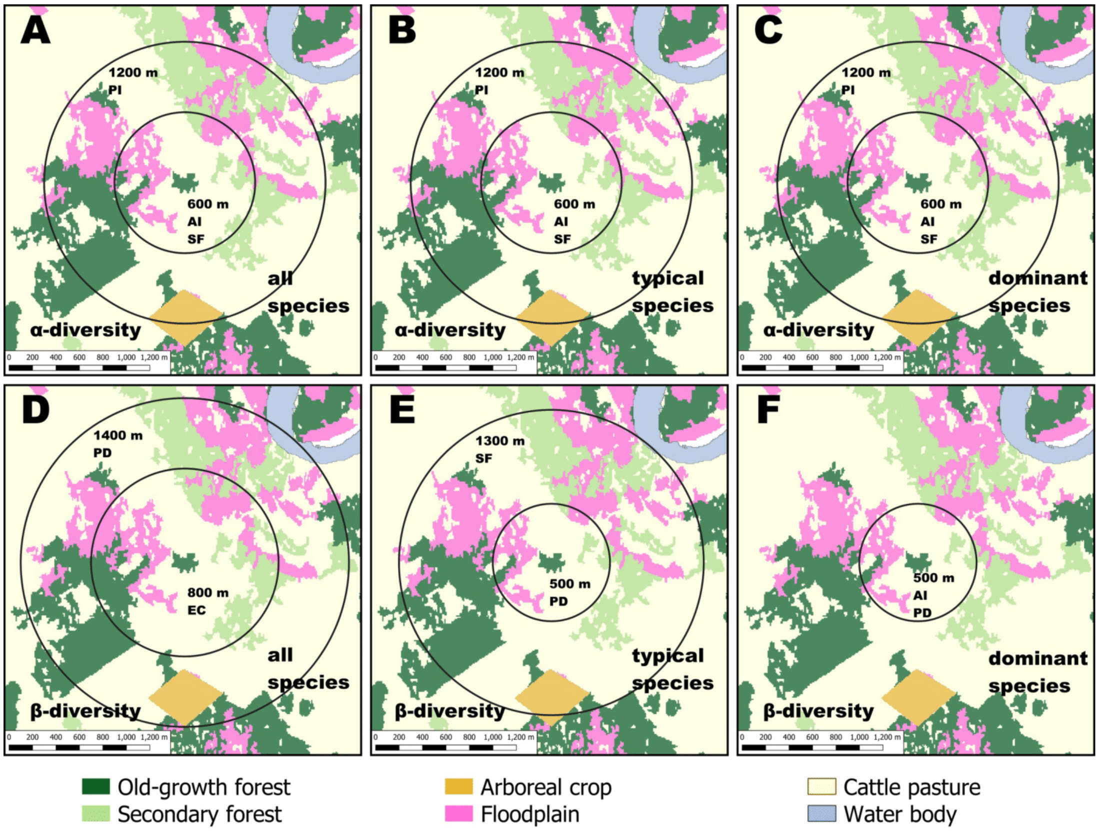


**Fig 2. Scale of effect of landscape metrics on seedling diversity within forest patches in a fragmented tropical rainforest in southern Mexico.** (A-C) Scale of effect on α-diversity. (D-F) Scale of effect on β-diversity. The landscape radius in meters and the associated landscape metrics are within each buffer. The landscape metrics are the aggregation index (AI), the edge contrast index (EC), the patch density (PD), patch isolation (PI), and the percentage of secondary forest (SF).

https://doi.org/10.1371/journal.pone.0253284.g002

diversity was the same for typical (807.52 ± 140.03 m; mean ± standard error) and dominant species (801.73 ± 132.57 m), whereas the scale of effect for all species was slightly lower (764.27 ± 144.06 m). The best-fitting models showed a positive effect of patch aggregation, and a negative effect of patch isolation and secondary forest cover (Table I in S1 Text). When assessing the importance and relative effect of these landscape metrics, we found that secondary forest was strongly associated ($\sum w_i > 0.75$; Fig 3A) to α-diversity loss, regardless diversity metrics (Fig 3C). We also found an important contribution of patch aggregation in species richness (Fig 3C).

In contrast, we found that scale of effect varied among β-diversity metrics (Fig 2D–2F). The bootstrapped data indicated that the scale of effect decreased in the predicted order (i.e. dominant < typical < all), where the scale of effect was higher for β-diversity of all species (1021.07 ± 133.74 m) than for typical (826.54 ± 84.72 m) and dominant species (577.91 ±101.79 m). The three β-diversity metrics were positively associated with patch

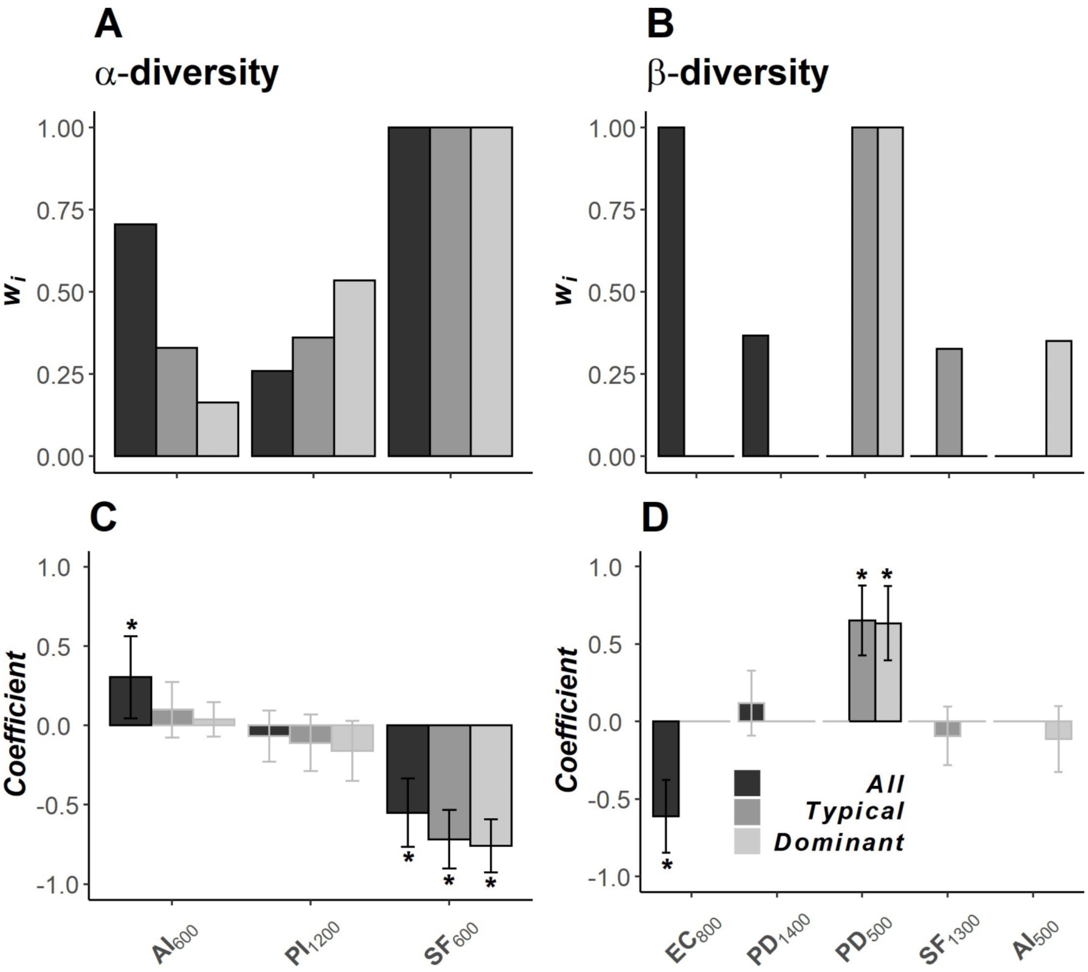


**Fig 3. Importance and relative effects of the landscape metrics on seedling diversity within forest patches in a fragmented tropical rainforest in southern Mexico.** We included the 95% confidence set of models for (A and C) α- and (B and D) β-diversity. The importance of each variable is represented by the sum of the Akaike weights ($\Sigma w_i$). The effects of each covariate were estimated through a model-averaged parameter estimate of information-theoretic-based model selection and multimodel inference. The whiskers represent the unconditional standard error (USE) and the asterisks indicate the influential variables (those for which the USE did not include zero). The landscape metrics are the aggregation index (AI), the edge contrast index (EC), the patch density (PD), patch isolation (PI), and the percentage of secondary forest (SF). The subscript numbers indicate the scale of effect of each variable.

https://doi.org/10.1371/journal.pone.0253284.g003

density, and negatively affected by secondary forest cover, patch aggregation, and edge contrast (Table I in S1 Text). The Akaike weighted values showed that landscape configuration was important for β-diversity (Fig 3B). Patch density was particularly relevant for β-diversity of typical and dominant species, while edge contrast was more important for β-diversity of all species (Fig 3D).

## Discussion

### Landscape effects on seedling diversity

This is the first study to assess the effects of landscape structure on the α- and β-diversity of the animal-dispersed tree seedling community at multiple spatial scales (but see [30]). As expected, we found that landscape composition affected α-diversity whereas β-diversity was influenced by landscape configuration. We also observed that the scale of effect varied among β-diversity metrics in the predicted order.

**Effects on α-diversity.** We found a decrease of α-diversity in forest patches surrounded by secondary forests, which are documented to exert a significant influence in the composition of tree communities within forest patches [32,33,96]. Altered microclimate and the opening of canopy gaps in small patches promote the proliferation of early-successional tree species while reducing the richness and abundance of old-growth species [74,97]. The arrival of early-successional species is driven by short-distance dispersal of generalist seed dispersers [98–100]. This may explain the high abundance of *I. punctata* seedlings, a species from seasonally flooded rainforests that is commonly found in secondary forests and as isolated trees in pastures [101–103]. Additionally, secondary forests restrict the arrival of some forest-specialist seed dispersers to forest patches at similar landscape sizes (100-ha or 564-m radius) [53,104] than the observed scale of effect of secondary forest on α-diversity (600-m radius). Thus, our findings support the contribution of the surrounding matrix on tree diversity within forest patches [32,33]. This results should be taken cautiously, because secondary forests are fundamental for forest regeneration and restoration in HMTLs [105,106], whether by increasing habitat amount, attracting pollinators and seed dispersers, buffering edge effects, and by providing seed sources that maximize the large-scale regeneration of disturbed abandoned fields [107,108]. Thus, conservation strategies in HMTLs should preferably promote secondary forests than agricultural fields in the surrounding matrix of forest patches [105,109].

Contrary to our predictions, we observed that α-diversity was also affected by landscape configuration, supporting the fragmentation threshold hypothesis [38]. The positive effect of patches aggregation on seedling richness suggests that seed sources and seed dispersal can be sustained where patches are highly aggregated. Previous studies predicted that dispersal distance of species may be limited in highly deforested landscapes, favoring species response to local characteristics, such as patches aggregation across the landscape [110,111]. In our study, the selected landscapes presented a low percentage of forest cover across the 13 buffer sizes (19.01±5.1%; mean ± standard deviation). The aggregation of forest patches facilitates the inter-patch movement of forest-dependent species in landscapes with low forest cover, where the distribution of species home range comprises several patches [77,112]. For example, frugivore birds can adjust their movement behavior according to landscape configuration, flying larger distances and visiting more forest patches in landscapes with decreasing forest cover [113]. These changes in the spatial configuration of forest patches also affect species foraging–which relies in resources from nearby patches (i.e. landscape supplementation dynamics [7])–and therefore, seed dispersal patterns. Some studies indicate that fruit removal increased and dispersal distance decreased where plants aggregation is high [114]. Thus, colonization of tree species in highly disturbed landscapes may be operating at smaller spatial scales [42].

**Effects on β-diversity.** Landscape configuration affected β-diversity, but seedling responses varied among diversity metrics. The β-diversity of all species was negatively associated with edge contrast of old-growth forests in the 800-m radius landscapes. The loss of β-diversity by edge contrast indicates an homogenization of seedling assemblages by edge effects, as well as by a limited heterogeneity of microclimate conditions, a processes observed in HMTLs with low forest cover [18,115]. Additionally, edge contrast can influence the presence of herbivorous mammals within patches [6], which promote β-diversity of tree seedlings through secondary seed dispersal, and seedling herbivory and trampling [22,23]. Accordingly, the association between seedling β-diversity and edge contrast suggests that low exposure to edge effects, a more heterogeneous microclimate and the presence of density-independent factors (i.e., terrestrial herbivores) promotes a broader species coexistence [35].

The overall increment of β-diversity for the typical and dominant species by patch density is not surprising. According to the "biotic differentiation hypothesis", the limited exchange of seeds and differences in disturbance regimes across forest patches promote floristic differentiation in highly deforested landscapes [68,96]. Spatial patterns that limit the species exchange influence β-diversity in the tropics [17,116]. These effects are intensified in fragmented rainforests, where differences in forest cover amount, disturbance source (i.e., slash-and-burn practices or tree removal by machinery), degree of fragmentation and connectivity, lead to contrasting regeneration dynamics within patches [96,117]. Consequently, the establishment of a wider array of species is facilitated by landscape configuration and a less evenly distributed number of individuals among dominant species [34,77]. These conditions can prevent competitive exclusion (i.e. excluding strong competitors that are weak dispersers), spread the risk of simultaneous extinctions and increase landscape complementation, favoring β-diversity [8,68]. This is consistent with the mechanisms involved in β-diversity increase through the colonization of different opportunistic species and the extinction of shared species among sites [118]. Thus, fragmentation is having positive effects on seedling diversity by facilitating the arrival and establishment of species otherwise poorly represented in old-growth forests [8].

## Scale of landscape effect on diversity metrics

Our results did not support the predicted order of the scale of effect (dominant < typical < all) for α-diversity metrics, which also showed a substantial uncertainty in the selected scale of effect (Fig C in S1 Text). These variations reinforce the findings that scale of effect does not vary in a predictable order among response variables [43,88]. The inconsistencies observed on α-diversity metrics may be associated to the temporal scale and landscape composition and configuration variables assessed [88]. Temporal scale variations regarding tree phenology and movement/foraging patterns of seed dispersers in fragmented HMTLs [54,119] may be obscuring the expected differences in the scale of effect. A study in the same region found that scale of effect of landscape composition on seed rain followed the predicted order [31,60]. The sampling period however, comprised a whole year in order to control for the temporal variation in the seed rain [60]. Additionally, the scale of effect was possibly influenced by the low forest cover of the study area (<25%), which can reduce the expected scale of effect to local factors, such as patch size [42]. However, comparative studies in HMTLs have found non-significant differences in the scale of effect among regions with contrasting disturbance levels [54,60]. Further studies including comparative assessments among regions are needed to fully understand the importance of regional context in landscape metrics and the scale of effect.

On the contrary, the scale of effect observed among β-diversity metrics did follow the predicted order. The scale of effect of edge contrast is similar to those observed for matrix contrast on stem density of understory vegetation in los Tuxtlas, Mexico (798 m), and for matrix openness in seed abundance and species richness of animal-dispersed seeds and forest generalist saplings (798–977 m) [30,31,47]. These studies suggested that matrix contrast operates at smaller scales, where it drives local edge effects involved in the mortality of animal-dispersed seedling species, and favors the dispersal and establishment of wind-dispersed seeds [31,47]. This also holds true for the scale of effect of patch density in our study (500 m) and those observed for richness of old-growth forest specialist- saplings (500 m) in the study area [30].

Patch density is positively related to habitat heterogeneity and to the number of subpopulations in the landscape, increasing community dissimilarity [8,35]. These findings suggest that matrix contrast is limiting the dispersal and recruitment of lower-density species, whereas forest fragmentation is promoting the coexistence of higher-density species.

### Study limitations

Our results are conservative as a larger number of landscapes are desirable to making further inferences. Also, the lack of information related to species composition of secondary forest trees and seed rain within forest patches limit our understanding about the contribution of secondary forests to seedlings α-diversity [60,120]. Finally, our study did not consider a long-term monitoring of tree seedlings to elucidate the contribution of patch microclimate, fruiting events, foraging behavior of seed dispersers, disturbance regimes, and density-dependent mortality factors, which strongly influence the composition and dynamics of seedling communities in the tropics [16,121,122].

For seedlings β-diversity, our findings should be taken cautiously, because we inferred the presence of mammals only through landscape metrics, regardless mammal species have different responses to landscape structure [6]. Furthermore, herbivorous mammal effects on seedling diversity vary according to the incidence, relative abundance and body mass [23,24], as well as by population fluctuations and food quality and availability [123]. In turn, these biological responses (i.e. abundance, richness, incidence and body size) are affected by landscape structure at varying spatial scales [39,42]. Finally, the mechanisms of β-diversity loss are highly sensitive to the ratio of winner-loser species and the spatial scale at which communities are assessed [118]. Nevertheless, the use of structural equation modeling in multi-scale assessments have permitted analyzing the direct and cascading effects of landscape structure on different biological responses in HMTLs [47]. This represents a promising approach to evaluate the response of interactions-mediated patterns and processes to landscape composition and configuration. Thus, further studies regarding cascading effects of landscape structure on different biological responses of herbivorous mammals and tree seedling communities are needed to fill these knowledge gaps.

## Conclusions and conservation implications

Contrary to studies performed in the same area [30], we found that forest fragmentation is a strong driver of seedling diversity at smaller spatial scales in highly deforested rainforests. Severe fragmentation of rainforests will occur in the short term [4], urging economic incentives and innovations in policy and governance that favor forest regrowth, matrix quality and patches number.

Implementation of payment for ecosystem services' schemes and REDD+ programs can prevent further loss of old-growth and secondary forests while promoting agroforestry management [124,125]. Favoring matrix quality and configurational patterns that increase habitat heterogeneity are feasible in landscapes with land-sharing schemes of smallholder agriculture [126]. In these rural landscapes, diversification of small-scale agroecosystems, intensification of agriculture and reduction of cattle ranching promotes forest regeneration and food security [127,128]. Additionally, enactment of programs of enrichment planting of trees with local commercial/ecological importance, and forest management policies that permit local governance for harvesting timber and non-timber products are needed to enhance the management and diversity of secondary forests [129]. Finally, is necessary to map and classify the biophysical and socio-ecological land use dimensions of land covers and naturally regenerated forests to identify restoration opportunities for assisted or unassisted natural regeneration [129,130].

Novel institutional and policy approaches in Costa Rica have proven that decreasing meat exports while supporting payment for environmental services, agricultural intensification and native species plantations lead to a forest transition in less than 15 years [131,132]. Incorporation of these conservation, management and restoration guidelines are urgently needed to preserve regeneration of forest patches and future conservation value of HMTLs.

## Supporting information

**S1 Text. Supporting file.**
(DOCX)

## Acknowledgments

We thank to the people of Quiringüicharo for their hospitality and support. We acknowledge the logistical and technical support provided by J. Manuel Lobato-García during the fieldwork. We thank Gilberto Jamangapé and Rafael Lombera for plant identification. Natura y Ecosistemas Mexicanos A.C. and Arca de Noe provided logistical assistance and accommodation. Adriana L. Luna-Nieves, Bianca A. Santini and four anonymous reviewers provided very valuable comments on earlier versions of the manuscript. SNA is a doctoral student from the Programa de Doctorado en Ciencias Biomédicas, Universidad Nacional Autónoma de México (UNAM), and Consejo Nacional de Ciencia y Tecnología (CONACyT).

## Author Contributions

**Conceptualization:** Sergio Nicasio-Arzeta, Julieta Benítez-Malvido.

**Data curation:** Sergio Nicasio-Arzeta.

**Formal analysis:** Sergio Nicasio-Arzeta, Isela E. Zermeño-Hernández.

**Funding acquisition:** Julieta Benítez-Malvido.

**Investigation:** Sergio Nicasio-Arzeta, Julieta Benítez-Malvido.

**Methodology:** Sergio Nicasio-Arzeta.

**Project administration:** Julieta Benítez-Malvido.

**Resources:** Julieta Benítez-Malvido.

**Software:** Sergio Nicasio-Arzeta.

**Supervision:** Julieta Benítez-Malvido.

**Validation:** Sergio Nicasio-Arzeta, Julieta Benítez-Malvido.

**Visualization:** Sergio Nicasio-Arzeta.

**Writing – original draft:** Sergio Nicasio-Arzeta, Susana Maza-Villalobos.

**Writing – review & editing:** Sergio Nicasio-Arzeta, Isela E. Zermeño-Hernández, Susana Maza-Villalobos, Julieta Benítez-Malvido.

## References

1. Mace G, Masundire H, Lead JB, Ricketts T, Brooks T, Hoffmann M, et al. Biodiversity. In: Carpenter SR, Pingali PL, Bennett EM, Zurek MB, editors. Ecosystems and Human Well-being: Scenarios. Island Press; 2005. pp. 77–122.

2. Gardner TA, Barlow J, Chazdon R, Ewers RM, Harvey CA, Peres CA, et al. Prospects for tropical forest biodiversity in a human-modified world. Ecol Lett. 2009; 12: 561–582. https://doi.org/10.1111/j.1461-0248.2009.01294.x PMID: 19504750
3. Kim DH, Sexton JO, Townshend JR. Accelerated deforestation in the humid tropics from the 1990s to the 2000s. Geophysical Research Letters. John Wiley & Sons, Ltd; 2015. pp. 3495–3501. https://doi.org/10.1002/2014GL062777 PMID: 27656010
4. Taubert F, Fischer R, Groeneveld J, Lehmann S, Müller MS, Rödig E, et al. Global patterns of tropical forest fragmentation. Nature. 2018; 554: 519–522. https://doi.org/10.1038/nature25508 PMID: 29443966
5. Hernández-Ruedas MA, Arroyo-Rodríguez V, Meave JA, Martínez-Ramos M, Ibarra-Manríquez G, Martínez E, et al. Conserving tropical tree diversity and forest structure: The value of small rainforest patches in moderately-managed landscapes. Mason NW, editor. PLoS One. 2014; 9: e98931. https://doi.org/10.1371/journal.pone.0098931 PMID: 24901954
6. Garmendia A, Arroyo-Rodríguez V, Estrada A, Naranjo EJ, Stoner KE. Landscape and patch attributes impacting medium- and large-sized terrestrial mammals in a fragmented rain forest. J Trop Ecol. 2013; 29: 331–344. https://doi.org/10.1017/S0266467413000370
7. Dunning JB, Danielson BJ, Pulliam HR. Ecological processes that affect populations in complex landscapes. Oikos. 1992; 65: 169–175. https://doi.org/10.2307/3544901
8. Fahrig L. Ecological Responses to Habitat Fragmentation Per Se. Annu Rev Ecol Evol Syst. 2017;48: annurev-ecolsys-110316-022612. https://doi.org/10.1146/annurev-ecolsys-110316-022612
9. Cudney S, Toledo-Aceves T, Andrade-Ponce GP. Does patch quality drive arboreal mammal assemblages in fragmented rainforests? Perspect Ecol Conserv. 2020. https://doi.org/10.1016/j.pecon.2020.12.004
10. Wies G, Nicasio Arzeta S, Martinez Ramos M. Critical ecological thresholds for conservation of tropical rainforest in Human Modified Landscapes. Biol Conserv. 2021; 255: 109023. https://doi.org/10.1016/j.biocon.2021.109023
11. Crouzeilles R, Curran M, Ferreira MS, Lindenmayer DB, Grelle CEV, Rey Benayas JM. A global meta-Analysis on the ecological drivers of forest restoration success. Nat Commun. 2016; 7: 1–8. https://doi.org/10.1038/ncomms11666 PMID: 27193756
12. Brancalion PHS, Niamir A, Broadbent E, Crouzeilles R, Barros FSM, Almeyda Zambrano AM, et al. Global restoration opportunities in tropical rainforest landscapes. Sci Adv. 2019; 5: 3223–3226. https://doi.org/10.1126/sciadv.aav3223 PMID: 31281881
13. Benitez-Malvido J. Impact of forest fragmentation on seedling abundance in a tropical rain forest. Conserv Biol. 1998; 12: 380–389. https://doi.org/10.1046/j.1523-1739.1998.96295.x
14. Benítez-Malvido J, Lemus-Albor A. The seedling community of tropical rain forest edges and its interaction with herbivores and pathogens. Biotropica. 2005; 37: 301–313. https://doi.org/10.1111/j.1744-7429.2005.00031.x
15. Sánchez-Gallen I, Álvarez-Sánchez FJ, Benítez-Malvido J. Structure of the advanced regeneration community in tropical rain forest fragments of Los Tuxtlas, Mexico. Biol Conserv. 2010; 143: 2111–2118. https://doi.org/10.1016/j.biocon.2010.05.021
16. Harms KEE, Wright SJJ, Calderón O, Hernández A, Herre EA a. Pervasive density-dependent recruitment enhances seedling diversity in a tropical forest. Nature. 2000; 404: 493–5. https://doi.org/10.1038/35006630 PMID: 10761916
17. Condit R, Pitman N, Leigh EG, Chave J, Terborgh J, Foster RB, et al. Beta-diversity in tropical forest trees. Science (80-). 2002; 295: 666–669. https://doi.org/10.1126/science.1066854 PMID: 11809969
18. Nicotra AB, Chazdon RL, Iriarte SVB. Spatial heterogeneity of light and woody seedling regeneration in tropical wet forests. Ecology. 1999; 80: 1908–1926. https://doi.org/10.1890/0012-9658(1999)080[1908:SHOLAW]2.0.CO;2
19. Comita LS, Muller-Landau HC, Aguilar S, Hubbell SP. Asymmetrie density dependence shapes species abundances in a tropical tree community. Science (80-). 2010; 329: 330–332. https://doi.org/10.1126/science.1190772 PMID: 20576853
20. Jordano P. Fruits and frugivory. 2nd ed. In: Fenner M, editor. Seeds: the ecology of regeneration in plant communities. 2nd ed. Wallingford, U.K.: CABI Publishing; 2000. pp. 125–166.
21. Terborgh J, Lopez L, Nuñez P V., Rao M, Shahabuddin G, Orihuela G, et al. Ecological meltdown in predator-free forest fragments. Science (80-). 2001; 294: 1923–1926. https://doi.org/10.1126/science.1064397 PMID: 11729317
22. Camargo-Sanabria AA, Mendoza E, Guevara R, Martínez-Rmos M, Dirzo R. Experimental defaunation of terrestrial mammalian herbivores alters tropical rainforest understorey diversity. Proc R Soc B Biol Sci. 2014;282. https://doi.org/10.1098/rspb.2014.2580 PMID: 25540281

**23.** Villar N, Siqueira T, Zipparro VB, Farah F, Schmaedecke G, Hortenci L, et al. The cryptic regulation of diversity by functionally complementary large tropical forest herbivores. Edwards D, editor. J Ecol. 2019; 1365–2745.13257. https://doi.org/10.1111/1365-2745.13257

**24.** Terborgh J, Nuñez-Iturri G, Pitman NCA, Valverde FHC, Alvarez P, Swamy V, et al. Tree recruitment in an empty forest. Ecology. 2008; 89: 1757–68. https://doi.org/10.1890/07-0479.1 PMID: 18589539

**25.** Tabarelli M, Peres CA, Melo FPL. The "few winners and many losers" paradigm revisited: Emerging prospects for tropical forest biodiversity. Biol Conserv. 2012; 155: 136–140. https://doi.org/10.1016/j.biocon.2012.06.020

**26.** Dirzo R, Young HS, Galetti M, Ceballos G, Isaac NJB, Collen B. Defaunation in the Anthropocene. Science. American Association for the Advancement of Science; 2014. pp. 401–406. https://doi.org/10.1126/science.1251817 PMID: 25061202

**27.** Perfecto I, Vandermeer J. Biodiversity conservation in tropical agroecosystems: A new conservation paradigm. Ann N Y Acad Sci. 2008; 1134: 173–200. https://doi.org/10.1196/annals.1439.011 PMID: 18566094

**28.** Lewis OT, Ewers RM, Lowman MD, Malhi Y. Conservation of tropical forests: maintaining ecological integrity and resilience. In: Macdonald DW, Willis KJ, editors. Key Topics in Conservation Biology 2. John Wiley & Sons; 2013. pp. 222–235. https://doi.org/10.1002/9781118520178

**29.** Rigueira DMG, da Rocha PLB, Mariano-Neto E. Forest cover, extinction thresholds and time lags in woody plants (Myrtaceae) in the Brazilian Atlantic Forest: Resources for conservation. Biodivers Conserv. 2013; 22: 3141–3163. https://doi.org/10.1007/s10531-013-0575-4

**30.** Arasa-Gisbert R, Arroyo-Rodríguez V, Galán-Acedo C, Meave JA, Martínez-Ramos M. Tree recruitment failure in old-growth forest patches across human-modified rainforests. J Ecol. 2021; 1–13. https://doi.org/10.1111/1365-2745.13643

**31.** San-José M, Arroyo-Rodríguez V, Meave JA. Regional context and dispersal mode drive the impact of landscape structure on seed dispersal. Ecol Appl. 2019;0: eap.2033. https://doi.org/10.1002/eap.2033 PMID: 31677313

**32.** Nascimento HEM, Andrade ACS, Camargo JLC, Laurance WF, Laurance SG, Ribeiro JEL. Effects of the Surrounding Matrix on Tree Recruitment in Amazonian Forest Fragments. Conserv Biol. 2006; 20: 853–860. https://doi.org/10.1111/j.1523-1739.2006.00344.x PMID: 16909577

**33.** Ewers RM, Andrade A, Laurance SG, Camargo JLJL, Lovejoy TE, Laurance WF. Predicted trajectories of tree community change in Amazonian rainforest fragments. Ecography (Cop). 2017; 40: 26–35. https://doi.org/10.1111/ecog.02585

**34.** Cook WM, Yao J, Foster BL, Holt RD, Patrick LB. Secondary succession in an experimentally fragmented landscape: community patterns across space and time. Ecology. 2005; 86: 1267–1279. https://doi.org/10.1890/04-0320.

**35.** Tscharntke T, Tylianakis JM, Rand TA, Didham RK, Fahrig L, Batáry P, et al. Landscape moderation of biodiversity patterns and processes—eight hypotheses. Biol Rev. 2012; 87: 661–685. https://doi.org/10.1111/j.1469-185X.2011.00216.x PMID: 22272640

**36.** Benítez-Malvido J, Martínez-Ramos M, Camargo JLC, Ferraz IDK. Responses of seedling transplants to environmental variations in contrasting habitats of Central Amazonia. J Trop Ecol. 2005; 21: 397–406. https://doi.org/10.1017/s0266467405002439

**37.** Galán-Acedo C, Arroyo-Rodríguez V, Estrada A, Ramos-Fernández G. Forest cover and matrix functionality drive the abundance and reproductive success of an endangered primate in two fragmented rainforests. Landsc Ecol. 2019; 34: 147–158. https://doi.org/10.1007/s10980-018-0753-6

**38.** Andren H. Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. Oikos. 1994; 355–366. https://doi.org/10.2307/3545823

**39.** Suárez-Castro AF, Simmonds JS, Mitchell MGE, Maron M, Rhodes JR. The Scale-Dependent Role of Biological Traits in Landscape Ecology: A Review. Curr Landsc Ecol Reports. 2018; 3: 12–22. https://doi.org/10.1007/s40823-018-0031-y

**40.** Smith AC, Fahrig L, Francis CM. Landscape size affects the relative importance of habitat amount, habitat fragmentation, and matrix quality on forest birds. Ecography (Cop). 2011; 34: 103–113. https://doi.org/10.1111/j.1600-0587.2010.06201.x

**41.** Jackson HB, Fahrig L. Are ecologists conducting research at the optimal scale? Glob Ecol Biogeogr. 2015; 24: 52–63. https://doi.org/10.1111/geb.12233

**42.** Miguet P, Jackson HB, Jackson ND, Martin AE, Fahrig L. What determines the spatial extent of landscape effects on species? Landsc Ecol. 2016; 31: 1177–1194. https://doi.org/10.1007/s10980-015-0314-1

**43.** Martin AE. The spatial scale of a species' response to the landscape context depends on which biological response you measure. Curr Landsc Ecol Reports. 2018; 3: 23–33. https://doi.org/10.1007/s40823-018-0030-z

**44.** Wright SJ. Plant diversity in tropical forests: A review of mechanisms of species coexistence. Oecologia. 2002; 130: 1–14. https://doi.org/10.1007/s004420100809 PMID: 28547014

**45.** Jackson HB, Fahrig L. What size is a biologically relevant landscape? Landsc Ecol. 2012; 27: 929–941. https://doi.org/10.1007/s10980-012-9757-9

**46.** Jianguo W, David JL. A spatially explicit hierarchical approach to modeling complex ecological systems: theory and applications. Ecol Modell. 2002; 153: 7–26. https://doi.org/10.1016/S0304-3800(01)00499-9

**47.** Hernández-Ruedas MA, Arroyo-Rodríguez V, Morante-Filho JC, Meave JA, Martínez-Ramos M. Fragmentation and matrix contrast favor understory plants through negative cascading effects on a strong competitor palm. Ecol Appl. 2018; 28: 1546–1553. https://doi.org/10.1002/eap.1740 PMID: 29727519

**48.** Pennington TD, Sarukhán J. Árboles tropicales de México. Manual para la identificación de las principales especies. 3rd ed. Mexico City: Universidad Nacional Autónoma de México; 2005.

**49.** González-Espinosa M, Ramírez-Marcial N, Ruiz-Montoya L. Diversidad biológica en Chiapas. Colegio de la Frontera Sur: Consejo de Ciencia y Tecnología del Estado de Chiapas, Plaza y Valdéz, editors. México; 2005.

**50.** Myers N, Mittermeier R a, Mittermeier CG, da Fonseca G a, Kent J. Biodiversity hotspots for conservation priorities. Nature. 2000; 403: 853–8. https://doi.org/10.1038/35002501 PMID: 10706275

**51.** Carabias J, De la Maza J, Cadena R. Conservación y desarrollo sustentable en la Selva Lacandona: 25 años de actividades y experiencia. Mexico City: Natura y Ecosistemas Mexicanos; 2015.

**52.** Kolb M, Galicia L. Scenarios and story lines: drivers of land use change in southern Mexico. Environ Dev Sustain. 2018; 20: 681–702. https://doi.org/10.1007/s10668-016-9905-5

**53.** Carrara E, Arroyo-Rodríguez V, Vega-Rivera JH, Schondube JE, de Freitas SM, Fahrig L. Impact of landscape composition and configuration on forest specialist and generalist bird species in the fragmented Lacandona rainforest, Mexico. Biol Conserv. 2015; 184: 117–126. https://doi.org/10.1016/j.biocon.2015.01.014

**54.** Galán-Acedo C, Arroyo-Rodríguez V, Estrada A, Ramos-Fernández G. Drivers of the spatial scale that best predict primate responses to landscape structure. Ecography (Cop). 2018; 41: 2027–2037. https://doi.org/10.1111/ecog.03632

**55.** Nicasio-Arzeta S, Zermeño-Hernández IE, Maza-Villalobos S, Benítez-Malvido J. Landscape structure shapes tree seedlings' diversity at multiple spatial scales in a fragmented tropical rainforest. bioRxiv. bioRxiv; 2019. p. 826339. https://doi.org/10.1101/826339

**56.** Martínez E, Ramos-A. CH, Chiang F. Lista florística de la Lacandona, Chiapas. Bot Sci. 1994; 0: 99–177. https://doi.org/10.17129/botsci.1430

**57.** Sousa M. Adiciones al género Inga para la flora Mesoamericana. Acta botánica Mex. 2009; 89: 25–41.

**58.** Ibarra-Manríquez G, Cornejo-Tenorio G. Diversidad de frutos de los árboles del bosque tropical perennifolio De México. Acta botánica Mex. 2010; 104: 51–104.

**59.** Ibarra-Manríquez G, Martínez Ramos M, Oyama K. Seedling functional types in a lowland rain forest in Mexico. Am J Bot. 2001; 88: 1801–1812. https://doi.org/10.2307/3558356 PMID: 21669613

**60.** San-José M, Arroyo-Rodríguez V, Jordano P, Meave JA, Martínez-Ramos M. The scale of landscape effect on seed dispersal depends on both response variables and landscape predictor. Landsc Ecol. 2019; 1–12. https://doi.org/10.1007/s10980-019-00821-y

**61.** Missouri Botanical Garden. Tropicos.org. 2019 [cited 4 Jun 2019]. Available: https://www.tropicos.org/.

**62.** Chao A, Ma KH, Hsieh TC, Chiu C-H. User's Guide for Online Program SpadeR (Species-richness Prediction And Diversity Estimation in R). Taiwan; 2016.

**63.** Chao A, Lee SM. Estimating the number of classes via sample coverage. J Am Stat Assoc. 1992; 87: 210–217. https://doi.org/10.1080/01621459.1992.10475194

**64.** Chao A, Jost L. Coverage-based rarefaction and extrapolation: Standardizing samples by completeness rather than size. Ecology. 2012; 93: 2533–2547. https://doi.org/10.1890/11-1952.1 PMID: 23431585

**65.** Jost L. Partitioning diversity into independent alpha and beta components. Ecology. 2007; 88: 2427–2439. https://doi.org/10.1890/06-1736.1 PMID: 18027744

**66.** Jost L. Entropy and diversity. Oikos. 2006; 113: 363–375. https://doi.org/10.1111/j.2006.0030–1299.14714.x

**67.** Chao A, Chiu CH, Hsieh TC. Proposing a resolution to debates on diversity partitioning. Ecology. 2012; 93: 2037–2051. https://doi.org/10.1890/11-1817.1 PMID: 23094376

**68.** Arroyo-Rodríguez V, Rös M, Escobar F, Melo FPL, Santos BA, Tabarelli M, et al. Plant β-diversity in fragmented rain forests: Testing floristic homogenization and differentiation hypotheses. J Ecol. 2013; 101: 1449–1458. https://doi.org/10.1111/1365-2745.12153

**69.** Tuomisto H. A diversity of beta diversities: Straightening up a concept gone awry. Part 1. Defining beta diversity as a function of alpha and gamma diversity. Ecography (Cop). 2010; 33: 2–22. https://doi.org/10.1111/j.1600-0587.2009.05880.x

**70.** Jost L. The relation between evenness and diversity. Diversity. 2010; 2: 207–232. https://doi.org/10.3390/d2020207

**71.** Oksanen J, Blanchet FG, Friendly M, Kindt R, Legendre P, McGlinn D, et al. vegan: Community Ecology Package. 2.3–3. 2019. Available: https://cran.r-project.org/web/packages/vegan/index.html.

**72.** GRASS Development Team. Geographic Resources Analysis Support System (GRASS GIS) Software, Version 7.2. 2017. Available: http://grass.osgeo.org.

**73.** Li BL, Archer S. Weighted mean patch size: A robust index for quantifying landscape structure. Ecol Modell. 1997; 102: 353–361. https://doi.org/10.1016/S0304-3800(97)00071-9

**74.** Laurance WF, Nascimento HEM, Laurance SG, Andrade AC, Fearnside PM, Ribeiro JEL, et al. Rain forest fragmentation and the proliferation of successional trees. Ecology. 2006; 87: 469–482. https://doi.org/10.1890/05-0064 PMID: 16637371

**75.** Boesing AL, Nichols E, Metzger JP. Biodiversity extinction thresholds are modulated by matrix type. Ecography (Cop). 2018; 1–14. https://doi.org/10.1111/ecog.03365

**76.** He HS, DeZonia BE, Mladenoff DJ. An aggregation index (AI) to quantify spatial patterns of landscapes. Landsc Ecol. 2000; 15: 591–601. https://doi.org/10.1023/A:1008102521322

**77.** Radford JQ, Bennett AF, Cheers GJ. Landscape-level thresholds of habitat cover for woodland-dependent birds. Biol Conserv. 2005; 124: 317–337. https://doi.org/10.1016/j.biocon.2005.01.039

**78.** Moilanen A, Nieminen M. Simple connectivity measures in spatial ecology. Ecology. 2002; 83: 1131–1145. https://doi.org/10.1890/0012-9658(2002)083[1131:SCMISE]2.0.CO;2

**79.** Stevens SM, Husband TP. The influence of edge on small mammals: evidence from Brazilian Atlantic forest fragments. Biol Conserv. 1998; 85: 1–8. https://doi.org/10.1016/S0006-3207(98)00003-2

**80.** Bowman J, Jaeger JAG, Fahrig L. Dispersal distance of mammals is proportional to home range size. Ecology. 2002; 83: 2049–2055. https://doi.org/10.1890/0012-9658(2002)083[2049:DDOMIP]2.0.CO;2

**81.** Sutherland GD, Harestad AS, Price K, Lertzman KP. Scaling of natal dispersal distances in terrestrial birds and mammals. Ecol Soc. 2000; 4. https://doi.org/10.5751/es-00184-040116

**82.** Holbrook KM. Home range and movement patterns of toucans: Implications for seed dispersal. Biotropica. 2011; 43: 357–364. https://doi.org/10.1111/j.1744-7429.2010.00710.x

**83.** Clark PJ, Evans FC. Distance to nearest neighbor as a measure of spatial relationships in populations. Ecology. 1954; 35: 445–453. https://doi.org/10.2307/1931034

**84.** Crawley MJ. The R Book. 2nd ed. John Wiley & Sons, Ltd.; 2013.

**85.** Shao J. Linear Model Selection by Cross-Validation. J Am Stat Assoc. 1993; 88: 486. https://doi.org/10.2307/2290328

**86.** Browne MW. Cross-validation methods. J Math Psychol. 2000; 44: 108–132. https://doi.org/10.1006/jmps.1999.1279 PMID: 10733860

**87.** Baumann K. Cross-validation as the objective function for variable-selection techniques. TrAC—Trends in Analytical Chemistry. Elsevier; 2003. pp. 395–406. https://doi.org/10.1016/S0165-9936(03)00607-1

**88.** Moraga AD, Martin AE, Fahrig L. The scale of effect of landscape context varies with the species' response variable measured. Landsc Ecol. 2019; 34: 703–715. https://doi.org/10.1007/s10980-019-00808-9

**89.** Zuckerberg B, Desrochers A, Hochachka WM, Fink D, Koenig WD, Dickinson JL. Overlapping landscapes: A persistent, but misdirected concern when collecting and analyzing ecological data. J Wildl Manage. 2012; 76: 1072–1080. https://doi.org/10.1002/jwmg.326

**90.** Cleary KA, Waits LP, Finegan B. Agricultural intensification alters bat assemblage composition and abundance in a dynamic Neotropical landscape. Biotropica. 2016; 48: 667–676. https://doi.org/10.1111/btp.12327

**91.** Fox J, Weisberg S. An R Companion to Applied Regression. 2nd ed. Thousand Oaks: SAGE Publications; 2011.

92. Kutner MH, Nachtsheim C, Neter J, Li W. Applied linear statistical models. 5th ed. McGraw-Hill; 2005.
93. Barton K. MuMIn: Multi-Model Inference. R Packag version 1421. 2018.
94. Burnham KP, Anderson DR. Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach (2nd ed). Ecological Modelling. Springer-Verlag; 2002. https://doi.org/10.1016/j.ecolmodel.2003.11.004
95. R Development Core Team. R: A Language and Environment for Statistical Computing. Vienna, Austria; 2018. Available: https://www.r-project.org/.
96. Laurance WF, Nascimento HEMM, Laurance SG, Andrade A, Ewers RM, Harms KE, et al. Habitat fragmentation, variable edge effects, and the landscape-divergence hypothesis. Bennett P, editor. PLoS One. 2007; 2: e1017. https://doi.org/10.1371/journal.pone.0001017 PMID: 17925865
97. Laurance WF, Nascimento HEM, Laurance SG, Andrade A, Ribeiro JELS, Giraldo JP, et al. Rapid decay of tree-community composition in Amazonian forest fragments. Proc Natl Acad Sci U S A. 2006; 103: 19010–19014. https://doi.org/10.1073/pnas.0609048103 PMID: 17148598
98. Sosa Vinicio J, Galindo Gonzalez J, Guevara S. Bat- and bird-generated seed rains at isolated trees in pastures in a tropical rainforest. Conserv Biol. 2000; 14: 1693–1703.
99. de la Peña-Cuéllar E, Stoner KE, Avila-Cabadilla LD, Martínez-Ramos M, Estrada A. Phyllostomid bat assemblages in different successional stages of tropical rain forest in Chiapas, Mexico. Biodivers Conserv. 2012; 21: 1381–1397. https://doi.org/10.1007/s10531-012-0249-7
100. Arroyo-Rodríguez V, Andresen E, Bravo SP, Stevenson PR. Seed dispersal by howler monkeys: Current knowledge, conservation implications, and future directions. Howler Monkeys: Behavior, Ecology, and Conservation. New York, NY: Springer New York; 2015. pp. 111–139. https://doi.org/10.1007/978-1-4939-1960-4_5
101. Ferreira LV. Effects of the duration of flooding on species richness and floristic composition in three hectares in the Jau National Park in floodplain forests in central Amazonia. Biodivers Conserv. 1997; 6: 1353–1363. https://doi.org/10.1023/A:1018385529531
102. Holl KD, Loik ME, Lin EHV, Samuels IA. Tropical montane forest restoration in Costa Rica: Overcoming barriers to dispersal and establishment. Restor Ecol. 2000; 8: 339–349. https://doi.org/10.1046/j.1526-100X.2000.80049.x
103. Barron AR, Purves DW, Hedin LO. Facultative nitrogen fixation by canopy legumes in a lowland tropical forest. Oecologia. 2011; 165: 511–520. https://doi.org/10.1007/s00442-010-1838-3 PMID: 21110206
104. Arroyo-Rodríguez V, Rojas C, Saldaña-Vázquez RA, Stoner KE. Landscape composition is more important than landscape configuration for phyllostomid bat assemblages in a fragmented biodiversity hotspot. Biol Conserv. 2016; 198: 84–92. https://doi.org/10.1016/j.biocon.2016.03.026
105. Melo FPL, Arroyo-Rodríguez V, Fahrig L, Martínez-Ramos M, Tabarelli M. On the hope for biodiversity-friendly tropical landscapes. Trends Ecol Evol. 2013; 28: 462–468. https://doi.org/10.1016/j.tree.2013.01.001 PMID: 23375444
106. Chazdon RL, Uriarte M. The Role of Natural Regeneration in Large-scale Forest and Landscape Restoration: Challenge and Opportunity. Biotropica. 2016; 48: 709–715.
107. Chazdon RL, Peres CA, Dent D, Sheil D, Lugo AE, Lamb D, et al. The potential for species conservation in tropical secondary forests. Conserv Biol. 2009; 23: 1406–1417. https://doi.org/10.1111/j.1523-1739.2009.01338.x PMID: 20078641
108. Martínez-Ramos M, Pingarroni A, Rodríguez-Velázquez J, Toledo-Chelala L, Zermeño-Hernández I, Bongers F. Natural forest regeneration and ecological restoration in human-modified tropical landscapes. Biotropica. 2016; 48: 745–757. https://doi.org/10.1111/btp.12382
109. Arroyo-Rodríguez V, Melo FPL, Martínez-Ramos M, Bongers F, Chazdon RL, Meave JA, et al. Multiple successional pathways in human-modified tropical landscapes: new insights from forest succession, forest fragmentation and landscape ecology research. Biol Rev. 2017; 92: 326–340. https://doi.org/10.1111/brv.12231 PMID: 26537849
110. Delattre T, Baguette M, Burel F, Stevens VM, Quénol H, Vernon P. Interactive effects of landscape and weather on dispersal. Oikos. 2013; 122: 1576–1585. https://doi.org/10.1111/j.1600-0706.2013.00123.x
111. Ricci B, Franck P, Valantin-Morison M, Bohan DA, Lavigne C. Do species population parameters and landscape characteristics affect the relationship between local population abundance and surrounding habitat amount? Ecol Complex. 2013; 15: 62–70. https://doi.org/10.1016/j.ecocom.2013.02.008
112. Gardiner R, Proft K, Comte S, Jones M, Johnson CN. Home range size scales to habitat amount and increasing fragmentation in a mobile woodland specialist. Ecol Evol. 2019; 14005–14014. https://doi.org/10.1002/ece3.5837 PMID: 31938498

**113.** Ramos DL, Pizo MA, Ribeiro MC, Cruz RS, Morales JM, Ovaskainen O. Forest and connectivity loss drive changes in movement behavior of bird species. Ecography (Cop). 2020; 43: 1–12. https://doi.org/10.1111/ecog.04888

**114.** Carlo TA, Morales JM. Inequalities in fruit-removal and seed dispersal: consequences of bird behaviour, neighbourhood density and landscape aggregation. J Ecol. 2008; 96: 609–618. https://doi.org/10.1111/j.1365-2745.2008.01379.x

**115.** Santo-Silva EE, Almeida WR, Melo FPL, Zickel CS, Tabarelli M. The nature of seedling assemblages in a fragmented tropical landscape: Implications for forest regeneration. Biotropica. 2013; 45: 386–394. https://doi.org/10.1111/btp.12013

**116.** Myers JA, Chase JM, Jiménez I, Jørgensen PM, Araujo-Murakami A, Paniagua-Zambrana N, et al. Beta-diversity in temperate and tropical forests reflects dissimilar mechanisms of community assembly. Ecol Lett. 2013; 16: 151–157. https://doi.org/10.1111/ele.12021 PMID: 23113954

**117.** Arroyo-Rodríguez V, González-Perez IM, Garmendia A, Solà M, Estrada A. The relative impact of forest patch and landscape attributes on black howler monkey populations in the fragmented Lacandona rainforest, Mexico. Landsc Ecol. 2013; 28: 1717–1727. https://doi.org/10.1007/s10980-013-9929-2

**118.** Olden JD, Poff NLR. Toward a mechanistic understanding and prediction of biotic homogenization. Am Nat. 2003; 162: 442–460. https://doi.org/10.1086/378212 PMID: 14582007

**119.** Ordóñez-Gómez JD, Arroyo-Rodríguez V, Nicasio-Arzeta S, Cristóbal-Azkarate J. Which is the appropriate scale to assess the impact of landscape spatial configuration on the diet and behavior of spider monkeys? Am J Primatol. 2015; 77: 56–65. https://doi.org/10.1002/ajp.22310 PMID: 25231365

**120.** Benítez-Malvido J, Martínez-Ramos M, Ceccon E. Seed rain vs. seed bank, and the effect of vegetation cover on the recruitment of tree seedlings in tropical successional vegetation. In: Gottsberger G, Liede S, editors. Life Forms and Dynamics in Tropical Forests. Stuttgart, Germany: Schweizerbart Science Publishers; 2001. pp. 1805–203.

**121.** Zermeño-Hernández I, Méndez-Toribio M, Siebe C, Benítez-Malvido J, Martínez-Ramos M. Ecological disturbance regimes caused by agricultural land uses and their effects on tropical forest regeneration. Appl Veg Sci. 2015; 18: 443–455. https://doi.org/10.1111/avsc.12161

**122.** Benítez-Malvido J, Zermeño-Hernández I, González-DiPierro AM, Lombera R, Estrada A. Frugivore choice and escape from pre-dispersal seed predators: the case of Dialium guianense and two sympatric primate species in southern Mexico. Plant Ecol. 2016; 217: 923–933. https://doi.org/10.1007/s11258-016-0617-6

**123.** Camargo-Sanabria AA, Mendoza E. Interactions between terrestrial mammals and the fruits of two neotropical rainforest tree species. Acta Oecologica. 2016; 73: 45–52. https://doi.org/10.1016/j.actao.2016.02.005

**124.** Barbier EB, Tesfaw AT. Can REDD+ save the forest? The role of payments and tenure. Forests. 2012; 3: 881–895. https://doi.org/10.3390/f3040881

**125.** Hajjar R, Engbring G, Kornhauser K. The impacts of REDD+ on the social-ecological resilience of community forests. Environ Res Lett. 2021; 16: 24001. https://doi.org/10.1088/1748-9326/abd7ac

**126.** Arroyo-Rodríguez V, Fahrig L, Tabarelli M, Watling JI, Tischendorf L, Benchimol M, et al. Designing optimal human-modified landscapes for forest biodiversity conservation. Ecol Lett. 2020. https://doi.org/10.1111/ele.13535 PMID: 32537896

**127.** Liao C, Brown DG. Assessments of synergistic outcomes from sustainable intensification of agriculture need to include smallholder livelihoods with food production and ecosystem services. Curr Opin Environ Sustain. 2018; 32: 53–59. https://doi.org/10.1016/j.cosust.2018.04.013

**128.** Ricciardi V, Mehrabi Z, Wittman H, James D, Ramankutty N. Higher yields and more biodiversity on smaller farms. Nat Sustain. 2021. https://doi.org/10.1038/s41893-021-00699-2

**129.** Chazdon RL, Lindenmayer D, Guariguata MR, Crouzeilles R, Rey Benayas JM, Lazos Chavero E. Fostering natural forest regeneration on former agricultural land through economic and policy interventions. Environ Res Lett. 2020; 15: 043002. https://doi.org/10.1088/1748-9326/ab79e6

**130.** Boillat S, Scarpa FM, Robson JP, Gasparri I, Aide TM, Aguiar APD, et al. Land system science in Latin America: challenges and perspectives. Curr Opin Environ Sustain. 2017;26–27: 37–46. https://doi.org/10.1016/j.cosust.2017.01.015

**131.** Jadin I, Meyfroidt P, Lambin EF. International trade, and land use intensification and spatial reorganization explain Costa Rica's forest transition. Environ Res Lett. 2016; 11: 035005. https://doi.org/10.1088/1748-9326/11/3/035005

**132.** Calvo-Alvarado J, Jiménez V, Calvo-Obando A, Castillo M. Current Perspectives on Forest Recovery Trends in Guanacaste, Costa Rica. Int For Rev. 2019; 21: 425–431. https://doi.org/10.1505/146554819827906825

## Supplemental information

Table A. Coefficient of determination ($R^2$) and p value (in parenthesis) between α- and β-diversity metrics and patch size and shape.

| Diversity | Diversity order | Patch size | Patch shape |
|---|---|---|---|
| α | *All ($^0\alpha$)* | 0.071 (0.16) | 0.054 (0.195) |
|  | *Typical ($^1\alpha$)* | 0.103 (0.122) | 0.037 (0.229) |
|  | *Dominant ($^2\alpha$)* | 0.098 (0.128) | 0.001 (0.33) |
| β | *All ($^0\beta$)* | -0.007 (0.358) | 0.023 (0.264) |
|  | *Typical ($^1\beta$)* | 0.043 (0.217) | 0.047 (0.208) |
|  | *Dominant ($^2\beta$)* | -0.027 (0.45) | -0.01 (0.373) |

Table B. Abbreviation and description of the landscape metrics employed in the analysis

| Landscape metric | Abbreviation | Formula | Description |
|---|---|---|---|
| Aggregation index | AI | $\mathrm{AI} = 100 \times \left[\frac{g_{ii}}{max \rightarrow g_{ii}}\right]$ | Where $g_{ii}$ is the number of joins between pixels of forest patch *i* and *max*→$g_{ii}$ is the maximum number of joins between pixels of forest patch *i* based on the single-count method |
| Edge contrast index | EC | $\mathrm{EC} = 100 \times \left[\frac{\sum_{k=1}^{m} p_{ijk} \cdot d_{ik}}{p_{ij}}\right]$ | Where $p_{ijk}$ is the edge length (m) of patch *ij* adjacent to cover type *k*, $d_{ik}$ is the edge contrast weight between patch *i* and cover *k*, and $p_{ij}$ is the length of perimeter of patch *ij* |
| Euclidean-nearest neighbor distance | ENN | $\mathrm{ENN} = \frac{\sum_{i=1}^{n} h_{ij}}{n_h}$ | Where $h_{ij}$ is the edge-to-edge distance between two patches *j* of the land cover *i*, and $n_h$ is the number of distances recorded |
| Forest cover | FC | $\mathrm{FC} = 100 \times \left[\frac{\sum_{j=1}^{n} a_i}{A}\right]$ | Where *a* is the area ($m^2$) of forest patch *i* and *A* the is the total landscape area |
| Secondary vegetation | SV | $\mathrm{SV} = 100 \times \left[\frac{\sum_{j=1}^{n} a_i}{A}\right]$ | Where *a* is the area ($m^2$) of cover patch *i* and *A* the is the total landscape area |
| Patch density | PD | $\mathrm{PD} = 100 \times \left[\frac{n_i}{A} \times (10{,}000)\right]$ | Where $n_i$ is the total number of patches in the landscape of the land cover *i* and *A* is the total landscape area ($m^2$) |

Table C. Correlation values among landscape metrics across the 13 spatial scales employed in the multi-scale analysis in a fragmented tropical forest in southeastern Mexico. Strong correlations (-0.7 > r > 0.7) are in bold.

| Landscape radius | | *AI* | *EC* | *PD* | *FC* |
|---|---|---|---|---|---|
| **300m** | *EC* | -0.475 | | | |
| | *PD* | -0.582 | 0.283 | | |
| | *FC* | 0.497 | -0.621 | -0.303 | |
| | *SF* | 0.333 | -0.102 | -0.464 | 0.202 |
| **400m** | *EC* | -0.071 | | | |
| | *PD* | -0.618 | -0.373 | | |
| | *FC* | 0.573 | -0.477 | -0.145 | |
| | *SF* | -0.066 | -0.278 | 0.186 | 0.127 |
| **500m** | *EC* | 0.171 | | | |
| | *PD* | -0.57 | -0.568 | | |
| | *FC* | 0.303 | -0.44 | 0.256 | |
| | *SF* | -0.188 | -0.156 | -0.119 | -0.273 |
| **600m** | *EC* | 0.084 | | | |
| | *PD* | -0.135 | -0.334 | | |
| | *FC* | 0.155 | -0.459 | 0.413 | |
| | *SF* | -0.413 | -0.123 | 0.076 | -0.417 |
| **700m** | *EC* | -0.051 | | | |
| | *PD* | -0.088 | -0.339 | | |
| | *FC* | 0.079 | -0.474 | 0.503 | |
| | *SF* | -0.528 | -0.073 | -0.189 | -0.438 |
| **800m** | *EC* | -0.102 | | | |
| | *PD* | -0.299 | -0.382 | | |
| | *FC* | -0.062 | -0.492 | 0.67 | |
| | *SF* | -0.307 | 0.033 | -0.498 | -0.398 |
| **900m** | *EC* | -0.331 | | | |
| | *PD* | -0.031 | -0.225 | | |

| | | | | | |
|---|---|---|---|---|---|
| | *FC* | **0.875** | -0.33 | 0.148 | |
| | *SF* | -0.38 | 0.056 | -0.237 | -0.451 |
| **1000m** | *EC* | -0.32 | | | |
| | *PD* | -0.355 | -0.226 | | |
| | *FC* | **0.882** | -0.354 | -0.124 | |
| | *SF* | -0.282 | 0.068 | -0.145 | -0.426 |
| **1100m** | *EC* | -0.195 | | | |
| | *PD* | -0.142 | -0.373 | | |
| | *FC* | **0.838** | -0.264 | 0.293 | |
| | *SF* | -0.265 | 0.128 | -0.211 | -0.371 |
| **1200m** | *EC* | -0.16 | | | |
| | *PD* | -0.039 | -0.687 | | |
| | *FC* | **0.817** | -0.376 | 0.291 | |
| | *SF* | -0.244 | 0.27 | -0.48 | -0.36 |
| **1300m** | *EC* | -0.321 | | | |
| | *PD* | -0.014 | -0.551 | | |
| | *FC* | **0.859** | -0.498 | 0.207 | |
| | *SF* | -0.291 | 0.444 | -0.291 | -0.427 |
| **1400m** | *EC* | -0.361 | | | |
| | *PD* | -0.02 | -0.609 | | |
| | *FC* | **0.906** | -0.525 | 0.019 | |
| | *SF* | -0.439 | 0.526 | -0.233 | -0.507 |
| **1500m** | *EC* | -0.34 | | | |
| | *PD* | 0.193 | -0.597 | | |
| | *FC* | **0.932** | -0.511 | 0.209 | |
| | *SF* | -0.539 | 0.583 | -0.218 | -0.56 |

Table D. Percentage of landscape overlap among circular buffers of different radius (300 to1500-m radius, at 100 m intervals) in a fragmented tropical forest in southeastern Mexico. We divided the total overlapped area by the sum of the 16 buffers' area for each landscape radius.

| Landscape radius | Overlapping (%) |
|---|---|
| **300m** | 2.139 |
| **400m** | 7.56 |
| **500m** | 13.159 |
| **600m** | 19.078 |
| **700m** | 25.026 |
| **800m** | 31.037 |
| **900m** | 37.676 |
| **1000m** | 44.865 |
| **1100m** | 52.491 |
| **1200m** | 60.964 |
| **1300m** | 70.349 |
| **1400m** | 80.433 |
| **1500m** | 91.091 |

Table E. Moran's I autocorrelation tests between the distance of sampling sites of tree seedling community and the reported α- and β-diversity (${}^{0}D$ = all species, ${}^{1}D$ = typical species and ${}^{2}D$ = abundant species) in a fragmented tropical forest in southeastern Mexico.

| Diversity | Order | Moran's I ± standard deviation | P value |
|---|---|---|---|
| α | ${}^{0}\alpha$ | -0.043 ± 0.065 | 0.721 |
| | ${}^{1}\alpha$ | -0.055 ± 0.065 | 0.853 |
| | ${}^{2}\alpha$ | -0.063 ± 0.065 | 0.957 |
| β | ${}^{0}\beta$ | -0.077 ± 0.059 | 0.861 |
| | ${}^{1}\beta$ | -0.161 ± 0.065 | 0.147 |
| | ${}^{2}\beta$ | -0.175 ± 0.063 | 0.088 |

Table F. Moran's I autocorrelation tests between the distance of sampling sites of tree seedling community and landscape metrics across the 13 spatial scales employed in the multi-scale analysis in a fragmented tropical forest in southeastern Mexico.

| Landscape metric | Landscape radius | Moran ± standard deviation | *P* value |
|---|---|---|---|
| AI | 300m | -0.025 ± 0.065 | 0.523 |
| | 400m | -0.021 ± 0.065 | 0.485 |
| | 500m | -0.033 ± 0.062 | 0.59 |

|  |  |  |  |
|---|---|---|---|
|  | 600m | 0.058 ± 0.064 | 0.054 |
|  | 700m | 0.053 ± 0.066 | 0.068 |
|  | 800m | -0.092 ± 0.066 | 0.698 |
|  | 900m | -0.004 ± 0.062 | 0.31 |
|  | 1000m | -0.002 ± 0.062 | 0.293 |
|  | 1100m | -0.044 ± 0.061 | 0.71 |
|  | 1200m | -0.036 ± 0.06 | 0.607 |
|  | 1300m | -0.047 ± 0.063 | 0.75 |
|  | 1400m | -0.047 ± 0.064 | 0.762 |
|  | 1500m | -0.066 ± 0.063 | 0.99 |
| EC | 300m | -0.035 ± 0.064 | 0.624 |
|  | 400m | -0.044 ± 0.064 | 0.722 |
|  | 500m | -0.062 ± 0.065 | 0.938 |
|  | 600m | -0.083 ± 0.065 | 0.806 |
|  | 700m | -0.111 ± 0.065 | 0.493 |
|  | 800m | -0.125 ± 0.065 | 0.373 |
|  | 900m | -0.111 ± 0.065 | 0.5 |
|  | 1000m | -0.071 ± 0.066 | 0.951 |
|  | 1100m | -0.01 ± 0.066 | 0.385 |
|  | 1200m | 0.044 ± 0.066 | 0.093 |
|  | 1300m | 0.051 ± 0.067 | 0.077 |
|  | 1400m | 0.057 ± 0.067 | 0.063 |
|  | 1500m | 0.034 ± 0.066 | 0.131 |
| PD | 300m | -0.024 ± 0.056 | 0.446 |
|  | 400m | -0.035 ± 0.066 | 0.635 |
|  | 500m | -0.076 ± 0.064 | 0.887 |
|  | 600m | -0.114 ± 0.065 | 0.469 |
|  | 700m | -0.028 ± 0.063 | 0.541 |
|  | 800m | -0.15 ± 0.061 | 0.176 |
|  | 900m | -0.017 ± 0.063 | 0.432 |

|  |  |  |  |
|---|---|---|---|
|  | 1000m | -0.023 ± 0.065 | 0.507 |
|  | 1100m | 0.04 ± 0.063 | 0.091 |
|  | 1200m | 0.038 ± 0.065 | 0.109 |
|  | 1300m | -0.124 ± 0.066 | 0.386 |
|  | 1400m | -0.038 ± 0.059 | 0.629 |
|  | 1500m | -0.038 ± 0.061 | 0.638 |
| FC | 300m | **0.067 ± 0.067** | **0.044*** |
|  | 400m | 0.04 ± 0.064 | 0.097 |
|  | 500m | -0.018 ± 0.058 | 0.4 |
|  | 600m | -0.043 ± 0.048 | 0.625 |
|  | 700m | -0.051 ± 0.04 | 0.7 |
|  | 800m | -0.052 ± 0.032 | 0.639 |
|  | 900m | -0.024 ± 0.045 | 0.346 |
|  | 1000m | 0.005 ± 0.06 | 0.228 |
|  | 1100m | 0.009 ± 0.065 | 0.246 |
|  | 1200m | -0.001 ± 0.065 | 0.319 |
|  | 1300m | -0.012 ± 0.065 | 0.402 |
|  | 1400m | -0.029 ± 0.064 | 0.557 |
|  | 1500m | -0.05 ± 0.063 | 0.793 |
| SF | 300m | -0.018 ± 0.066 | 0.459 |
|  | 400m | -0.044 ± 0.066 | 0.73 |
|  | 500m | -0.038 ± 0.065 | 0.657 |
|  | 600m | -0.038 ± 0.064 | 0.652 |
|  | 700m | -0.069 ± 0.06 | 0.971 |
|  | 800m | -0.075 ± 0.06 | 0.886 |
|  | 900m | -0.071 ± 0.059 | 0.946 |
|  | 1000m | -0.071 ± 0.058 | 0.935 |
|  | 1100m | -0.073 ± 0.058 | 0.911 |
|  | 1200m | -0.073 ± 0.059 | 0.911 |

| | | |
|---|---|---|
| 1300m | -0.074 ± 0.06 | 0.903 |
| 1400m | -0.078 ± 0.061 | 0.855 |
| 1500m | -0.069 ± 0.062 | 0.972 |

* Significant autocorrelation values

Table G. Moran's I autocorrelation tests between the distance of sampling sites of the biotic-dispersed tree seedling community and the residuals of the linear models between α- and β-diversity metrics ($^{0}D$ = all species, $^{1}D$ = typical species and $^{2}D$ = dominant species) and landscape metrics in a fragmented tropical forest in southeastern Mexico. The numbers in parenthesis indicate de standard deviation. The subscript numbers indicate the scale of effect of each variable.

| **Diversity** | **Order** | **Landscape metric** | **Moran's I** | ***P* value** |
|---|---|---|---|---|
| **α** | $^{0}\alpha$ | AI$_{600}$ | -0.036 (0.064) | 0.632 |
| | | SF$_{600}$ | -0.064 (0.066) | 0.967 |
| | | PI$_{1200}$ | -0.067 (0.065) | 0.999 |
| | $^{1}\alpha$ | AI$_{600}$ | -0.045 (0.064) | 0.74 |
| | | SF$_{600}$ | -0.1 (0.065) | 0.61 |
| | | PI$_{1200}$ | -0.032 (0.064) | 0.588 |
| | $^{2}\alpha$ | A$_{I600}$ | -0.057 (0.064) | 0.877 |
| | | SF$_{600}$ | -0.096 (0.063) | 0.643 |
| | | PI$_{1200}$ | -0.023 (0.065) | 0.496 |
| **β** | $^{0}\beta$ | EC$_{800}$ | -0.134 (0.057) | 0.24 |
| | | PD$_{1400}$ | -0.055 (0.053) | 0.827 |
| | $^{1}\beta$ | AI$_{500}$ | -0.073 (0.065) | 0.922 |
| | | SF$_{1300}$ | -0.164 (0.064) | 0.129 |
| | $^{2}\beta$ | AI$_{500}$ | -0.123 (0.064) | 0.383 |
| | | PD$_{500}$ | -0.173 (0.064) | 0.098 |

Table H. Tree seedlings recorded during the sampling period in the Lacandona rainforest, at southeastern Mexico. Seedling dispersal syndromes were categorized whether by abiotic (A) or biotic (B) dispersion.

| ***Family*** | **Genus** | **Species** | **Dispersal** | **Number** |
|---|---|---|---|---|
| **ACANTHACEAE** | *Bravaisia* | *B. integerrima* | A | 29 |
| **ANACARDIACEAE** | *Spondias* | *S. mombin* | B | 6 |
| | | *S. radlkoferi* | B | 4 |
| | *Astronium* | *A. graveolens* | B | 1 |
| **ANNONACEAE** | *Annona* | *A. sp1* | B | 4 |
| | *Xylopia* | *X. frutescens* | B | 1 |
| **APOCYNACEAE** | *Stemmadenia* | *S. galeottiana* | B | 2 |
| **BIGNONIACEAE** | *Tabebuia* | *T. rosea* | A | 1 |

| | | | | |
|---|---|---|---|---|
| **BORAGINACEAE** | *Cordia* | *C. odorata* | B | 4 |
| | | *C. bicolor* | B | 2 |
| **BURSERACEAE** | *Bursera* | *B. simaruba* | B | 1 |
| | *Protium* | *P. copal* | B | 1 |
| **CAPPARACEAE** | *Capparis* | *C. quiriguensis* | B | 1 |
| **CHRYSOBALANACEAE** | *Hirtella* | *H. americana* | B | 15 |
| | *Licania* | *L. hypoleuca* | B | 8 |
| | | *L. platypus* | B | 1 |
| **CLUSIACEAE** | *Calophyllum* | *C. brasilense* | B | 10 |
| | *Garcinia* | *G. intermedia* | B | 4 |
| **EUPHORBIACEAE** | *Croton* | *C. schiedeanus* | B | 11 |
| **FABACEAE** | *Acacia* | *A. mayana* | B | 11 |
| | *Albizia* | *A. leucocalyx* | A | 5 |
| | *Andira* | *A. inermis* | B | 4 |
| | *Cojoba* | *C. arboreum* | B | 4 |
| | *Dialium* | *D. guianense* | B | 10 |
| | *Inga* | *I. edulis* | B | 3 |
| | | *I. pavoniana* | B | 1 |
| | | *I. punctata* | B | 418 |
| | | *I. vera* | B | 2 |
| | | *I. sp1* | B | 4 |
| | | *I. sp2* | B | 2 |
| | *Lonchocarpus* | *L. cruentus* | A | 2 |
| | | *L. pubescens* | A | 8 |
| | *Platymiscium* | *P. yucatanum* | A | 10 |
| | *Pterocarpus* | *P. hayesii* | A | 1 |
| | | *P. yucatanum* | A | 1 |
| **ICACINACEAE** | *Calatola* | *C. costaricanum* | B | 3 |
| **LASCISTEMATACEAE** | *Lacistema* | *L. agreggatum* | B | 2 |
| **LAURACEAE** | *Licaria* | *L. capitata* | B | 8 |
| | *Nectandra* | *N. ambigiens* | B | 17 |
| | | *N. reticulata* | B | 5 |
| **MALVACEAE** | *Hampea* | *H. stipitata* | B | 4 |
| | *Luehea* | *L. seemannii* | A | 4 |
| | *Quararibea* | *Q. funebris* | B | 4 |
| **MELIACEAE** | *Cedrela* | *C. odorata* | A | 3 |
| | *Guarea* | *G. excelsa* | B | 8 |
| | | *G. glabra* | B | 9 |
| | | *G. grandifolia* | B | 5 |
| | *Trichilia* | *T. havanensis* | B | 3 |
| **MORACEAE** | *Brosimum* | *B. alicastrum* | B | 147 |

| | | | | |
|---|---|---|---|---|
| | | *B. latescens* | B | 20 |
| | *Castilla* | *Castilla elastica* | B | 32 |
| | *Maclura* | *M. tinctoria* | B | 3 |
| | *Trophis* | *T. racemosa* | B | 93 |
| **PRIMULACEAE** | *Ardisia* | *A. paschalis* | B | 27 |
| **MYRTACEAE** | *Eugenia* | *E. edulis* | B | 4 |
| | | *E. mexicana* | B | 57 |
| | | *E. nigrita* | B | 5 |
| **POLYGONACEAE** | *Coccoloba* | *C. barbadensis* | B | 1 |
| **RUBIACEAE** | *Faramea* | *F. occidentalis* | B | 20 |
| | *Posoqueria* | *P. latifolia* | B | 13 |
| | | *P. sp1* | B | 5 |
| **SALICACEAE** | *Pleuranthodendron* | *P. lindenii* | B | 18 |
| **SAPINDACEAE** | *Cupania* | *C. dentata* | B | 8 |
| | | *C. glabra* | B | 14 |
| | *Sapindus* | *S. saponaria* | B | 1 |
| **SAPOTACEAE** | *Chrysophyllum* | *C. mexicanum* | B | 10 |
| | *Pouteria* | *P. durlandii* | B | 4 |
| **ULMACEAE** | *Ampelocera* | *A. hottlei* | B | 173 |
| **VOCHYSIACEAE** | *Vochysia* | *V. guatemalensis* | A | 7 |
| **Unknown** | | Morpho 1 | | 1 |
| | | Morpho 2 | | 3 |
| | | Morpho 3 | | 1 |

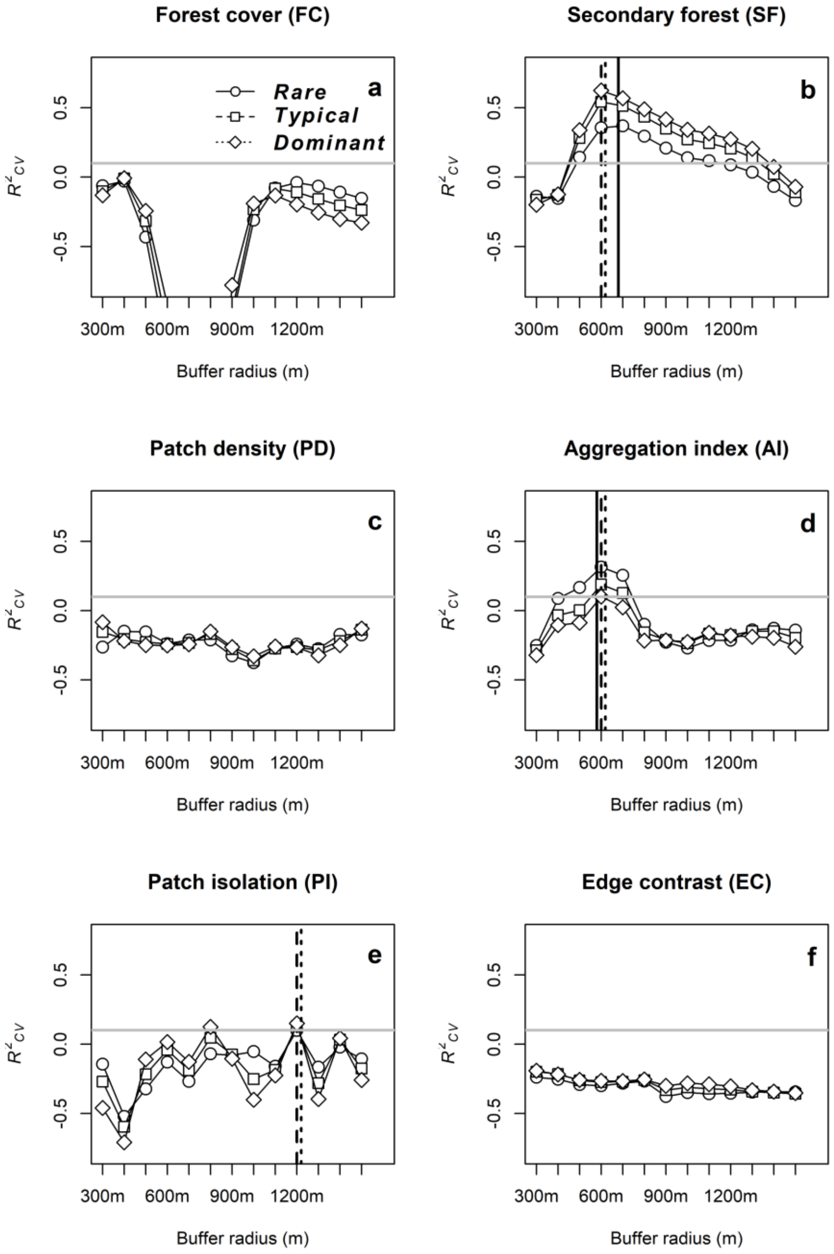
Table I. Model selection results of the linear models that explain each α- and β-diversity metric ($^{0}D$ = all species, $^{1}D$ = typical species and $^{2}D$ = dominant species) of the animal-dispersed tree seedling community in a fragmented tropical rainforest at southern Mexico. The models log-likelihood (*LL*), the corrected Akaike index criterion (*AICc*), the Akaike difference from the best model (*Δ*), the Akaike weight ($w_i$) and the coefficient of determination ($R^2$). The landscape metrics are the aggregation index (AI), the edge contrast index (EC), patch isolation (PI), and the percentage of secondary forest (SF). The subscript numbers indicate the scale of effect (radius meters) of each landscape metric. The superscript symbols indicate the positive (+) or negative (-) effects of landscape metrics. The values in italic correspond to the null model.

| | Diversity metric | Model | $R^2$ | *LL* | *AICc* | *Δ* | $w_i$ |
|---|---|---|---|---|---|---|---|
| α-diversity | All species | $^{0}\alpha \sim {}^{+}AI_{600} + {}^{-}SF_{600}$ | 0.6 | -8.38 | 28.39 | 0 | 0.52 |
| | | $^{0}\alpha \sim {}^{-}SF_{600}$ | 0.45 | -11.46 | 30.91 | 2.52 | 0.15 |
| | | $^{0}\alpha \sim {}^{-}PI_{1200} + {}^{-}SF_{600}$ | 0.52 | -9.87 | 31.38 | 2.98 | 0.12 |
| | | $^{0}\alpha \sim {}^{+}AI_{600} + {}^{-}PI_{1200} + {}^{-}SF_{600}$ | 0.6 | -7.69 | 31.39 | 2.99 | 0.12 |
| | | $^{0}\alpha \sim {}^{+}AI_{600}$ | 0.39 | -12.33 | 32.66 | 4.27 | 0.06 |
| | | $^{0}\alpha \sim {}^{+}AI_{600} + {}^{-}PI_{1200}$ | 0.43 | -11.25 | 34.13 | 5.74 | 0.03 |

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| | | $^{0}\alpha \sim {}^{-}PI_{1200}$ | 0.24 | -14.1 | 36.21 | 7.82 | 0.01 |
| | | $^{0}\alpha \sim 1$ | *0* | *-16.84* | *38.61* | *10.22* | *0* |
| | Typical species | | | | | | |
| | | $^{1}\alpha \sim {}^{-}PI_{1200} + {}^{-}SF_{600}$ | 0.67 | -1.84 | 15.31 | 0 | 0.32 |
| | | $^{1}\alpha \sim {}^{+}AI_{600} + {}^{-}SF_{600}$ | 0.67 | -1.93 | 15.5 | 0.19 | 0.29 |
| | | $^{1}\alpha \sim {}^{-}SF_{600}$ | 0.61 | -3.81 | 15.63 | 0.32 | 0.27 |
| | | $^{1}\alpha \sim {}^{+}AI_{600} + {}^{-}PI_{1200} + {}^{-}SF_{600}$ | 0.69 | -0.78 | 17.57 | 2.26 | 0.1 |
| | | $^{1}\alpha \sim {}^{+}AI_{600}$ | 0.29 | -8.64 | 25.29 | 9.98 | 0 |
| | | $^{1}\alpha \sim {}^{-}PI_{1200}$ | 0.26 | -8.99 | 25.98 | 10.67 | 0 |
| | | $^{1}\alpha \sim {}^{+}AI_{600} + {}^{-}PI_{1200}$ | 0.36 | -7.25 | 26.13 | 10.82 | 0 |
| | | $^{1}\alpha \sim 1$ | *0* | *-11.94* | *28.8* | *13.49* | *0* |
| | Dominant species | | | | | | |
| | | $^{2}\alpha \sim {}^{-}PI_{1200} + {}^{-}SF_{600}$ | 0.74 | 2.42 | 6.8 | 0 | 0.49 |
| | | $^{2}\alpha \sim {}^{-}SF_{600}$ | 0.67 | 0.03 | 7.95 | 1.14 | 0.28 |
| | | $^{2}\alpha \sim {}^{+}AI_{600} + {}^{-}SF_{600}$ | 0.7 | 1.23 | 9.17 | 2.37 | 0.15 |
| | | $^{2}\alpha \sim {}^{+}AI_{600} + {}^{-}PI_{1200} + {}^{-}SF_{600}$ | 0.73 | 2.88 | 10.23 | 3.43 | 0.09 |
| | | $^{2}\alpha \sim {}^{-}PI_{1200}$ | 0.27 | -6.39 | 20.79 | 13.99 | 0 |
| | | $^{2}\alpha \sim {}^{+}AI_{600}$ | 0.23 | -6.83 | 21.65 | 14.85 | 0 |
| | | $^{2}\alpha \sim {}^{+}AI_{600} + {}^{-}PI_{1200}$ | 0.33 | -5.19 | 22.02 | 15.22 | 0 |
| | | $^{2}\alpha \sim 1$ | *0* | *-9.49* | *23.91* | *17.11* | *0* |
| β-diversity | All species | | | | | | |
| | | $^{0}\beta \sim {}^{-}EC_{800}$ | 0.4 | -11.04 | 30.08 | 0 | 0.56 |
| | | $^{0}\beta \sim {}^{-}EC_{800} + {}^{+}PD_{1400}$ | 0.45 | -9.77 | 31.17 | 1.08 | 0.32 |
| | | $^{0}\beta \sim {}^{+}PD_{1400}$ | 0.25 | -12.79 | 33.59 | 3.5 | 0.1 |
| | | $^{0}\beta \sim 1$ | *0* | *-15.68* | *36.27* | *6.19* | *0.03* |
| | Typical species | | | | | | |
| | | $^{1}\beta \sim {}^{+}PD_{500}$ | 0.44 | -13.71 | 35.41 | 0 | 0.63 |
| | | $^{1}\beta \sim {}^{+}PD_{500} + {}^{-}SF_{1300}$ | 0.48 | -12.61 | 36.86 | 1.44 | 0.3 |
| | | $^{1}\beta \sim {}^{-}SF_{1300}$ | 0.24 | -16.19 | 40.37 | 4.96 | 0.05 |
| | | $^{1}\beta \sim 1$ | *0* | *-18.94* | *42.8* | *7.39* | *0.02* |
| | Dominant species | | | | | | |

| | | | | | |
|---|---|---|---|---|---|
| $^{2}\beta \sim {}^{+}PD_{500} + {}^{-}SF_{1300}$ | 0.45 | -9.81 | 27.62 | 0 | 0.56 |
| $^{2}\beta \sim {}^{-}AI_{500} + {}^{+}PD_{500} + {}^{-}SF_{1300}$ | 0.49 | -8.6 | 28.84 | 1.23 | 0.3 |
| $^{2}\beta \sim {}^{-}AI_{500} + {}^{-}SF_{1300}$ | 0.34 | -11.32 | 30.64 | 3.02 | 0.12 |
| $^{2}\beta \sim 1$ | *0* | *-15.17* | *35.26* | *7.64* | *0.01* |

Figure A. Association between buffer size and the coefficient of prediction ($R^2_{CV}$) between each landscape metric and each α-diversity metric (all, typical and dominant species) of the animal-dispersed tree seedling community in a fragmented rainforest in southeastern Mexico. Each point represents the $R^2_{CV}$ value of a simple linear regression between a diversity metric and single landscape metric measured at each buffer size. The points above the horizontal grey line indicate the proportion of variation that can be predicted by the model, whereas those points below the horizontal line indicate the prediction power of the model is worse than for a null model. The scale of effect is indicated within each panel with vertical lines.



Forest cover (FC)

Secondary forest (SF)

Patch density (PD)

Aggregation index (AI)

Patch isolation (PI)

Edge contrast (EC)

Figure B. Association between buffer size and the coefficient of prediction ($R^2_{CV}$) between each landscape metric and each β-diversity metric (all, typical and dominant species) of the animal-dispersed tree seedling community in a fragmented rainforest in southeastern Mexico. Each point represents the $R^2_{CV}$ value of a simple linear regression between a diversity metric and single landscape metric measured at each buffer size. The points above the horizontal grey line indicate the proportion of variation that can be predicted by the model, whereas those points below the horizontal line indicate the prediction power of the model is worse than for a null model. The scale of effect is indicated within each panel with vertical lines.

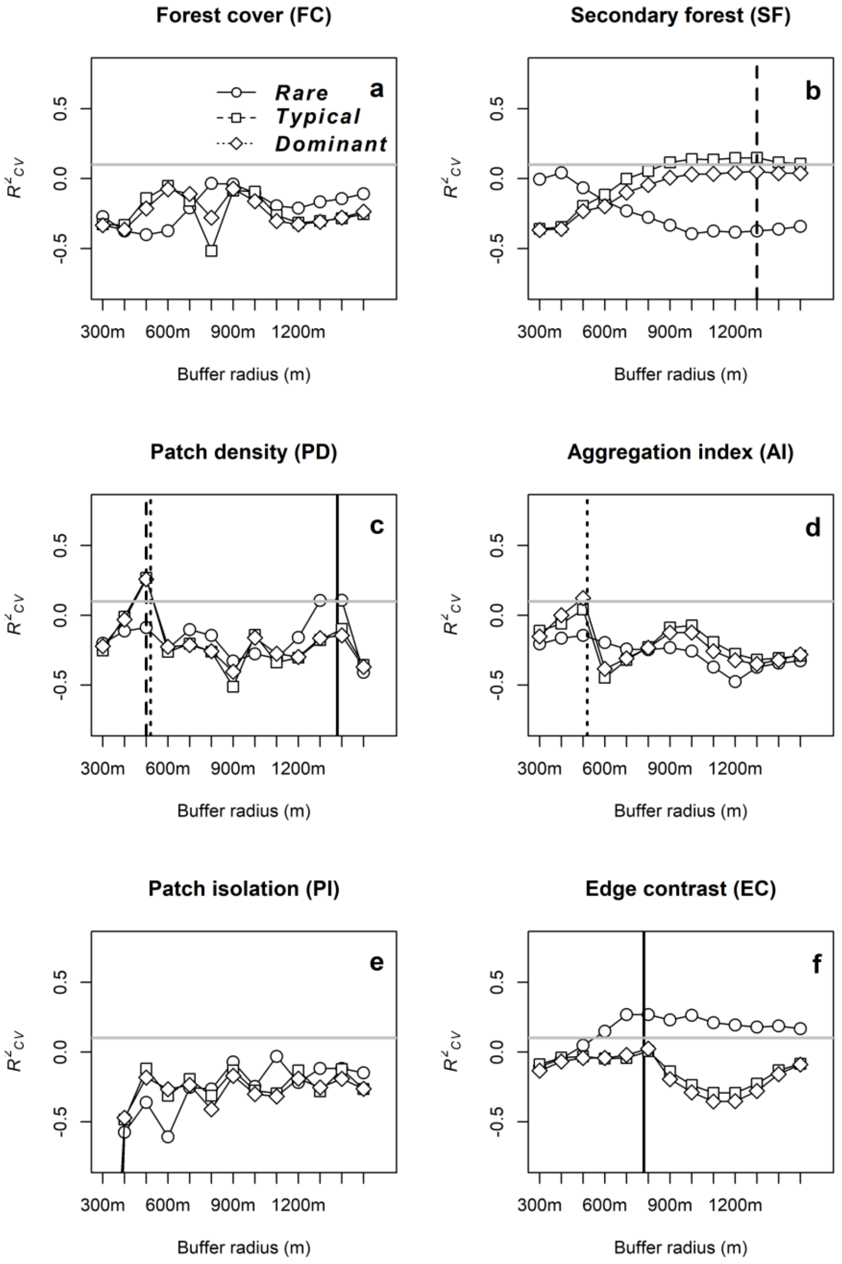


Figure C. Uncertainty around the estimated scale of effect between each landscape metric and each α-diversity metric (all, typical and dominant species) of the animal-dispersed tree seedling community, estimated by bootstrapping. For each landscape-diversity combination we randomly re-sampled the data from *n* patches, with replacement, from the set of the 16 forest patches, 1000 times. We then estimated the scale of effect for each resampled data. The total number of times (out of 1000) that each buffer size was selected as the scale of effect is plotted. The estimated scale of effect (red arrow) is the buffer size with the highest $R^2_{CV}$ for the complete data set (see Fig A).

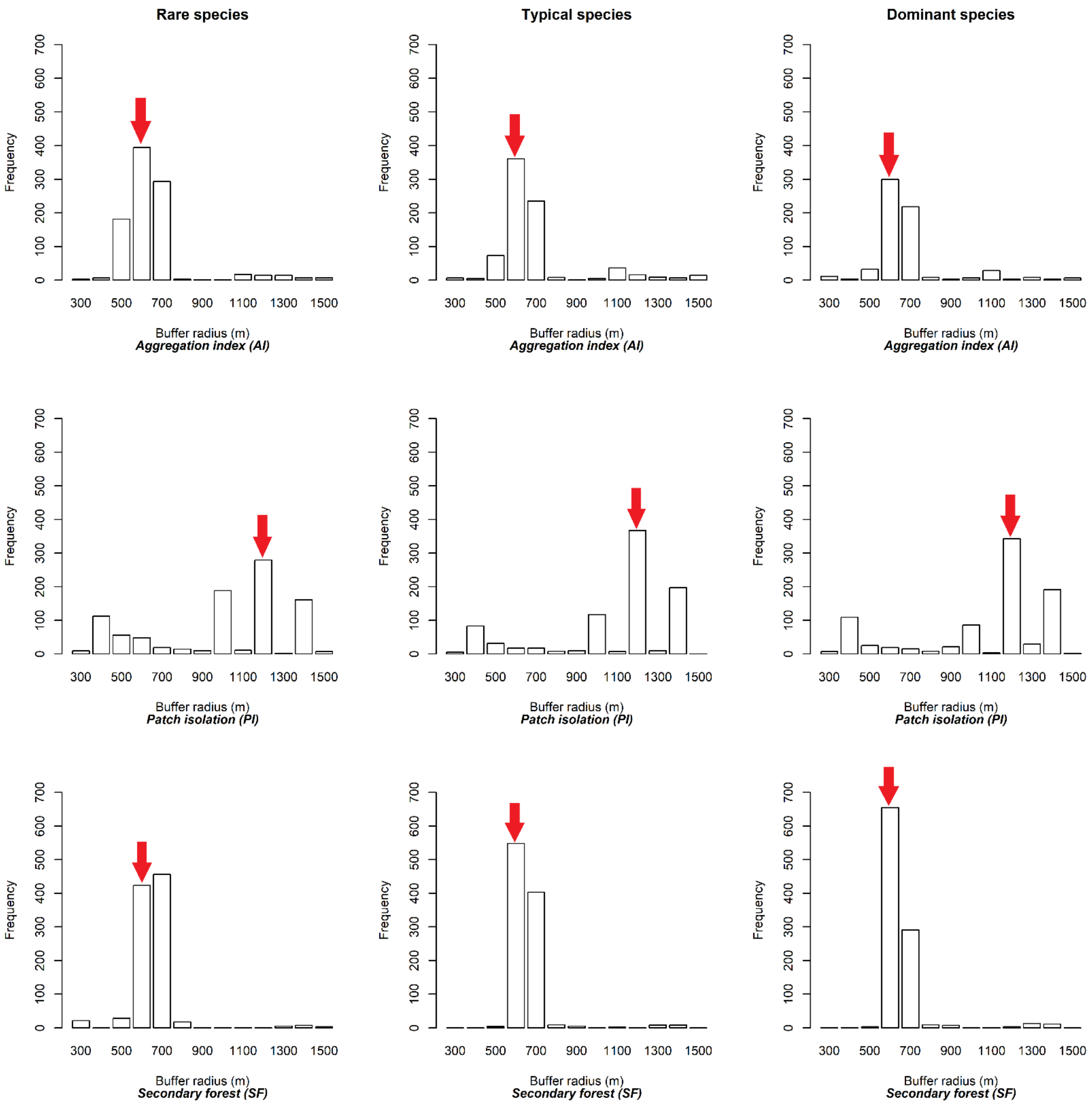


Figure D. Uncertainty around the estimated scale of effect between each landscape metric and each β-diversity metric (all, typical and dominant species) of the animal-dispersed tree seedling community, estimated by bootstrapping. For each landscape-diversity combination we randomly re-sampled the data from *n* patches, with replacement, from the set of the 16 forest patches, 1000 times. We then estimated the scale of effect for each resampled data. The total number of times (out of 1000) that each buffer size was selected as the scale of effect is plotted. The estimated scale of effect (red arrow) is the buffer size with the highest $R^2_{CV}$ for the complete data set (see Fig B).

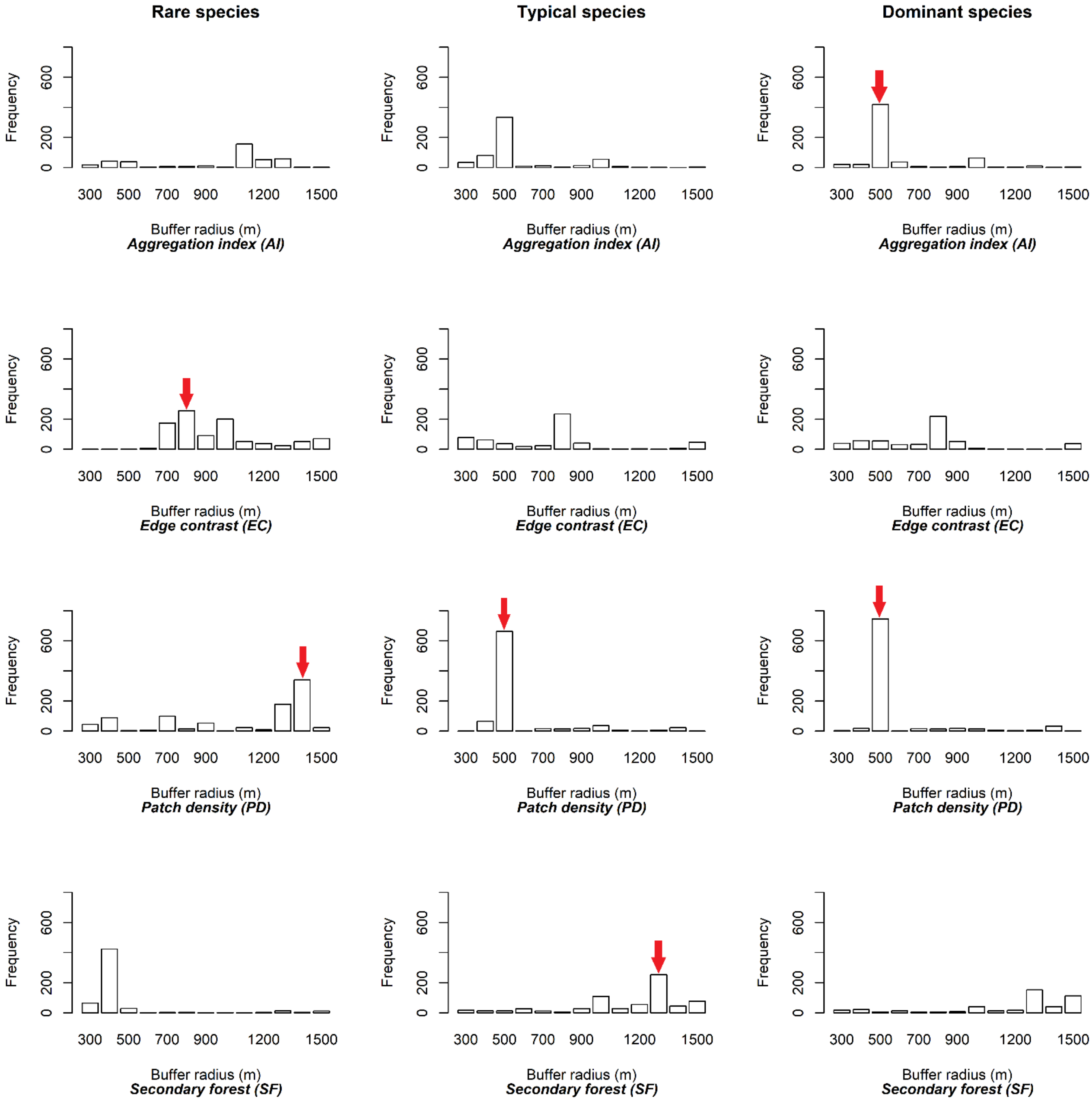


Figure E. Values of a) α- and b) β-diversity orders for tree seedlings within the patches' sampling plots in a fragmented tropical forest in southeastern Mexico. We observed ${}^{0}\alpha$-diversity was significantly higher (2.703 ± 0.716) than ${}^{1}\alpha$ (2.295 ± 0.527) and ${}^{2}\alpha$ (2.114 ± 0.452) within sampling plots ($\chi^2 = 6.99$; *d.f.* = 2; $P = 0.0302$). This also held true for β-diversity ($\chi^2 = 32.511$; *d.f.* = 2; $P < 0.001$; Figure 2b), which had ${}^{0}\beta$ values higher (4.303 ± 0.665) than ${}^{1}\beta$ (2.258 ± 0.816) and ${}^{2}\beta$ (1.617 ± 0.644).

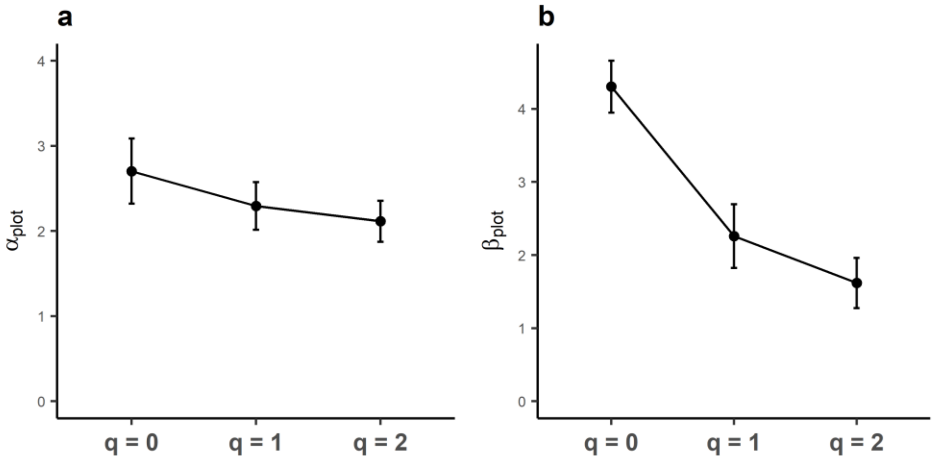
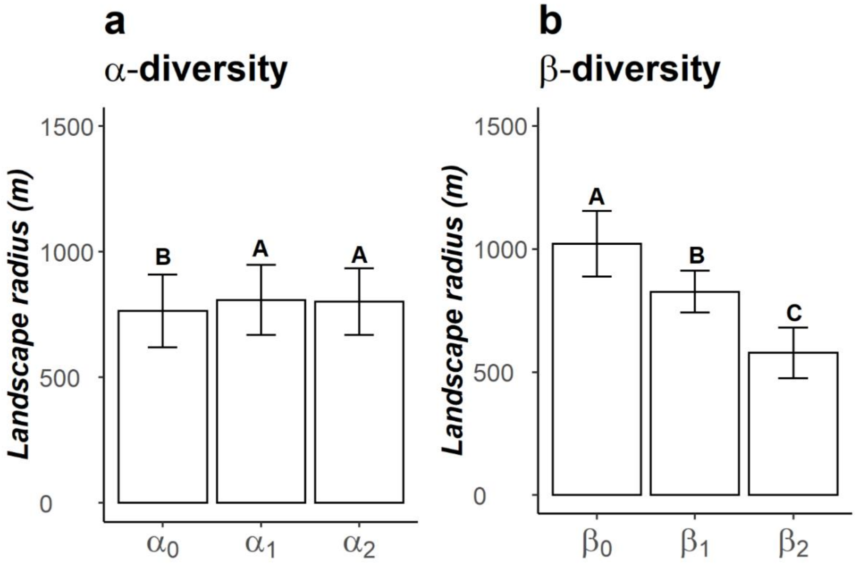


Figure F. Differences in the scale of effect between each landscape metric and each α- and β-diversity metric of the animal-dispersed tree seedling community. The values employed were estimated by bootstrapping. For each landscape-diversity combination we randomly re-sampled the data from *n* patches, with replacement, from the set of the 16 forest patches, 1000 times. We then estimated the scale of effect for each resampled data. The bars represent the mean and the whiskers the standard error.



# CAPÍTULO IV. THE ROLE OF LANDSCAPE MATRIX EFFECTS ON MAMMAL OCCUPANCY WITHIN RAINFOREST PATCHES

# The role of landscape matrix effects on mammals' occupancy within rainforest patches

Sergio Nicasio-Arzeta[1], Julieta Benítez-Malvido[1]

Ecología del Hábitat Alterado, Instituto de Investigaciones en Ecosistemas y Sustentabilidad,
Universidad Nacional Autónoma de México, Morelia, Michoacán, México

Corresponding author:
Sergio Nicasio-Arzeta[1]
Antigua Carretera a Pátzcuaro no. 8701, Morelia, Michoacán, 58190, México
Email address: sergio.nicasio@gmail.com

## Abstract

Landscape matrix plays a key role to sustain patch occupancy of terrestrial mammals in fragmented habitats, whether by contributing to habitat amount or by restraining the inter-patch movement. Nevertheless, the magnitude and spatial extent at which these matrix effects operate remains unexplored. We assessed the relative importance of matrix effects on habitat amount and resistance to movement on patch occupancy of four terrestrial mammals in a fragmented rainforest in southeastern Mexico. We monitored the incidence of each species within 16 forest patches. We then employed landscape composition metrics to measure matrix effects on habitat amount and textural variables from satellite imagery to estimate matrix resistance. We assessed both matrix effects on patch occupancy at four spatial scales (200, 300, 400 and 500 ha). We found a negative effect of both matrix effects on patch occupancy. However, matrix effects on habitat amount were more important for mammals with small home-range sizes than matrix effects on resistance to movement. Consequently, we observed that matrix effects on habitat amount operated at smaller spatial scales than matrix resistance. Our results suggest that the magnitude and contribution of matrix effects differ among species and spatial scales, urging to assess these effects separately in fragmentation studies. We also highlight the key role of remote sensing techniques to estimate matrix resistance at multiple spatial scales in the tropics.

## Introduction

The conversion of natural habitats to different land uses accounts for ca. 70% of forest loss, threatening biodiversity worldwide (Leadley et al., 2014; Song et al., 2018). Tropical rainforests are particularly vulnerable, because 10% of their remaining area persists as small and isolated patches within human-modified landscapes (Gibbs et al., 2010; Hansen et al., 2013; Lewis et al., 2015; Taubert et al., 2018). Biodiversity conservation in these habitats urges to understand how landscape structure promote the persistence of the remaining species within forest patches (Chazdon et al., 2009; Gardner et al., 2009).

Landscape matrix plays a key role in biodiversity conservation within fragmented habitats (Kupfer et al., 2006; Watling et al., 2011). The matrix influences species persistence mainly through effects on resources' availability (Driscoll et al., 2013) and functional connectivity (Eycott et al., 2010; Prevedello & Vieira, 2010). These effects are driven by matrix traits and species-specific requirements. On the one hand, matrix effects on resources availability (i.e., species breeding/foraging requirements) is associated to the composition of its land covers (Tscharntke et al., 2012; Watling et al., 2011). On the other hand, matrix can facilitate/impede the inter-patch movement throughout the structural resemblance of matrix vegetation with forest patches, as well as species movement requirements (Daniel et al., 2010; Driscoll et al., 2013; Prevedello & Vieira, 2010). Accordingly, understanding the role of matrix effects on the remaining species is crucial for reinforcing conservation strategies in fragmented landscapes (Driscoll et al., 2013; Lindenmayer et al., 2008; Watling et al., 2011).

Studies that appropriately differentiate among matrix effects, however, are lacking, leading to ineffective management practices (but see Watson et al. 2014). Untangling matrix effects can be achieved using composition metrics from landscape studies (Garmendia et al., 2013; Umetsu et al., 2008) and resistance measurements based on circuit theory (McRae et al., 2008; McRae & Beier, 2007). The latter has been successfully employed to measure the inter-patch movement resistance in a variety of scenarios derived from vegetation data (S. J. Watson et al., 2014). Nonetheless, resistance measurements are usually derived from expert-based estimations of categorical data (Ayram et al., 2015; Zeller et al., 2012), leading to inaccurate representations of connectivity (Koenig & Bender, 2018; Muratet et al., 2013). These shortcomings can be avoided by using satellite sensor data (Cavender-Bares et al., 2020; Muratet et al., 2013). The spectral values of satellite imagery are associated with different vegetation components (Lausch et al., 2020; Madritch et al., 2020; Pettorelli et al., 2014; Vihervaara et al., 2017) and are widely employed to map forest structure, disturbance, and suitability for species persistence in a variety of ecosystems (Baccini et al., 2012; M. Pfeifer et al., 2016; Strassburg et al., 2010; Turner et al., 2003). Textural variables are of particular importance in the tropics, since they have proven to overcome the limitations associated with the saturation of spectral bands at high biomass levels (Castillo-Santiago et al., 2010; Gallardo-Cruz et al., 2012; Gallardo-Cruz et al., 2018; Solórzano et al., 2017).

Furthermore, there is also a lack of knowledge regarding the spatial extent at which matrix effects are operating. The scale effect (SE) represents the spatial extent where landscape structure exerts its strongest effects on particular species (Fahrig, 2013; H. B. Jackson & Fahrig, 2012). The SE can be influenced by species traits (i.e. ranging behavior, habitat specialization, dispersal movements) and landscape predictors (habitat amount/fragmentation measures), suggesting that SE of landscape structure may vary among species and landscape patterns Jackson & Fahrig, 2012, 2015; Miguet et al., 2016). This is a critical issue since the species' responses can be overlooked if assessed at an incorrect scale, misleading conservation plans (Lenore Fahrig, 2013; H. B. Jackson & Fahrig, 2015). Nonetheless, the SE of landscape structure remains unexplored for most species (Lenore Fahrig, 2013; H. B. Jackson & Fahrig, 2012; McGarigal et al., 2016), and to our knowledge, no one has ever tested between matrix effects (Driscoll et al., 2013; Miguet et al., 2016).

Terrestrial mammals play a key role in the long-term functioning of rainforests (Galetti & Dirzo, 2013; Stoner et al., 2007; Terborgh, 2013). Nevertheless, they are highly vulnerable to habitat loss and fragmentation (Ahumada et al., 2011; Lyra-Jorge et al., 2010; M. Pfeifer et al., 2017; Wearn et al., 2017). Several studies have found that the proportion of tree cover in the surrounding matrix is associated with the abundance, occupancy and richness of mammals within forest patches at varying spatial scales (García-Marmolejo et al., 2015; Garmendia et al., 2013; Nagy-Reis et al., 2017; Umetsu et al., 2008). These studies, however, have overlooked the identity and the scale of matrix effects involved in the persistence of terrestrial mammals. Therefore, the aim of this study is to assess the role of matrix effects on (1) habitat amount and (2) resistance to movement on patch occupancy by four large terrestrial mammals using a multi-scale spatial approach. We untangled matrix effects by using composition metrics to represent matrix effects on habitat amount and matrix resistance estimations derived from satellite imagery to represent resistance to movement. Thereafter, we assessed the contribution of each parameter through occupancy models' selection and their variables' importance at different spatial extents. Following the hypothesis described by Miguet et al. (2016), we expected that the scale of effect of matrix effects on habitat amount should be smaller than those on resistance movement.

## Material & Methods

### *Study area*

We conducted the fieldwork at the Lacandona rainforest in southeastern Mexico (Fig 1a). The land-cover change to cattle pastures has shrunk its extension by two thirds in the last 40 years (De Jong et al., 2000; Kolb & Galicia, 2018; Mendoza & Dirzo, 1999). This region, however, encompasses the largest tropical rainforest of Mesoamerica (González-Espinosa et al., 2005). The vegetation is dominated by lowland tropical forest, reaching up to 40 m in height in alluvial terraces (Pennington & Sarukhán, 2005). The average monthly temperature is 24 to 26 ºC, and the annual precipitation ranges from 2500 to 3500 mm (Mendoza & Dirzo, 1999). We selected 16 fragments of floodplain forest, ranging between 1 ha and 63 ha (Fig 1b).

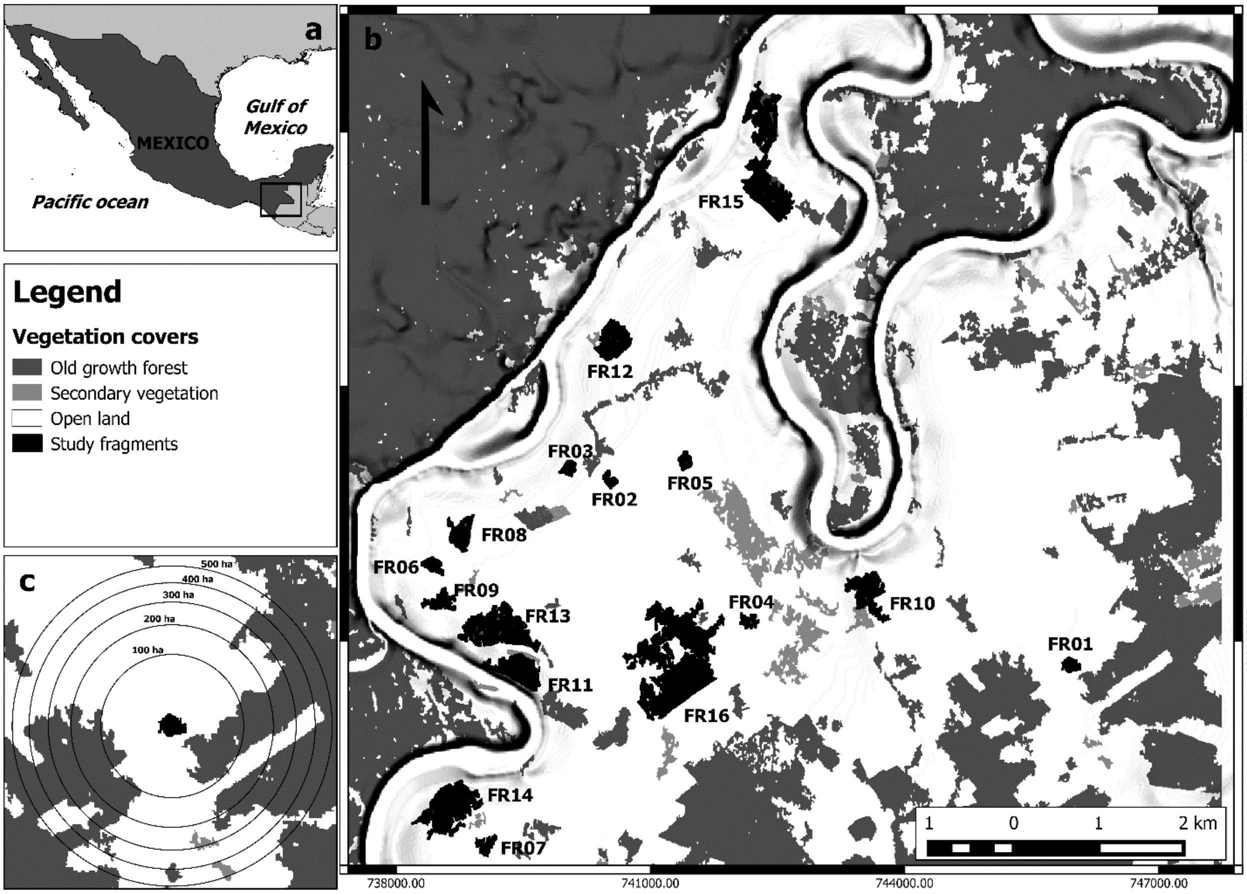


**Fig 1. Location of the study area in the Lacandona rain forest in Chiapas, southeastern Mexico (a)**. We show the location of the 16 study forest fragments (black) in the Marqués de

Comillas Region (b). The five buffer sizes around the geographic center of the focal patch are also indicated (c).

### *Experimental design*

We surveyed the terrestrial mammal community from February to June of 2012, during the peak of mammal activity (Haugaasen & Peres, 2007). We combined two sampling methods to obtain a more accurate estimation of species number within each fragment in a short period of time. Firstly, we used camera traps (Cuddeback IR) for 30 consecutive days. At the end of the sampling period, we identified each mammal species following field guides (Reid, 2009). Secondly, we established two 500 × 3 m trails within each fragment and recorded the presence of mammals through sightings and indirect evidence (i.e., footprints, feces, feeding sites) three times a week for four weeks. We only considered terrestrial mammals with a body mass ≥ 1 kg (Medellin, 1994). We detected 15 species (Table S1), but we focused our analysis on 4 large-sized species: the white-tailed deer (*Odocoileus virginianus*), the ocelot (*Leopardus pardalis*), the white-collared peccary (*Pecari tajacu*) and the jaguar (*Panthera onca*).

### *Image classification*

We employed a multispectral SPOT-5 satellite image recorded in March 2012. We carried out a supervised classification by using ground control points evenly distributed across different cover classes categorized as old-growth forest, secondary forest, arboreal crops, cattle pasture, anthropogenic features, bare soil, semiaquatic vegetation and water bodies. We used the GRASS GIS software (GRASS Development Team, 2017) for the complete procedure. The overall classification accuracy was 79%.

### *Landscape metrics*

We measured three landscape metrics relevant to terrestrial mammal persistence in fragmented tropical forests (Garmendia et al., 2013; Goulart et al., 2009; Thornton et al., 2011; Umetsu et al., 2008) and one resistance distance within four spatial extents (buffers with sizes of 200, 300, 400 and 500 ha; Fig 1c) around the centroid of each patch (Table 1). Although the overlapping between buffers of nearby sampling points was high in the larger spatial extents (400 and 500 ha), the degree of spatial autocorrelation in the model residuals is not necessarily associated with the extent of landscape overlap but rather with the proximity between sampling sites (Cleary et al., 2016; Zuckerberg et al., 2012). According to Moran's I autocorrelation tests, we did not find spatial autocorrelation between the distance of sampling sites and the number of detection records of each species (Table S2).

**Table 1. Landscape metrics and resistance estimators employed for the analysis**

| **Landscape metric** | **Formula** | **Description** |
|---|---|---|
| FC | $\mathrm{FC} = 100 \times \left[\frac{\sum_{j=1}^{n} a_i}{A}\right]$ | Where *a* is the area (m$^2$) of forest patch *i* and *A* the is the total landscape area |
| PD | $\mathrm{PD} = \frac{n_i}{A}(10{,}000)(100)$ | Where $n_i$ is the total number of patches in the landscape of the land cover *i* and *A* is the total landscape area (m$^2$) |
| MH | $\mathrm{MH} = 100 \times \left[\sum_{i=1}^{6}\left(\frac{a_i \cdot Q_i}{A}\right)\right]$ | Where $a_i$ is the total area (m$^2$) of the land cover *i*, $Q_i$ is a relative quality index obtained by dividing the suitability values of each land cover (as seen in Methods) by seven (the maximum suitability |

|  |  |  |
|---|---|---|
|  |  | value, corresponding to the old-growth forest cover) and $A$ is the total landscape area ($m^2$) |
| MR | $\mathrm{VAR} = \sum_{i,j=0}^{N-1} P_{i,j}\,(i - \mathrm{MEAN})^2$ | Where $P_{i,j}$ is the ($i,j$) element of the GLCM, and represents the probability of finding the reference pixel value $i$ in combination with a neighbor pixel value $j$ |

We selected two metrics related to landscape composition and one related to landscape configuration. The composition metrics were the percentage of old-growth forest cover (FC) and the percentage of habitat accounting the amount high-quality matrix (MH). The FC is associated to habitat available, whereas MH is an indicator of additional habitat when accounting for high-quality matrices (Umetsu et al., 2008). The configuration metric was the density of patches (PD), which is an accurate descriptor of habitat fragmentation (Lenore Fahrig, 2013, 2017; Rayfield et al., 2011).

### *Matrix effect on habitat amount*

We constructed the MH metric by assigning quality values to each land cover of the study area. The quality values were based on the assumption that overall species presence declines along a land-use gradient (Gardner et al., 2009). We ranked the quality of each land-cover type based on the suitability of vegetation structure for terrestrial mammals´ feeding, movement and/or habitat on a six-point scale (Garmendia et al., 2013): 1 (water bodies, with the lowest suitability); 2 (anthropogenic cover); 3 (cattle pasture); 4 (arboreal crops); 5 (semiaquatic vegetation); and 6 (secondary forest, with the highest suitability). Then, we calculated the relative quality of land covers by dividing each value by seven (the quality value of old-growth forest). Finally, we related the relative quality values to the area of each land cover to re-calculate the percentage of total matrix (Table 1).

### *Matrix effect on resistance movement*

We constructed the matrix resistance metric (MR) through the “variance” texture variable of the red (*R*) and near-infrared (*NIR*) spectral bands from the SPOT-5 satellite image (Table 1). The spectral values of the *R* and *NIR* layers are strongly associated to the canopy cover and aboveground biomass of woody vegetation of tropical rainforests, respectively (Castillo-Santiago et al., 2010; José Alberto Gallardo-Cruz et al., 2018; Sarker & Nichol, 2011). The texture variables were estimated by constructing a gray-level co-occurrence matrix (GLCM). Firstly, we transformed the pixel values to 64 levels of gray, and then we calculated the texture metrics within a window size of 9 × 9 pixels using an offset of one pixel in four angle directions (0°, 45°, 90º and 135°). We averaged the metrics calculated in the four directions to obtain a directionless metric. These are the optimal features for assessing the vegetation structure in the study site (Castillo-Santiago et al., 2010). We applied a mask to each band to eliminate water bodies and bare ground from the analysis. We employed the *glcm* package for the entire procedure (Zvoleff, 2016).

Next, we employed a natural breaks classification to divide the distribution of the resulting cell values into 20 resistance classes (from 10 to 200). We added a buffer around each resistance layer to minimize the overestimation of resistance distances caused by artificial boundaries (Koen et al., 2010). Finally, we estimated patch isolation by matrix resistance using the Circuitscape software (McRae et al., 2008). We modeled the resistance distance across all pairs of forest patches within each buffer and obtained the mean resistance distance for each buffer size.

### *Statistical analysis*

We used occupancy modeling with a likelihood-based approach (D. I. MacKenzie et al., 2006) to estimate patch occupancy ($\psi$) of each species while accounting for detection probability ($p$). We regarded occupancy as a measure of mammal habitat use instead of true occupancy because the home range size of each species exceeds that of the sampling units (Hines et al., 2010; D.I. MacKenzie & Nichols, 2004; Nagy-Reis et al., 2017). This supposition did not violate the assumption that the sampling sites are closed to changes in occupancy during repeated surveys (D.I. MacKenzie, 2005). We employed a single-season approach, wherein data from camera trapping and trail sampling were included in different sampling occasions.

We determined a general model for $p$ by developing models where $\psi$ remained constant ($\psi(.)$) while allowing $p$ to vary as a function of either a single or a combination of the following observation covariates: survey method of each sampling occasion (camera trapping/trail sampling), patch use by cattle (presence/absence), and patch flooding during the rainy season (flooded/not flooded). We assessed the goodness of fit of these models using the Mackenzie and Bailey goodness of fit test for single-season occupancy (Darryl I. MacKenzie & Bailey, 2004). First, we calculated the Pearson $\chi^2$ from the observed and expected values based on the detection histories and single-season occupancy model, respectively (D. I. MacKenzie et al., 2006; Darryl I. MacKenzie & Bailey, 2004). Then, we employed a parametric bootstrap approach (100 simulation per model) to obtain the p-value of the $\chi^2$ statistic and the overdispersion parameter ($\hat{c}$) of each model using the *AICcmodavg* package (Mazerolle, 2020). We selected the best-fit models (i.e., those with non-significant $\chi^2$ values and $\hat{c} < 2$; Table S3) and ranked them using the corrected version of the Akaike information criterion for small sample sizes (AICc). We accounted for those models with an AICc difference lower than two ($\Delta$AICc<2) from the topranking model as best-supported by the data (Burnham & Anderson, 2002). The model of survey method (*p(s)*) provided enough evidence of changes in detection probability for three species, whereas models that where *p* remained constant (null model) and that included patch flooding (*p(f)*) were the best supported by data for *P. tajacu* (Table S4).

We determined the SE of site covariates (Table 1) for each species by developing a general model for *p* while allowing $\psi$ to be constant or to vary as a function of the same covariate measured at the different buffer sizes (D I MacKenzie, 2006). We previously assessed the resistance distances that best represented the MR metric, and we selected the $R_v$ values for all species (Table S5). We estimated the Nagelkerke's $R^2$ index (Trust, 1991) and selected the model with the highest $R^2$ to determine the scale of effect of the covariate when different spatial extents were equally plausible (Table S6). We employed the *unmarked* package for the entire procedure (Fiske & Chandler, 2011). Once selected the SE of each covariate, we assessed the contribution and relative importance of landscape metrics on patch occupancy. We constructed a global model and developed the set of sub-models using the dredge function of the *MuMIn* package (Barton, 2018). We excluded those models that did not converge or had abnormal convergences (Welsh et al., 2013). Furthermore, we ranked the models as mentioned above and selected the subset of models for which the sum of the Akaike weights ($\sum w_i$) were ≤ 0.95 (Burnham & Anderson, 2002). We employed the selected models to estimate the relative contribution of each covariate through a model-average approach, and assessed their relative importance by summing the Akaike weights ($w_i$) of the models where the covariate was present (Burnham & Anderson, 2002).

Finally, we tested for differences in the SE between landscape metrics and among species with a nonparametric Kruskal-Wallis test using the R 3.5.2 statistical computing environment (R Development Core Team, 2018).

## Results

### *Relative importance and effects of landscape metrics*

We observed a high importance of patch density and forest cover on patch occupancy of all species. On one hand, density of patches was present in the best-supported models (Table 2) and represented the most important variable ($\sum w_i > 0.5$) for *O. virginianus*, *L. pardalis* and *P. onca* occupancy (Figs 2a, 2e and 2g). According to the averaged estimators, patch occupancy increased as the number of patches per unit area increased (Figs 2b, 2f and 2h). This was not true for *P. tajacu*, whose occupancy was not affected by the density of patches (Figs 2c, and 2d). The percentage of forest cover represented the second most important variable for *O. virginianus, P. tajacu* and *P. onca* (Figs 2a, 2c and 2g), and promoted patch occupancy between the 300-500ha spatial scales (Figs 2b, 2d and 2h).

**Table 2. Set of occupancy models of four terrestrial mammals employed for the model selection assessment and model-average approach in the Lacandona rainforest in Mexico.**

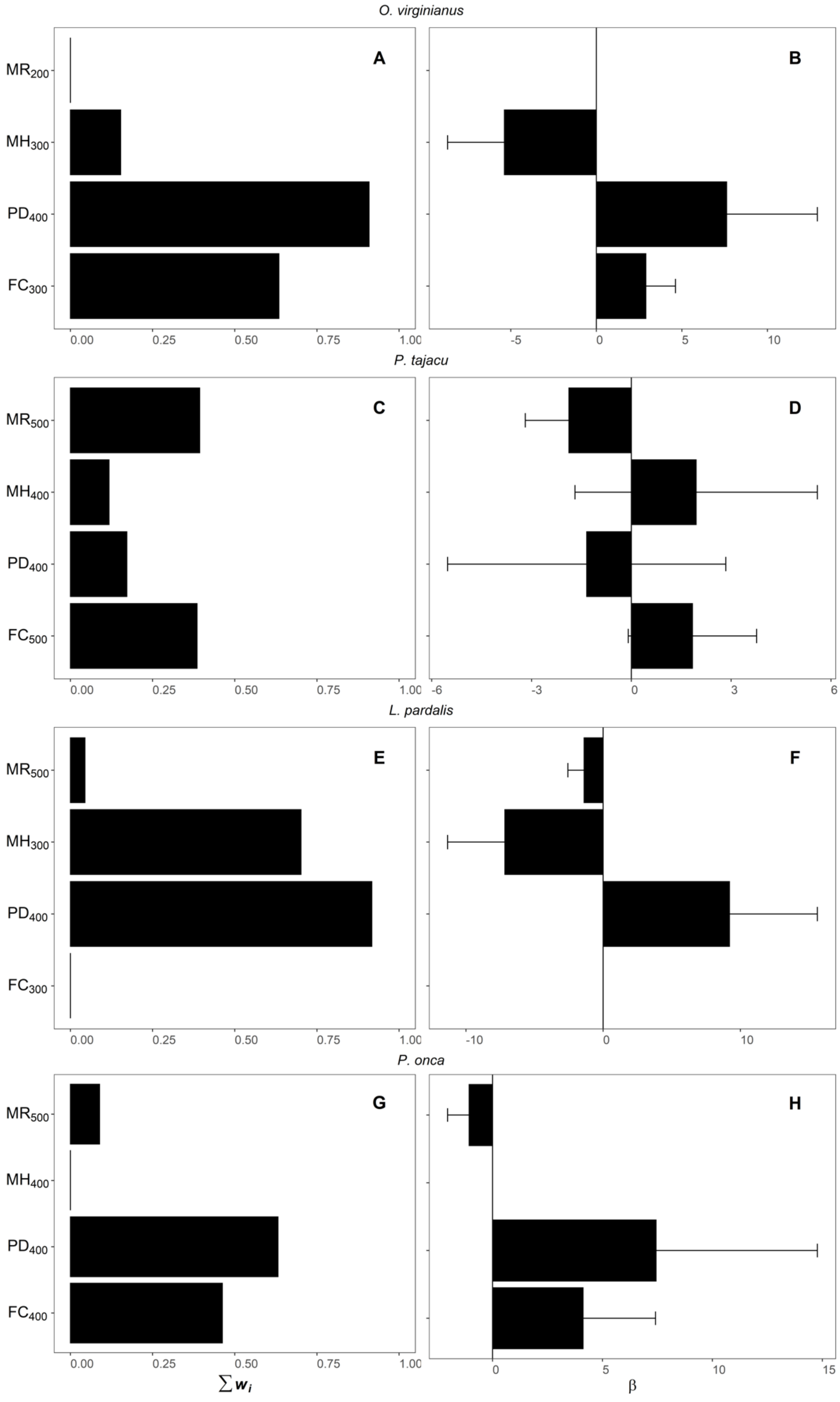
| Specie | Model | *LL* | *AICc* | $\Delta_i$ | $w_i$ | $R^2$ | $\chi^2$ | *P* | $\hat{c}$ |
|---|---|---|---|---|---|---|---|---|---|
| ***O. virginianus*** | $p(s)\psi(FC_{300}+PD_{400})$ | -21.53 | 59.07 | 0 | 0.59 | 0.77 | 84.4 | 0.39 | 1.24 |
| | $p(s)\psi(MH_{300}+PD_{400})$ | -22.96 | 61.92 | 2.85 | 0.14 | 0.73 | 84.37 | 0.36 | 1.43 |
| | $p(s)\psi(PD_{400})$ | -25.37 | 62.38 | 3.31 | 0.11 | 0.62 | 84.21 | 0.37 | 1.12 |
| | $p(s)\psi(.)$ | -27.47 | 62.94 | 3.87 | 0.08 | 0.51 | 84.18 | 0.37 | 1.25 |
| | $p(s)\psi(MR_{200}+PD_{400})$ | -24.3 | 64.61 | 5.54 | 0.04 | 0.67 | 84.17 | 0.48 | 0.9 |
| | $p(s)\psi(MR_{200})$ | -27.29 | 66.21 | 7.14 | 0.02 | 0.52 | 84.18 | 0.34 | 1.17 |
| | $p(s)\psi(MH_{300}+MR_{200}+PD_{400})$ | -22.68 | 66.69 | 7.62 | 0.01 | 0.74 | 84.42 | 0.48 | 1.13 |
| | $p(.)\psi(MH_{300}+PD_{400})$ | -28.56 | 68.75 | 9.68 | 0 | 0.43 | 131.76 | 0.75 | 0.72 |
| | $p(.)\psi(PD_{400})$ | -30.92 | 69.84 | 10.77 | 0 | 0.23 | 131.27 | 0.7 | 0.71 |
| | $p(.)\psi(.)$ | -33 | 70.92 | 11.86 | 0 | 0 | 131.07 | 0.63 | 0.82 |
| | $p(.)\psi(MR_{200}+PD_{400})$ | -29.84 | 71.31 | 12.24 | 0 | 0.33 | 131.07 | 0.64 | 0.72 |

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | $p(.)\psi(MR_{200})$ | -32.81 | 73.63 | 14.56 | 0 | 0.02 | 131.05 | 0.74 | 0.65 |
| ***P. tajacu*** | $p(.)\psi(MR_{500})$ | -51.39 | 110.78 | 0 | 0.24 | 0.21 | 346.05 | 0.02 | 1.48 |
| | $p(.)\psi(.)$ | -53.23 | 111.38 | 0.6 | 0.18 | 0 | 345.92 | 0.02 | 1.38 |
| | $p(.)\psi(FC_{500})$ | -51.79 | 111.59 | 0.81 | 0.16 | 0.16 | 345.84 | 0.03 | 1.42 |
| | $p(.)\psi(FC_{500}+MR_{500})$ | -50.84 | 113.31 | 2.53 | 0.07 | 0.26 | 345.92 | 0.02 | 1.43 |
| | $p(.)\psi(FC_{500}+MH_{400})$ | -50.92 | 113.47 | 2.69 | 0.06 | 0.25 | 345.98 | 0.05 | 1.4 |
| | $p(.)\psi(FC_{500}+PD_{400})$ | -50.97 | 113.58 | 2.8 | 0.06 | 0.25 | 355.69 | 0.05 | 1.48 |
| | $p(.)\psi(MR_{500}+PD_{400})$ | -51.15 | 113.94 | 3.16 | 0.05 | 0.23 | 346.05 | 0.02 | 1.41 |
| | $p(.)\psi(PD_{400})$ | -53.02 | 114.04 | 3.26 | 0.05 | 0.03 | 345.98 | 0.04 | 1.46 |
| | $p(.)\psi(MH_{400})$ | -53.08 | 114.16 | 3.38 | 0.04 | 0.02 | 345.91 | 0.05 | 1.41 |
| | $p(.)\psi(MH_{400}+MR_{500})$ | -51.36 | 114.35 | 3.57 | 0.04 | 0.21 | 346.04 | 0.03 | 1.47 |
| | $p(.)\psi(FC_{500}+MH_{400}+MR_{500})$ | -50.17 | 116.34 | 5.56 | 0.01 | 0.32 | 346.12 | 0.03 | 1.41 |
| | $p(.)\psi(FC_{500}+MR_{500}+PD_{400})$ | -50.72 | 117.44 | 6.66 | 0.01 | 0.27 | 346.03 | 0.07 | 1.42 |
| | $p(.)\psi(MH_{400}+PD_{400})$ | -52.93 | 117.49 | 6.71 | 0.01 | 0.04 | 345.79 | 0.04 | 1.44 |
| | $p(.)\psi(FC_{500}+MH_{400}+PD_{400})$ | -50.91 | 117.82 | 7.04 | 0.01 | 0.25 | 355.9 | 0.06 | 1.49 |
| | $p(.)\psi(MH_{400}+MR_{500}+PD_{400})$ | -51.14 | 118.29 | 7.51 | 0.01 | 0.23 | 345.98 | 0.02 | 1.43 |
| | $p(.)\psi(FC_{500}+MH_{400}+MR_{500}+PD_{400})$ | -50.02 | 121.38 | 10.6 | 0 | 0.33 | 345.99 | 0.03 | 1.44 |
| ***L. pardalis*** | $p(s)\psi(MH_{300}+PD_{400})$ | -30.02 | 76.04 | 0 | 0.58 | 0.72 | 102.12 | 0.57 | 0.64 |
| | $p(s)\psi(PD_{400})$ | -33.48 | 78.59 | 2.55 | 0.16 | 0.56 | 101.18 | 0.53 | 0.74 |
| | $p(.)\psi(MH_{300}+PD_{400})$ | -34.12 | 79.88 | 3.83 | 0.08 | 0.53 | 182.9 | 0.6 | 0.91 |
| | $p(s)\psi(.)$ | -36.02 | 80.03 | 3.99 | 0.08 | 0.4 | 101.15 | 0.54 | 0.73 |
| | $p(s)\psi(MR_{500}+PD_{400})$ | -32.65 | 81.3 | 5.26 | 0.04 | 0.61 | 101.13 | 0.58 | 0.56 |
| | $p(s)\psi(MR_{500})$ | -35.46 | 82.55 | 6.51 | 0.02 | 0.44 | 101.25 | 0.56 | 0.75 |
| | $p(.)\psi(PD_{400})$ | -37.52 | 83.04 | 6.99 | 0.02 | 0.27 | 184.26 | 0.67 | 0.85 |
| | $p(.)\psi(MR_{500}+PD_{400})$ | -36.69 | 85.01 | 8.97 | 0.01 | 0.35 | 184.52 | 0.64 | 0.84 |
| | $p(.)\psi(.)$ | -40.05 | 85.03 | 8.99 | 0.01 | 0 | 184.39 | 0.65 | 0.84 |
| | $p(.)\psi(MR_{500})$ | -39.5 | 86.99 | 10.95 | 0 | 0.07 | 184.28 | 0.63 | 0.89 |
| ***P. onca*** | $p(s)\psi(FC_{400}+PD_{400})$ | -15.3 | 46.59 | 0 | 0.43 | 0.81 | 10.93 | 0.63 | 0.82 |
| | $p(s)\psi(.)$ | -19.8 | 47.59 | 1 | 0.26 | 0.65 | 10.91 | 0.67 | 0.87 |
| | $p(s)\psi(PD_{400})$ | -18.48 | 48.6 | 2.01 | 0.16 | 0.7 | 10.95 | 0.59 | 0.9 |

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| $p(s)\psi(MR_{500})$ | -19.13 | 49.9 | 3.31 | 0.08 | 0.68 | 10.92 | 0.64 | 0.85 |
| $p(s)\psi(FC_{400}+MR_{500})$ | -17.14 | 50.29 | 3.7 | 0.07 | 0.76 | 10.64 | 0.68 | 0.84 |
| $p(.)\psi(.)$ | -27.67 | 60.26 | 13.67 | 0 | 0 | 116.61 | 0.74 | 0.7 |
| $p(.)\psi(PD_{400})$ | -26.37 | 60.74 | 14.15 | 0 | 0.15 | 117.15 | 0.72 | 0.7 |
| $p(.)\psi(MR_{500})$ | -27.01 | 62.02 | 15.43 | 0 | 0.08 | 116.82 | 0.76 | 0.66 |
| $p(.)\psi(MR_{500}+PD_{400})$ | -25.4 | 62.44 | 15.85 | 0 | 0.25 | 117.46 | 0.78 | 0.64 |
| $p(.)\psi(MH_{400}+MR_{500}+PD_{400})$ | -24.01 | 64.03 | 17.44 | 0 | 0.38 | 116.85 | 0.73 | 0.72 |

The covariates are the percentage of forest cover (FC), patch density (PD), the percentage of habitat from matrix (MH) and matrix resistance (MR). The subscript numbers indicate the buffer size (in hectares) of each covariate. The null model does not include a covariate (.). The models' log-likelihood (LL), Akaike Information Criterion (AIC), Akaike differences ($\Delta_i$), Akaike weights ($w_i$), the Nagelkerke's $R^2$ ($R^2$), the models' Pearson chi-square ($\chi^2$), significance ($P$) and overdispersion parameter ($\hat{c}$) of each model are shown.

The relative contribution of matrix effects was lower than for forest cover and patch density. Interestingly, the importance between matrix effects varied among species, and were characterized for presenting contrasting values. The percentage of matrix habitat was more important than matrix resistance for *O. virginianus* and *L. pardalis* (Figs 2a and 2e), and affected negatively patch occupancy (Figs 2b and 2f). Contrarily, matrix resistance was more important than matrix habitat for *P. tajacu* and *P. onca* (Figs 2c and 2g), whose occupancy decreased as patch isolation by resistance increased (Figs 2d and 2h). We must emphasize that matrix resistance had significant effects for all species, with the exception of *O. virginianus*.



O. virginianus
A
B
MR200
MH300
PD400
FC300
0.00
0.25
0.50
0.75
1.00
-5
0
5
10
P. tajacu
C
D
MR500
MH400
PD400
FC500
0.00
0.25
0.50
0.75
1.00
-6
-3
0
3
6
L. pardalis
E
F
MR500
MH300
PD400
FC300
0.00
0.25
0.50
0.75
1.00
-10
0
10
P. onca
G
H
MR500
MH400
PD400
FC400
0.00
0.25
0.50
0.75
1.00
0
5
10
15
∑wi
β

**Fig 2. Relative importance and effects of covariates on patch occupancy of four terrestrial mammals in the Lacandona rainforest in Mexico**. The importance of each covariate is represented by the sum of the Akaike weights ($\sum w_i$). The effects of each covariate were estimated through a model-averaged parameter estimate (β) of information-theoretic-based model selection and multimodel inference for occupancy. The whiskers represent the unconditional standard error (USE) and those for which the USE did not include zero are the influential covariates. The covariates are the percentage of forest cover (FC), patch density (PD), the percentage of habitat when accounting for suitable matrix (MH) and matrix resistance (MR). The subscript numbers indicate the scale of effect of each covariate.

### *Differences in the scale of effect among landscape metrics*

Although we did not find differences in the scale of effect among species ($\chi^2 = 8.4$, d.f. = 3, P = 0.26), the scale of effect varied among landscape metrics ($\chi^2 = 8.25$, d.f. = 3, P = 0.04) when accounting for those with significant effects (Fig 2). The scale of effect of landscape metrics increased as follows: MH < FC < PD < MR. We also observed a consistent scale of effect for percentage of matrix habitat (300ha), patch density (400ha) and matrix resistance (500ha), regardless species.

## Discussion

We aimed to investigate the mechanisms that sustain patch occupancy by terrestrial mammals at multiple spatial scales by untangling two matrix effects in the landscape. Our results showed matrix effects had negative effects on patch occupancy at varying spatial scales. Matrix effects on habitat amount affected patch occupancy at smaller spatial scales than matrix resistance. We also observed that the importance of these effects shifted among species. Such differences may be associated with the scale of interaction between landscape structure and species' home range, habitat requirements and dispersal distance (Miguet et al., 2016).

### *Matrix effects on habitat amount*

Previous studies have associated matrix covers that provide food resources or improve habitat quality within species home range with the provision of complementary/supplementary resources near habitat patches (Asensio et al., 2009; Garmendia et al., 2013). In our study, the amount of habitat provided by the matrix increased along the proportion of semiaquatic vegetation and secondary forests, suggesting these covers are critical for the persistence of the herbivore mammals assessed. It is well documented that floodplains provide fruits and suitable conditions for collared peccaries (A. Keuroghlian & Eaton, 2008). Secondary forests are preferred by the white-tailed deer because of the high availability of leaves and stems, which represent most of their diet (Arceo et al., 2005; García-Marmolejo et al., 2015; Tejeda-Cruz et al., 2009). Nevertheless, they require old-growth forest landscapes for their long-term persistence (García-Marmolejo et al., 2015). The latter is consistent with the high importance of forest cover and patch density observed. We must emphasize that our study site is highly deforested (< 25% of forest cover) and the dominant land covers in the matrix are cattle pastures, which explains the negative relationship between forest cover and matrix habitat ($r = -0.82$). Accordingly, the negative effect of the percentage of matrix habitat on the occupancy of *O. virginianus* may be related with a low habitat quality and depauperate food resources from the dominant matrix covers within their home-range, suggesting the role of landscape matrix to sustain complementation/supplementation processes at smaller scales (Dunning et al., 1992).

The negative effect of matrix habitat on *L. pardalis* occupancy and its null effect for *P. onca* supports their condition as forest-dependent species. For *L. pardalis*, the use of matrix as complimentary habitat is possibly restricted to secondary forests, as ocelots tend to avoid flooded areas (Trolle & Kéry, 2005) and prefer large patches of densely-forested vegetation (Garmendia et al., 2013; V. L. Jackson et al., 2005; Pérez-Irineo & Santos-Moreno, 2016). This also holds true for the jaguar, a species with large home range requirements and a preference for primary forest over human-modified habitats (Cullen-Junior et al., 2013; de la Torre et al., 2017; Morato et al., 2016). We must emphasize that jaguar records were restricted in landscapes near to large patches of undisturbed old-growth forest (> 100 ha), a pattern observed in similar cattle ranching areas (de Souza et al., 2018; Zimbres et al., 2017). These conditions, as well as the null association of matrix habitat to patch occupancy, suggest that jaguar presence may result from spillover effects.

### *Matrix effects on resistance to movement*

Matrix resistance was important only at larger spatial scales (500ha) and decreased patch occupancy. These findings, along the positive effects of patch density at similar spatial scales (400ha) suggest that functional connectivity is driven by vegetation quality of matrix and by fragmentation *per se* (Bowman, Cappuccino, et al., 2002; Holzschuh et al., 2010; Radford et al., 2005; Saura & Rubio, 2010; Tischendorf & Fahrig, 2000).

An increase of patches in the landscape promotes the availability of habitat across the landscape, as well as the amount of forest edges, which had positive effects in mammals' richness in the study area at the same spatial scales (Garmendia et al., 2013). The same study also found the positive effects of forest patches and edges increased when accounting the positive effect of matrix quality at smaller spatial scales. The latter suggests that matrix quality promotes functional connectivity at large spatial scales, as observed elsewhere (Powney et al. 2011, 2012; Muratet et al., 2013). It is interesting that matrix effects on resistance movement were more important for mammals with large home-range sizes and dispersal distances, such as ocelots, collared-peccaries and jaguars (de la Torre et al., 2017; Di Bitetti et al., 2006; Alexine Keuroghlian et al., 2004). This is supported by Miguet et al. (2016), who predicted that scale of effect increases with the mean dispersal distance, a trait strongly related with home range size (Bowman, Jaeger, et al., 2002).

In this sense, our findings indicate that connectivity loss has a negative effect on terrestrial mammals at large scales in fragmented rainforests and that matrix resistance plays a key role in driving the inter-patch movement of mammals with large dispersal distances (Thornton et al. 2011; Garmendia et al. 2013). Nonetheless, since we observed these effects in the largest spatial scale, more studies are needed to accurately find the scale of effect of matrix resistance, which might be operating at larger spatial scales (H. B. Jackson & Fahrig, 2015).

### *The role of remote sensing techniques to estimate matrix resistance*

Our results indicate that resistance estimations from satellite can provide of realistic connectivity measurements. Although quality indices has been employed as indicator of matrix permeability in fragmented rainforests (Arroyo-Rodríguez, González-Perez, et al., 2013; Galán-Acedo et al., 2018, 2019; Garmendia et al., 2013), it does not represent isolation distances and/or movement rates (Rayfield et al., 2011; Tischendorf & Fahrig, 2000). Additionally, the use of textural variables on spectral data allow to obtain a more heterogeneous range of values associated to the structure of matrix vegetation than vegetation indices or spectral bands alone. This is critical in the tropics, where textural variables outperform vegetation indices when estimating forest structure (J. V. Solórzano et al., 2018, 2017).

Mammal species were only affected by *Rv* matrix resistance. In the tropics, the red band captures the reflectance of the crown area of canopy vegetation (Bourgoin et al., 2018; Steininger, 2000), and the textural variables are associated with the spatial variability of canopy structure (J. Alberto Gallardo-Cruz et al., 2012; M. Pfeifer et al., 2016; J. V. Solórzano et al., 2018). Tree canopy plays a key role in sustaining biodiversity in human-modified landscapes by regulating both a forest's understory and edge microclimate (Ewers & Banks-Leite 2013; Hardwick et al. 2015). The association between forest canopy with terrestrial mammal's composition suggests that canopy cover also promote animal movement along human-modified landscapes (Pardo et al., 2018). Accordingly, our results indicate that matrix resistance for our species is driven by canopy structure through microclimate regulation.

Estimating more heterogeneous resistance values improves connectivity assessments. Connectivity networks that derived from NDVI values improved model fit more than their homogeneous counterparts when assessing community dissimilarity among habitat patches in an urban landscape (Muratet et al., 2013). We must emphasize, however, that the use of satellite imagery in connectivity assessments is considered in its infancy, and more studies are needed to evaluate its suitability to measure, map and understand functional connectivity for a variety of species in human-modified landscapes (Muratet et al., 2013; Pettorelli et al., 2014). Estimations of vegetation structure and matrix heterogeneity can be affected by the scale of the site, the image resolution and the temporal range of the image generation (Gamon et al., 2020; Hernando et al., 2017).

Forthcoming approaches aimed at improving our understanding regarding the role of landscape matrix on biodiversity conservation should consider untangling matrix effects at varying spatial scales. We must emphasize that further studies are needed to fully understand how mammals respond to canopy structure, as well as to perform analysis at larger spatial scales to determine the scale of effect of landscape matrix on connectivity. We also encourage more detailed connectivity assessments using satellite imagery for long-term monitoring purposes.

## Conclusions

We conclude that the interaction between landscape matrix with species home range and dispersal requirements drives the scale of effect and importance of the different matrix effects. Mammals with small home-range sizes rely on the nearby matrix covers to fulfill their food and habitat requirements within their home range. Species with larger home ranges and long dispersion distances rely on the canopy structure of matrix vegetation to facilitate their inter-patch movement at larger spatial scales. Our findings also represent an important step in conservation planning because mammal's conservation in human-modified landscapes should favor the preservation of matrix covers that increase habitat amount and quality. Meanwhile, management practices that favor canopy cover at larger spatial extents –such as alley cropping, extensive silvopasture or riparian buffers– would reduce matrix resistance for vagile species (Martínez-Ramos et al., 2016). These recommendations support a land-sharing strategy to improve the conservation value of the remaining forest patches (Lenore Fahrig, 2017), particularly where forest is already hyper-fragmented (Hernández-Ruedas et al., 2018).

## Acknowledgments

We thank the Velasco and Quintana families, as well as the people of Quiringüicharo for their hospitality and support. We acknowledge the logistical and technical support provided by J. Manuel Lobato-García during the fieldwork. P. Ávila-Romano supported the field sampling. Estación Chajul and Arca de Noe provided logistic assistance and accommodation. CentroGeo facilitated the satellite images. SNA is a doctoral student from Programa de Doctorado en Ciencias Biomédicas, Universidad Nacional Autónoma de México (UNAM), and was supported by CONACyT, Mexico and DGAPA-UNAM.

# References

Ahumada JA, Silva CEF, Gajapersad K, Hallam C, Hurtado J, Martin E, McWilliam A, Mugerwa B, O'Brien T, Rovero F, Sheil D, Spironello WR, Winarni N, Andelman SJ. 2011. Community structure and diversity of tropical forest mammals: data from a global camera trap network. *Philosophical transactions of the Royal Society of London. Series B, Biological sciences* 366:2703–11. DOI: 10.1098/rstb.2011.0115.

Arceo G, Mandujano S, Gallina S, Perez-Jimenez LA. 2005. Diet diversity of white-tailed deer (Odocoileus virginianus) in a tropical dry forest in Mexico. *Mammalia* 69:159–168. DOI: 10.1515/mamm.2005.014.

Arroyo-Rodríguez V, González-Perez IM, 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* 28:1717–1727. DOI: 10.1007/s10980-013-9929-2.

Asensio N, Arroyo-Rodríguez V, Dunn JC, Cristóbal-Azkarate J. 2009. Conservation value of landscape supplementation for howler monkeys living in forest patches. *Biotropica* 41:768–773. DOI: 10.1111/j.1744-7429.2009.00533.x.

Ayram CAC, Mendoza ME, Etter A, Salicrup DRP. 2015. Habitat connectivity in biodiversity conservation A review of recent studies and applications. *Progress in Physical Geography*:0309133315598713. DOI: 10.1177/0309133315598713.

Baccini A, Goetz SJ, Walker WS, Laporte NT, Sun M, Sulla-Menashe D, Hackler J, Beck PSA, Dubayah R, Friedl MA, Samanta S, Houghton RA. 2012. Estimated carbon dioxide emissions from tropical deforestation improved by carbon-density maps. *Nature Climate Change* 2:182–185. DOI: 10.1038/nclimate1354.

Barton K. 2018. MuMIn: Multi-Model Inference. *R package version 1.42.1*.

Di Bitetti MS, Paviolo A, De Angelo C. 2006. Density, habitat use and activity patterns of ocelots (Leopardus pardalis) in the Atlantic Forest of Misiones, Argentina. *Journal of Zoology* 270:153–163. DOI: 10.1111/j.1469-7998.2006.00102.x.

Bourgoin C, Blanc L, Bailly JS, Cornu G, Berenguer E, Oszwald J, Tritsch I, Laurent F, Hasan AF, Sist P, Gond V. 2018. The potential of multisource remote sensing for mapping the biomass of a degraded Amazonian forest. *Forests* 9. DOI: 10.3390/f9060303.

Bowman J, Cappuccino N, Fahrig L. 2002. Patch size and population density: The effect of immigration behavior. *Ecology and Society* 6:art9. DOI: 9\nArtn 9.

Bowman J, Jaeger JAG, Fahrig L. 2002. Dispersal distance of mammals is proportional to home range size. *Ecology* 83:2049–2055. DOI: 10.1890/0012-9658(2002)083[2049:DDOMIP]2.0.CO;2.

Burnham KP, Anderson DR. 2002. *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach (2nd ed)*. Springer-Verlag. DOI: 10.1016/j.ecolmodel.2003.11.004.

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

Castillo-Santiago MA, Ricker M, De Jong BHJJ. 2010. Estimation of tropical forest structure from spot-5 satellite images. *International Journal of Remote Sensing* 31:2767–2782. DOI: 10.1080/01431160903095460.

Cavender-Bares J, Schweiger AK, Pinto-Ledezma JN, Meireles JE. 2020. Applying Remote Sensing to Biodiversity Science. In: Cavender-Bares J, Gamon JA, Townsend PA eds. *Remote Sensing of Plant Biodiversity*. Cham: Springer International Publishing, 13–42. DOI: 10.1007/978-3-030-33157-3_2.

Chazdon RL, Harvey CA, Komar O, Griffith DM, Ferguson BG, Martínez-Ramos M, Morales H, Nigh R, Soto-Pinto L, Van Breugel M, Philpott SM. 2009. Beyond reserves: A research agenda for conserving biodiversity in human-modified tropical landscapes. *Biotropica* 41:142–153. DOI: 10.1111/j.1744-7429.2008.00471.x.

Cleary KA, Waits LP, Finegan B. 2016. Agricultural intensification alters bat assemblage composition and abundance in a dynamic Neotropical landscape. *Biotropica* 48:667–676. DOI: 10.1111/btp.12327.

Cullen-Junior L, Sana DA, Lima F, Abreu KC de, Uezu A. 2013. Selection of habitat by the jaguar, Panthera onca (Carnivora: Felidae), in the upper Paraná River, Brazil. *Zoologia (Curitiba)* 30:379–387. DOI: 10.1590/S1984-46702013000400003.

Daniel K, Brian H, Haddad NM, Morris And WF, Nicole T. 2010. The conflicting role of matrix habitats as conduits and barriers for dispersal. *Ecology* 91:944–950. DOI: 10.1890/09-0614.1.

Driscoll DA, Banks SC, Barton PS, Lindenmayer DB, Smith AL. 2013. Conceptual domain of the matrix in fragmented landscapes. *Trends in Ecology and Evolution* 28:605–613. DOI: 10.1016/j.tree.2013.06.010.

Dunning JB, Danielson BJ, Pulliam HR. 1992. Ecological processes that affect populations in complex landscapes. *Oikos* 65:169–175. DOI: 10.2307/3544901.

Ewers RM, Banks-Leite C. 2013. Fragmentation impairs the microclimate buffering effect of tropical forests. *PLoS ONE* 8:e58093. DOI: 10.1371/journal.pone.0058093.

Eycott A, Watts K, Brandt G, Buyung-Ali L, Bowler D, Stewart G, Pullin A. 2010.CEE review 08-006 (SR43). Collaboration for Environmental Evidence. *Available at www.environmentalevidence.org/SR43.html.*

Fahrig L. 2013. Rethinking patch size and isolation effects: The habitat amount hypothesis. *Journal of Biogeography* 40:1649–1663. DOI: 10.1111/jbi.12130.

Fahrig L. 2017. Ecological Responses to Habitat Fragmentation Per Se. *Annual Review of Ecology, Evolution, and Systematics* 48:annurev-ecolsys-110316-022612. DOI: 10.1146/annurev-ecolsys-110316-022612.

Fiske I, Chandler R. 2011. unmarked: An R Package for Fitting Hierarchical Models of Wildlife Occurrence and Abundance. *Journal of Statistical Software* 43:1–23.

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* 41:2027–2037. DOI: 10.1111/ecog.03632.

Galán-Acedo C, Arroyo-Rodríguez V, Estrada A, Ramos-Fernández G. 2019. Forest cover and matrix functionality drive the abundance and reproductive success of an endangered primate in two fragmented rainforests. *Landscape Ecology* 34:147–158. DOI: 10.1007/s10980-018-0753-6.

Galetti M, Dirzo R. 2013. Ecological and evolutionary consequences of living in a defaunated world. *Biological Conservation* 163:1–6. DOI: 10.1016/j.biocon.2013.04.020.

Gallardo-Cruz JA, Hernández-Stefanoni JL, Moser D, Martínez-Yrizar A, Llobet S, Meave JA. 2018. Relating species richness to the structure of continuous landscapes: alternative methodological approaches. *Ecosphere* 9. DOI: 10.1002/ecs2.2189.

Gallardo-Cruz JA, Meave JA, González EJ, Lebrija-Trejos EE, Romero-Romero MA, Pérez-García EA, Gallardo-Cruz R, Hernández-Stefanoni JL, Martorell C. 2012. Predicting tropical dry forest successional attributes from space: Is the key hidden in image texture? *PLoS ONE* 7:e30506. DOI: 10.1371/journal.pone.0030506.

Gamon JA, Wang R, Gholizadeh H, Zutta B, Townsend PA, Cavender-Bares J. 2020. Consideration of Scale in Remote Sensing of Biodiversity. In: Cavender-Bares J, Gamon JA, Townsend PA eds. *Remote Sensing of Plant Biodiversity*. Cham: Springer International Publishing, 425–447. DOI: 10.1007/978-3-030-33157-3_16.

García-Marmolejo G, Chapa-Vargas L, Weber M, Huber-Sannwald E. 2015. Landscape composition influences abundance patterns and habitat use of three ungulate species in fragmented secondary deciduous tropical forests, Mexico. *Global Ecology and Conservation* 3:744–755. DOI: 10.1016/j.gecco.2015.03.009.

Gardner TA, Barlow J, Chazdon R, Ewers RM, Harvey CA, Peres CA, Sodhi NS. 2009. Prospects for tropical forest biodiversity in a human-modified world. *Ecology Letters* 12:561–582. DOI: 10.1111/j.1461-0248.2009.01294.x.

Garmendia A, Arroyo-Rodríguez V, Estrada A, Naranjo EJ, Stoner KE. 2013. Landscape and patch attributes impacting medium- and large-sized terrestrial mammals in a fragmented rain forest. *Journal of Tropical Ecology* 29:331–344. DOI: 10.1017/S0266467413000370.

Gibbs HK, Ruesch AS, Achard F, Clayton MK, Holmgren P, Ramankutty N, Foley JA. 2010. Tropical forests were the primary sources of new agricultural land in the 1980s and 1990s. *Proceedings of the National Academy of Sciences* 107:16732–16737. DOI: 10.1073/pnas.0910275107.

Goulart FVB, Cáceres NC, Graipel ME, Tortato MA, Ghizoni IR, Oliveira-Santos LGR, Ghizoni Jr IR, Oliveira-Santos LGR. 2009. Habitat selection by large mammals in a southern Brazilian Atlantic Forest. *Mammalian Biology - Zeitschrift für Säugetierkunde* 74:182–190. DOI: 10.1016/j.mambio.2009.02.006.

GRASS Development Team. 2017.Geographic Resources Analysis Support System (GRASS GIS) Software, Version 7.2. *Available at http://grass.osgeo.org*

Hansen MC, Potapov P V, Moore R, Hancher M, Turubanova SA, Tyukavina A, Thau D, Stehman S V, Goetz SJ, Loveland TR, Kommareddy A, Egorov A, Chini L, Justice CO, Townshend JRG. 2013. High-Resolution Global Maps of 21st-Century Forest Cover Change. *Science* 342:850–853. DOI: 10.1126/science.1244693.

Hardwick SR, Toumi R, Pfeifer M, Turner EC, Nilus R, Ewers RM. 2015. The relationship between leaf area index and microclimate in tropical forest and oil palm plantation: Forest disturbance drives changes in microclimate. *Agricultural and Forest Meteorology* 201:187–195. DOI: 10.1016/j.agrformet.2014.11.010.

Haugaasen T, Peres CA. 2007. Vertebrate responses to fruit production in Amazonian flooded and unflooded forests. *Biodiversity and Conservation* 16:4165–4190. DOI: 10.1007/s10531-007-9217-z.

Hernández-Ruedas MA, Arroyo-Rodríguez V, Morante-Filho JC, Meave JA, Martínez-Ramos M. 2018. Fragmentation and matrix contrast favor understory plants through negative cascading effects on a strong competitor palm. *Ecological Applications* 28:1546–1553. DOI: 10.1002/eap.1740.

Hernando A, Velázquez J, Valbuena R, Legrand M, García-Abril A. 2017. Influence of the resolution of forest cover maps in evaluating fragmentation and connectivity to assess habitat conservation status. *Ecological Indicators* 79:295–302. DOI: 10.1016/j.ecolind.2017.04.031.

Hines JE, Nichols JD, Royle JA, MacKenzie DI, Gopalaswamy AM, Kumar NS, Karanth KU. 2010. Tigers on trail: occupancy modeling for cluster sampling. *Ecological applications* 20:1456–1466.

Holzschuh A, Steffan-Dewenter I, Tscharntke T. 2010. How do landscape composition and configuration, organic farming and fallow strips affect the diversity of bees, wasps and their parasitoids? *Journal of Animal Ecology* 79:491–500. DOI: 10.1111/j.1365-2656.2009.01642.x.

Jackson HB, Fahrig L. 2012. What size is a biologically relevant landscape? *Landscape Ecology* 27:929–941. DOI: 10.1007/s10980-012-9757-9.

Jackson HB, Fahrig L. 2015. Are ecologists conducting research at the optimal scale? *Global Ecology and Biogeography* 24:52–63. DOI: 10.1111/geb.12233.

Jackson VL, Laack LL, Zimmerman EG. 2005. Landscape metrics associated with habitat use by ocelots in South Texas. *Journal of Wildlife Management* 69:733–738. DOI: 10.2193/0022-541X(2005)069[0733:LMAWHU]2.0.CO;2.

De Jong BHJ, Ochoa-Gaona S, Castillo-Santiago MA, Ramírez-Marcial N, Cairns MA. 2000. Carbon flux and patterns of land-use/land-cover change in the selva Lacandona, Mexico. *AMBIO: A Journal of the Human Environment* 29:504–511. DOI: 10.1579/0044-7447-29.8.504.

Keuroghlian A, Eaton DP. 2008. Importance of rare habitats and riparian zones in a tropical forest fragment: Preferential use by Tayassu pecari, a wide-ranging frugivore. *Journal of Zoology* 275:283–293. DOI: 10.1111/j.1469-7998.2008.00440.x.

Keuroghlian A, Eaton DP, Longland WS. 2004. Area use by white-lipped and collared peccaries (Tayassu pecari and Tayassu tajacu) in a tropical forest fragment. *Biological Conservation* 120:415–429. DOI: 10.1016/j.biocon.2004.03.016.

Koen EL, Garroway CJ, Wilson PJ, Bowman J. 2010. The effect of map boundary on estimates of landscape resistance to animal movement. *PLoS ONE* 5:e11785. DOI: 10.1371/journal.pone.0011785.

Koenig SJ, Bender DJ. 2018. Generalizing matrix structure affects the identification of least-cost paths and patch connectivity. *Theoretical Ecology* 11:95–109. DOI: 10.1007/s12080-017-0351-2.

Kolb M, Galicia L. 2018. Scenarios and story lines: drivers of land use change in southern Mexico. *Environment, Development and Sustainability* 20:681–702. DOI: 10.1007/s10668-016-9905-5.

Kupfer JA, Malanson GP, Franklin SB. 2006. Not seeing the ocean for the islands: The mediating influence of matrix-based processes on forest fragmentation effects. *Global Ecology and Biogeography* 15:8–20. DOI: 10.1111/j.1466-822X.2006.00204.x.

de la Torre JA, Núñez JM, Medellín RA. 2017. Spatial requirements of jaguars and pumas in Southern Mexico. *Mammalian Biology* 84:52–60. DOI: 10.1016/j.mambio.2017.01.006.

Lausch A, Heurich M, Magdon P, Rocchini D, Schulz K, Bumberger J, King DJ. 2020. A Range of Earth Observation Techniques for Assessing Plant Diversity. In: Cavender-Bares J, Gamon JA, Townsend PA eds. *Remote Sensing of Plant Biodiversity*. Springer International Publishing, 309–348. DOI: 10.1007/978-3-030-33157-3_13.

Leadley P, Proença V, Fernández-Manjarrés J, Pereira HM, Alkemade R, Biggs R, Bruley E, Cheung W, Cooper D, Figueiredo J, Gilman E, Guénette S, Hurtt G, Mbow C, Oberdorff T, Revenga C, Scharlemann JPW, Scholes R, Smith MS, Sumaila UR, Walpole M. 2014. Interacting regional-scale regime shifts for biodiversity and ecosystem services. *BioScience* 64:665–679. DOI: 10.1093/biosci/biu093.

Lewis SL, Edwards DP, Galbraith D. 2015. Increasing human dominance of tropical forests. *Science* 349:827–832. DOI: 10.1126/science.aaa9932.

Lindenmayer D, Hobbs RJ, Montague-Drake R, Alexandra J, Bennett A, Burgman M, Cale P, Calhoun A, Cramer V, Cullen P, Driscoll D, Fahrig L, Fischer J, Franklin J, Haila Y, Hunter M, Gibbons P, Lake S, Luck G, MacGregor C, McIntyre S, Nally R Mac, Manning A, Miller J, Mooney H, Noss R, Possingham H, Saunders D, Schmiegelow F, Scott M, Simberloff D, Sisk T, Tabor G, Walker B, Wiens J, Woinarski J, Zavaleta E, Mac Nally R, Manning A, Miller J, Mooney H, Noss R, Possingham H, Saunders D, Schmiegelow F, Scott M, Simberloff D, Sisk T, Tabor G, Walker B, Wiens J, Woinarski J, Zavaleta E. 2008. A checklist for ecological management of landscapes for conservation. *Ecology Letters* 11:78–91. DOI: 10.1111/j.1461-0248.2007.01114.x.

Lyra-Jorge MC, Ribeiro MC, Ciocheti G, Tambosi LR, Pivello VR. 2010. Influence of multi-scale landscape structure on the occurrence of carnivorous mammals in a human-modified savanna, Brazil. *European Journal of Wildlife Research* 56:359–368. DOI: 10.1007/s10344-009-0324-x.

MacKenzie DI. 2005. What are the issues with presence-absence data for wildlife managers? *The Journal of Wildlife Management* 69:849–860. DOI: 10.2193/0022-541X(2005)069[0849:WATIWP]2.0.CO;2.

MacKenzie DI. 2006. Modeling the probability of resource use: The effect of, and dealing with, detecting a species imperfectly. *Journal of Wildlife Management* 70:367–374. DOI: Doi 10.2193/0022-541x(2006)70[367:Mtporu]2.0.Co;2.

MacKenzie DI, Bailey LL. 2004. Assessing the fit of site-occupancy models. *Journal of Agricultural, Biological, and Environmental Statistics* 9:300–318. DOI: 10.1198/108571104X3361.

MacKenzie DI, Nichols JD. 2004. Occupancy as a surrogate for abundance estimation. *Animal Biodiversity and Conservation* 1:461–467.

MacKenzie DI, Nichols JD, Royle JA, Pollock KH, Bailey L, Hines JE. 2006. *Occupancy Estimation and Modeling: Inferring Patterns and Dynamics of Species Occurrence*. Academic Press.

Madritch M, Cavender-Bares J, Hobbie SE, Townsend PA. 2020. Linking Foliar Traits to Belowground Processes. In: Cavender-Bares J, Gamon JA, Townsend PA eds. *Remote Sensing of Plant Biodiversity*. Cham: Springer International Publishing, 173–197. DOI: 10.1007/978-3-030-33157-3_8.

Martínez-Ramos M, Pingarroni A, Rodríguez-Velázquez J, Toledo-Chelala L, Zermeño-Hernández I, Bongers F. 2016. Natural forest regeneration and ecological restoration in human-modified tropical landscapes. *Biotropica* 48:745–757. DOI: 10.1111/btp.12382.

Mazerolle MJ. 2020. AICcmodavg: Model selection and multimodel inference based on (Q)AIC(c).

McGarigal K, Wan HY, Zeller KA, Timm BC, Cushman SA. 2016. Multi-scale habitat selection modeling: a review and outlook. *Landscape Ecology* 31:1161–1175. DOI: 10.1007/s10980-016-0374-x.

McRae BH, Beier P. 2007. Circuit theory predicts gene flow in plant and animal populations. *Proceedings of the National Academy of Sciences* 104:19885–90. DOI: 10.1073/pnas.0706568104.

McRae BH, Dickson BG, Keitt TH, Shah VB. 2008. Using circuit theory to model connectivity in ecology, evolution, and conservation. *Ecology* 89:2712–24. DOI: 10.1890/07-1861.1.

Medellin RA. 1994. Mammal diversity and conservation in the selva Lacandona, Chiapas, Mexico. *Conservation Biology* 8:780–799. DOI: 10.1046/j.1523-1739.1994.08030780.x.

Mendoza E, Dirzo R. 1999. Deforestation in Lacandonia (southeast Mexico): evidence for the declaration of the northernmost tropical hot-spot. *Biodiversity & Conservation* 8:1621–1641. DOI: 10.1023/A:1008916304504.

Miguet P, Jackson HB, Jackson ND, Martin AE, Fahrig L. 2016. What determines the spatial extent of landscape effects on species? *Landscape Ecology* 31:1177–1194. DOI: 10.1007/s10980-015-0314-1.

Morato RRG, Stabach JA, Fleming CH, Calabrese JMJ, De Paula RC, Ferraz KMPMPM, Kantek DLZZ, Miyazaki SS, Pereira TDCC, Araujo GR, Paviolo A, De Angelo C, Di Bitetti MS, Cruz P, Lima F, Cullen L, Sana DA, Ramalho EEE, Carvalho MM, Soares FHSS, Zimbres B, Silva MX, Moraes MDFF, Vogliotti A, May JA, Haberfeld M, Rampim L, Sartorello L, Ribeiro MCM, Leimgruber P, Paula RC De, Ferraz KMPMPM, Kantek DLZZ, Miyazaki SS, Pereira TDCC, Araujo GR, Paviolo A, Angelo C De, Bitetti MDMDS Di, Cruz P, Lima F, Cullen L, Sana DA, Ramalho EEE, Carvalho MM, Soares FHSS, Zimbres B, Silva MX, Moraes MDFF, Vogliotti A, Jr. JAM, Haberfeld M, Rampim L, Sartorello L, Ribeiro MCM, Leimgruber P, Chapman B, Hulthen K, Wellenreuther M, Hansson L-A, Nilsson J, Bronmark C, Nowell K, Jackson P, Macdonald D, Crooks K, Cardillo M, Purvis A, Sechrest W, Gittleman J, Bielby J, Mace G, Fahrig L, Nathan R, Chetkiewicz C-L, Boyce M, Rodríguez-Soto C, Monroy-Vilchis O, Maiorano L, Boitani L, Faller J, Briones M, Horne J, Garton E, Fleming CH, Fagan W, Mueller T, Olson K a, Leimgruber P, Calabrese JMJ, Sanderson E, Redford K, Chetkiewicz C-L, Medellin R, Rabinowitz A, Robinson J, Morato RRG, Beisiegel B, Ramalho EEE, Boulhosa L, G A, E C, Angelo C De, Bitetti MDMDS Di, Lucherini M, Muzzachiodi N, Schaller G, Crawshaw P, Rabinowitz A, Jr. BN, Astete S, Sollmann R, Silveira L, Azevedo F de, Murray D, Cavalcanti S, Gese E, Conde D a., Colchero F, Zarza H, Christensen N, Sexton J, Manterola C, Colchero F, Conde D a., Manterola C, Chávez C, Rivera A, Ceballos G, Sollmann R, Furtado M, Gardner B, Hofer H, Jácomo A, Tôrres N, Calabrese JMJ, Fleming CH, Gurarie E, Fleming CH, Subaşl Y, Calabrese JMJ, Fleming CH, Calabrese JMJ, Mueller T, Olson K a, Leimgruber P, Fagan W, Fleming CH, Calabrese JMJ, Mueller T, Olson K a, Leimgruber P, Fagan W, Blackwell P, Niu M, Lambert M, Lapoint S, Jr. PC, Jr. LC, Abreu K De, Sana DA, Nava A, Azevedo F de, Murray D, Ribeiro MCM, Metzger J, Martensen A, Ponzoni F, Hirota M, Leal I, Silva J, Tabarelli M, Jr. TL, Robinson T, Wint GW, Conchedda G, Boeckel T Van, Ercoli V, Palamara E, Morato RRG, Conforti V a., Azevedo F de, Jacomo a. T a, Silveira L, Sana DA, Balme G, Slotow R, Hunter L, Sikes R, Gannon W, Fleming CH, Calabrese JMJ, Akaike H, Kéry M, McCarthy M, Royston P, Gelman A, Rubin D, Gelman A, Hill J, Liu J, Taylor W, Ouyang Z, Groop R, Tan Y, Zhang H, Angelo C De, Paviolo A, Wiegand T, Kanagaraj R, Bitetti MDMDS Di, McCarthy M, McCarthy M, Crawshaw P, Quigley H, Powell R, Mitchell M, Singh N, Börger L, Dettki H, Bunnefeld N, Ericsson G, Borger L, Boone R, Thirgood S, Hopcraft J, Stabach JA, Wittemyer G, Boone R, Reid R, Worden JS, Schaller G, Mauritzen M, Derocher A, Oysten W, May R, Dijk J van, Landa A, Andersen R, Andersen R, Kittle A, Anderson M, Avgar T, Baker J, Brown G, Hagens J, Mikael S, Angelo C De, Paviolo A, Bitetti MDMDS Di, Carvalho E a. R, Zarco-González M, Monroy-Vilchis O, Morato RRG. 2016. Space use and movement of a neotropical top predator: The endangered jaguar. *PLoS ONE* 11:e0168176. DOI: 10.1371/JOURNAL.PONE.0168176.

Muratet A, Lorrillière R, Clergeau P, Fontaine C. 2013. Evaluation of landscape connectivity at community level using satellite-derived NDVI. *Landscape Ecology* 28:95–105. DOI: 10.1007/s10980-012-9817-1.

Nagy-Reis MB, Nichols JD, Chiarello AG, Ribeiro MC, Setz EZF. 2017. Landscape use and co-occurrence patterns of Neotropical spotted cats. *PLoS ONE* 12:e0168441. DOI: 10.1371/journal.pone.0168441.

Pardo LE, Campbell MJ, Edwards W, Clements GR, Laurance WF. 2018. Terrestrial mammal responses to oil palm dominated landscapes in Colombia. *PLoS ONE* 13:e0197539. DOI: 10.1371/journal.pone.0197539.

Pennington TD, Sarukhán J. 2005. *Árboles tropicales de México. Manual para la identificación de las principales especies*. Mexico City: Universidad Nacional Autónoma de México.

Pérez-Irineo G, Santos-Moreno A. 2016. Abundance and activity patterns of medium-sized felids (Felidae, Carnivora) In Southeastern Mexico. *The Southwestern Naturalist* 61:33–39. DOI: 10.1894/0038-4909-61.1.33.

Pettorelli N, Laurance WF, O'Brien TG, Wegmann M, Nagendra H, Turner W. 2014. Satellite remote sensing for applied ecologists: Opportunities and challenges. *Journal of Applied Ecology* 51:839–848. DOI: 10.1111/1365-2664.12261.

Pfeifer M, Kor L, Nilus R, Turner E, Cusack J, Lysenko I, Khoo M, Chey VK, Chung AC, Ewers RM. 2016. Mapping the structure of Borneo's tropical forests across a degradation gradient. *Remote Sensing of Environment* 176:84–97. DOI: 10.1016/j.rse.2016.01.014.

Pfeifer M, Lefebvre V, Peres CA, Banks-Leite C, Wearn OR, Marsh CJ, Butchart SHM, Arroyo-Rodríguez V, Barlow J, Cerezo A, Cisneros L, D'Cruze N, Faria D, Hadley A, Harris SM, Klingbeil BT, Kormann U, Lens L, Medina-Rangel GF, Morante-Filho JC, Olivier P, Peters SL, Pidgeon A, Ribeiro DB, Scherber C, Schneider-Maunoury L, Struebig M, Urbina-Cardona N, Watling JI, Willig MR, Wood EM, Ewers RM. 2017. Creation of forest edges has a global impact on forest vertebrates. *Nature* 551:187–191. DOI: 10.1038/nature24457.

Powney GD, Broaders LK, Oliver TH. 2012. Towards a measure of functional connectivity: Local synchrony matches small scale movements in a woodland edge butterfly. *Landscape Ecology* 27:1109–1120. DOI: 10.1007/s10980-012-9771-y.

Powney GD, Roy DB, Chapman D, Brereton T, Oliver TH. 2011. Measuring functional connectivity using long-term monitoring data. *Methods in Ecology and Evolution* 2:527–533. DOI: 10.1111/j.2041-210X.2011.00098.x.

Prevedello JA, Vieira M V. 2010. Does the type of matrix matter? A quantitative review of the evidence. *Biodiversity and Conservation* 19:1205–1223. DOI: 10.1007/s10531-009-9750-z.

R Development Core Team. 2018.R: A Language and Environment for Statistical Computing. *Available at https://www.r-project.org/*

Radford JQ, Bennett AF, Cheers GJ. 2005. Landscape-level thresholds of habitat cover for woodland-dependent birds. *Biological Conservation* 124:317–337. DOI: 10.1016/j.biocon.2005.01.039.

Rayfield B, Fortin MJ, Fall A. 2011. Connectivity for conservation: A framework to classify network measures. *Ecology* 92:847–858. DOI: 10.1890/09-2190.1.

Reid A. 2009. *A Field Guide to the Mammals of Central America and Southeast México.* Oxford University Press. DOI: 10.1644/11-MAMM-R-008.1.

Sarker LR, Nichol JE. 2011. Improved forest biomass estimates using ALOS AVNIR-2 texture indices. *Remote Sensing of Environment* 115:968–977. DOI: 10.1016/j.rse.2010.11.010.

Saura S, Rubio L. 2010. A common currency for the different ways in which patches and links can contribute to habitat availability and connectivity in the landscape. *Ecography* 33:523–537. DOI: 10.1111/j.1600-0587.2009.05760.x.

Solórzano JV, Gallardo-Cruz JA, González EJ, Peralta-Carreta C, Hernández-Gómez M, Oca AF-M de, Cervantes-Jiménez LG. 2018. Contrasting the potential of Fourier transformed ordination and gray level co-occurrence matrix textures to model a tropical swamp forest's structural and diversity attributes. *Journal of Applied Remote Sensing* 12:1. DOI: 10.1117/1.JRS.12.036006.

Solórzano J V., Meave JA, Gallardo-Cruz JA, González EJ, Hernández-Stefanoni JL. 2017. Predicting old-growth tropical forest attributes from very high resolution (VHR)-derived surface metrics. *International Journal of Remote Sensing* 38:492–513. DOI: 10.1080/01431161.2016.1266108.

Song XP, Hansen MC, Stehman S V., Potapov P V., Tyukavina A, Vermote EF, Townshend JR. 2018. Global land change from 1982 to 2016. *Nature* 560:639–643. DOI: 10.1038/s41586-018-0411-9.

de Souza JC, da Silva RM, Gonçalves MPR, Jardim RJD, Markwith SH. 2018. Habitat use, ranching, and human-wildlife conflict within a fragmented landscape in the Pantanal, Brazil. *Biological Conservation* 217:349–357. DOI: 10.1016/j.biocon.2017.11.019.

Steininger MK. 2000. Satellite estimation of tropical secondary forest above-ground biomass: Data from Brazil and Bolivi. *International Journal of Remote Sensing* 21:1139–1157. DOI: 10.1080/014311600210119.

Stoner KE, Riba-Hernández P, Vulinec K, Lambert JE. 2007. The Role of Mammals in Creating and Modifying Seedshadows in Tropical Forests and Some Possible Consequences of Their Elimination. *Biotropica* 39:316–327. DOI: 10.1111/j.1744-7429.2007.00292.x.

Strassburg BBN, Kelly A, Balmford A, Davies RG, Gibbs HK, Lovett A, Miles L, Orme CDL, Price J, Turner RK, Rodrigues ASL. 2010. Global congruence of carbon storage and biodiversity in terrestrial ecosystems. *Conservation Letters* 3:98–105. DOI: 10.1111/j.1755-263X.2009.00092.x.

Taubert F, Fischer R, Groeneveld J, Lehmann S, Müller MS, Rödig E, Wiegand T, Huth A. 2018. Global patterns of tropical forest fragmentation. *Nature* 554:519–522. DOI: 10.1038/nature25508.

Tejeda-Cruz C, Naranjo EJ, Cuarón AD, Perales H, Cruz-Burguete JL. 2009. Habitat use of wild ungulates in fragmented landscapes of the Lacandon Forest, Southern Mexico. *Mammalia* 73:211–219. DOI: 10.1515/MAMM.2009.044.

Terborgh J. 2013. Using Janzen-Connell to predict the consequences of defaunation and other disturbances of tropical forests. *Biological Conservation* 163:7–12. DOI: 10.1016/j.biocon.2013.01.015.

Thornton DH, Branch LC, Sunquist ME. 2011. The relative influence of habitat loss and fragmentation: Do tropical mammals meet the temperate paradigm? *Ecological Applications* 21:2324–2333. DOI: 10.1890/10-2124.1.

Tischendorf L, Fahrig L. 2000. How should we measure landscape connectivity? *Landscape Ecology* 15:633–641. DOI: 10.1023/A:1008177324187.

Trolle M, Kéry M. 2005. Estimation of Ocelot Density in the Pantanal Using Capture–Recapture Analysis of Camera-Trapping Data. *Journal of Mammalogy* 84:607–614. DOI: 10.1644/1545-1542(2003)084<0607:eoodit>2.0.co;2.

Trust B. 1991. A note on a general definition of the coefficient of determination. *Biometrika* 78:691–692.

Tscharntke T, Tylianakis JM, Rand TA, Didham RK, Fahrig L, Batáry P, Bengtsson J, Clough Y, Crist TO, Dormann CF, Ewers RM, Fründ J, Holt RD, Holzschuh A, Klein AM, Kleijn D, Kremen C, Landis DA, Laurance W, Lindenmayer D, Scherber C, Sodhi N, Steffan-Dewenter I, Thies C, van der Putten WH, Westphal C. 2012. Landscape moderation of biodiversity patterns and processes - eight hypotheses. *Biological Reviews* 87:661–685. DOI: 10.1111/j.1469-185X.2011.00216.x.

Turner W, Spector S, Gardiner N, Fladeland M, Sterling E, Steininger M. 2003. Remote sensing for biodiversity science and conservation. *Trends in Ecology & Evolution* 18:306–314. DOI: 10.1016/S0169-5347(03)00070-3.

Umetsu F, Paul Metzger J, Pardini R. 2008. Importance of estimating matrix quality for modeling species distribution in complex tropical landscapes: a test with Atlantic forest small mammals. *Ecography* 31:359–370. DOI: 10.1111/j.0906-7590.2008.05302.x.

Vihervaara P, Auvinen AP, Mononen L, Törmä M, Ahlroth P, Anttila S, Böttcher K, Forsius M, Heino J, Heliölä J, Koskelainen M, Kuussaari M, Meissner K, Ojala O, Tuominen S, Viitasalo M, Virkkala R. 2017. How Essential Biodiversity Variables and remote sensing can help national biodiversity monitoring. *Global Ecology and Conservation* 10:43–59. DOI: 10.1016/j.gecco.2017.01.007.

Watling JI, Nowakowski AJ, Donnelly M a., Orrock JL. 2011. Meta-analysis reveals the importance of matrix composition for animals in fragmented habitat. *Global Ecology and Biogeography* 20:209–217. DOI: 10.1111/j.1466-8238.2010.00586.x.

Watson SJ, Watson DM, Luck GW, Spooner PG. 2014. Effects of landscape composition and connectivity on the distribution of an endangered parrot in agricultural landscapes. *Landscape Ecology* 29:1249–1259. DOI: 10.1007/s10980-014-0065-4.

Wearn OR, Rowcliffe JM, Carbone C, Pfeifer M, Bernard H, Ewers RM. 2017. Mammalian species abundance across a gradient of tropical land-use intensity: A hierarchical multi-species modelling approach. *Biological Conservation* 212:162–171. DOI: 10.1016/j.biocon.2017.05.007.

Welsh AH, Lindenmayer DB, Donnelly CF. 2013. Fitting and Interpreting Occupancy Models. *PLoS ONE* 8:e52015. DOI: 10.1371/journal.pone.0052015.

Zeller KA, McGarigal K, Whiteley AR. 2012. Estimating landscape resistance to movement: a review. *Landscape Ecology* 27:777–797. DOI: 10.1007/s10980-012-9737-0.

Zimbres B, Peres CA, Machado RB. 2017. Terrestrial mammal responses to habitat structure and quality of remnant riparian forests in an Amazonian cattle-ranching landscape. *Biological Conservation* 206:283–292. DOI: 10.1016/j.biocon.2016.11.033.

Zuckerberg B, Desrochers A, Hochachka WM, Fink D, Koenig WD, Dickinson JL. 2012. Overlapping landscapes: A persistent, but misdirected concern when collecting and analyzing ecological data. *Journal of Wildlife Management* 76:1072–1080. DOI: 10.1002/jwmg.326.

Zvoleff A. 2016.glcm: Calculate Textures from Grey-Level Co-Occurrence Matrices (GLCMs). *Available at https://cran.r-project.org/package=glcm*

## Supplemental information

### Table S1. Terrestrial mammals recorded during the field surveys in the Lacandona rainforest, Mexico

| Common name | Scientific name |
|---|---|
| Striped hog-nosed skunk | *Conepatus semistriatus* |
| Lowland paca | *Cuniculus paca* |
| Common opossum | *Didelphis virginiana* |
| Ocelot | *Leopardus pardalis* |
| Margay | *Leopardus wiedii* |
| Red brocket | *Mazama temama* |
| White-nosed coati | *Nasua narica* |
| White-tailed deer | *Odocoileus virginianus* |
| Jaguar | *Panthera onca* |
| White-collared peccary | *Pecari tajacu* |
| Northern raccoon | *Procyon lotor* |
| Jaguarundi | *Puma yagouaroundi* |
| Tapeti | *Sylvilagus brasiliensis* |
| Baird's tapir | *Tapirus bairdii* |
| White-lipped peccary | *Tayassu pecari* |

**Table S2. Moran's I autocorrelation tests between the sampling sites distance and the number of detection records of four terrestrial mammal species in the Lacandona rainforest, Mexico.**

| **Specie** | **Moran's I** | **P value** |
|---|---|---|
| *O. virginianus* | - 0.0284 (0.0635) | 0.547 |
| *P. tajacu* | - 0.0684 (0.0669) | 0.978 |
| *L. pardalis* | 0.0075 (0.0640) | 0.246 |
| *P. onca* | - 0.0879 (0.0626) | 0.734 |

**Table S3. Goodness of fit of detectability models of four terrestrial mammals in the Lacandona rainforest, Mexico.**

| Specie | Model | $\chi^2$ | $P$ | $\hat{c}$ |
|---|---|---|---|---|
| *O. virginianus* | *ψ(.)p(.)* | 131.07 | 0.63 | 0.75 |
| | *ψ(.)p(c)* | 127.24 | 0.82 | 0.65 |
| | *ψ(.)p(f)* | 153.14 | 0.36 | 1.12 |
| | *ψ(.)p(s)* | 84.18 | 0.47 | 0.81 |
| | *ψ(.)p(f+s)* | 101.57 | 0.2 | 1.5 |
| | *ψ(.)p(c+s)* | 80.99 | 0.49 | 0.85 |
| | *ψ(.)p(c+f)* | 157.03 | 0.46 | 0.99 |
| | *ψ(.)p(c+f+s)* | 81.11 | 0.51 | 0.9 |
| *P. tajacu* | *ψ(.)p(.)* | 345.92 | 0.03 | 1.45 |
| | *ψ(.)p(c)* | 347.42 | 0 | 1.46 |
| | *ψ(.)p(f)* | 419.47 | 0.02 | 1.79 |
| | *ψ(.)p(s)* | 793.3 | 0.01 | 6.53 |
| | *ψ(.)p(f+s)* | 842.78 | 0.01 | 9.17 |

|  |  |  |  |  |
|---|---|---|---|---|
|  | *ψ(.)p(c+s)* | 795.26 | 0 | 7.35 |
|  | *ψ(.)p(c+f)* | 415.15 | 0 | 1.76 |
|  | *ψ(.)p(c+f+s)* | 907.25 | 0.02 | 6.62 |
| *L. pardalis* | *ψ(.)p(.)* | 184.39 | 0.75 | 0.86 |
|  | *ψ(.)p(c)* | 184.33 | 0.73 | 0.9 |
|  | *ψ(.)p(f)* | 214.47 | 0.51 | 1.01 |
|  | *ψ(.)p(s)* | 101.15 | 0.52 | 0.62 |
|  | *ψ(.)p(f+s)* | 116.65 | 0.42 | 0.75 |
|  | *ψ(.)p(c+s)* | 98.74 | 0.58 | 0.75 |
|  | *ψ(.)p(c+f)* | 226.39 | 0.38 | 1.05 |
|  | *ψ(.)p(c+f+s)* | 121.44 | 0.45 | 0.7 |
| *P. onca* | *ψ(.)p(.)* | 116.61 | 0.72 | 0.71 |
|  | *ψ(.)p(c)* | 134.99 | 0.52 | 0.9 |
|  | *ψ(.)p(f)* | 126.81 | 0.56 | 0.94 |
|  | *ψ(.)p(s)* | 10.91 | 0.59 | 0.88 |
|  | *ψ(.)p(f+s)* | 11.62 | 0.63 | 0.82 |
|  | *ψ(.)p(c+s)* | 12.34 | 0.46 | 0.95 |
|  | *ψ(.)p(c+f)* | 144.77 | 0.66 | 0.85 |
|  | *ψ(.)p(c+f+s)* | 15.2 | 0.41 | 1 |

The covariates are the survey method used in each sampling occasion (s), the use of the patch by cattle (c), and patch flooding during the rainy season (f). The null model does not include a covariate (.). The models' Pearson chi-square ($\chi^2$), significance (*P*) and overdispersion parameter ($\hat{c}$) are shown.

**Table S4. Model selection analysis for detection probability (*p*) covariates for four terrestrial mammals in the Lacandona rainforest, Mexico.**

| Specie | Model | *df* | *LL* | *AICc* | $\Delta_i$ | $w_i$ |
|---|---|---|---|---|---|---|
| *O. virginianus* | ***ψ(.)p(s)*** | **3** | **-27.47** | **62.94** | **0** | **0.68** |
| | *ψ(.)p(f+s)* | 4 | -27.21 | 66.06 | 3.11 | 0.14 |
| | *ψ(.)p(c+s)* | 4 | -27.26 | 66.16 | 3.22 | 0.14 |
| | *ψ(.)p(c+f+s)* | 5 | -27.26 | 70.51 | 7.57 | 0.02 |
| | *ψ(.)p(.)* | 2 | -33 | 70.92 | 7.98 | 0.01 |
| | *ψ(.)p(f)* | 3 | -32.67 | 73.34 | 10.4 | 0 |
| | *ψ(.)p(c)* | 3 | -32.93 | 73.85 | 10.91 | 0 |
| | *ψ(.)p(c+f)* | 4 | -32.62 | 76.88 | 13.94 | 0 |
| *P. tajacu* | ***ψ(.)p(.)*** | **2** | **-53.23** | **111.38** | **0** | **0.59** |
| | ***ψ(.)p(f)*** | **3** | **-52.67** | **113.35** | **1.97** | **0.22** |
| | *ψ(.)p(c)* | 3 | -53.23 | 114.45 | 3.07 | 0.13 |
| | *ψ(.)p(c+f)* | 4 | -52.24 | 116.11 | 4.72 | 0.06 |
| *L. pardalis* | ***ψ(.)p(s)*** | **3** | **-36.02** | **80.03** | **0** | **0.58** |
| | *ψ(.)p(f+s)* | 4 | -35.21 | 82.05 | 2.02 | 0.21 |
| | *ψ(.)p(c+s)* | 4 | -36 | 83.63 | 3.6 | 0.09 |
| | *ψ(.)p(.)* | 2 | -40.05 | 85.03 | 5 | 0.05 |
| | *ψ(.)p(c+f+s)* | 5 | -34.87 | 85.73 | 5.7 | 0.03 |
| | *ψ(.)p(f)* | 3 | -39.19 | 86.38 | 6.35 | 0.02 |

| | | | | | | |
|---|---|---|---|---|---|---|
| | $\psi(.)p(c)$ | 3 | -40.05 | 88.11 | 8.08 | 0.01 |
| | $\psi(.)p(c+f)$ | 4 | -38.83 | 89.3 | 9.27 | 0.01 |
| *P. onca* | **$\psi(.)p(s)$** | **3** | **-19.8** | **47.59** | **0** | **0.7** |
| | $\psi(.)p(c+s)$ | 4 | -19.61 | 50.86 | 3.27 | 0.14 |
| | $\psi(.)p(f+s)$ | 4 | -19.66 | 50.97 | 3.37 | 0.13 |
| | $\psi(.)p(c+f+s)$ | 5 | -18.91 | 53.83 | 6.24 | 0.03 |
| | $\psi(.)p(.)$ | 2 | -27.67 | 60.26 | 12.67 | 0 |
| | $\psi(.)p(c)$ | 3 | -27.42 | 62.85 | 15.26 | 0 |
| | $\psi(.)p(f)$ | 3 | -27.51 | 63.02 | 15.43 | 0 |
| | $\psi(.)p(c+f)$ | 4 | -26.92 | 65.48 | 17.89 | 0 |

The covariates are the survey method used in each sampling occasion (s), the use of the patch by cattle (c), and patch flooding during the rainy season (f). The null model does not include a covariate (.). The models' degrees of freedom (*df*), log-likelihood (*LL*), Akaike Information Criterion for small samples (*AICc*), Akaike differences ($\Delta_i$), and Akaike weights ($w_i$) are shown. The selected models for further analysis are in bold.

**Table S5. Model selection analysis for occupancy ($\psi$) covariates measured at different spatial extents (buffer sizes) for four terrestrial mammals in the Lacandona rainforest, Mexico.**

| Specie | Scale | Model | K | AICc | ΔAICc | $w_i$ | LL | $R^2$ |
|---|---|---|---|---|---|---|---|---|
| ***L. pardalis*** | 200ha | $\psi(.)\ p(s)$ | 3 | 79.23 | 0 | 0.76 | -35.53 | 0 |
| | | $\psi(R_v)\ p(s)$ | 4 | 82.76 | 3.53 | 0.13 | -35.38 | 0.02 |
| | | $\psi(NIR_v)\ p(s)$ | 4 | 83.05 | 3.81 | 0.11 | -35.52 | 0 |
| | 300ha | $\psi(.)\ p(s)$ | 3 | 80.03 | 0 | 0.86 | -36.02 | 0 |
| | | $\psi(R_v)\ p(s)$ | 4 | 83.65 | 3.61 | 0.14 | -36 | 0 |
| | | $\psi(NIR_v)\ p(s)$ | 4 | 100.28 | 20.25 | 0 | -44.32 | -1.84 |
| | 400ha | $\psi(.)\ p(s)$ | 3 | 80.03 | 0 | 0.65 | -36.02 | 0 |
| | | $\psi(NIR_v)\ p(s)$ | 4 | 82.57 | 2.54 | 0.18 | -35.47 | 0.07 |
| | | $\psi(R_v)\ p(s)$ | 4 | 82.78 | 2.75 | 0.16 | -35.57 | 0.05 |
| | 500ha | $\psi(.)\ p(s)$ | 3 | 80.03 | 0 | 0.65 | -36.02 | 0 |
| | | $\psi(R_v)\ p(s)$ | 4 | 82.56 | 2.53 | 0.18 | -35.46 | 0.07 |
| | | $\psi(NIR_v)\ p(s)$ | 4 | 82.77 | 2.74 | 0.17 | -35.57 | 0.06 |

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | 200ha | $\psi(.)\ p(s)$ | 3 | 62.35 | 0 | 0.77 | -27.08 | 0 |
| | | $\psi(NIR_v)\ p(s)$ | 4 | 66.1 | 3.75 | 0.12 | -27.05 | 0 |
| | | $\psi(R_v)\ p(s)$ | 4 | 66.12 | 3.77 | 0.12 | -27.06 | 0 |
| | 300ha | $\psi(.)\ p(s)$ | 3 | 62.94 | 0 | 0.85 | -27.47 | 0 |
| | | $\psi(R_v)\ p(s)$ | 4 | 66.36 | 3.42 | 0.15 | -27.36 | 0.01 |
| ***O. virginianus*** | 400ha | $\psi(.)\ p(s)$ | 3 | 62.94 | 0 | 0.65 | -27.47 | 0 |
| | | $\psi(NIR_v)\ p(s)$ | 4 | 65.05 | 2.11 | 0.23 | -26.71 | 0.09 |
| | | $\psi(R_v)\ p(s)$ | 4 | 66.35 | 3.41 | 0.12 | -27.36 | 0.01 |
| | 500ha | $\psi(.)\ p(s)$ | 3 | 62.94 | 0 | 0.65 | -27.47 | 0 |
| | | $\psi(NIR_v)\ p(s)$ | 4 | 65.02 | 2.08 | 0.23 | -26.69 | 0.1 |
| | | $\psi(R_v)\ p(s)$ | 4 | 66.24 | 3.3 | 0.12 | -27.3 | 0.02 |
| | 200ha | $\psi(.)\ p(s)$ | 3 | 47.18 | 0 | 0.76 | -19.5 | 0 |
| | | $\psi(R_v)\ p(s)$ | 4 | 50.65 | 3.47 | 0.13 | -19.32 | 0.02 |
| | | $\psi(NIR_v)\ p(s)$ | 4 | 51 | 3.82 | 0.11 | -19.5 | 0 |
| | 300ha | $\psi(.)\ p(s)$ | 3 | 47.59 | 0 | 0.86 | -19.8 | 0 |
| | | $\psi(R_v)\ p(s)$ | 4 | 51.22 | 3.63 | 0.14 | -19.79 | 0 |
| ***P. onca*** | 400ha | $\psi(.)\ p(s)$ | 3 | 47.59 | 0 | 0.69 | -19.8 | 0 |
| | | $\psi(NIR_v)\ p(s)$ | 4 | 50.25 | 2.66 | 0.18 | -19.31 | 0.06 |
| | | $\psi(R_v)\ p(s)$ | 4 | 51.03 | 3.44 | 0.12 | -19.7 | 0.01 |
| | 500ha | $\psi(.)\ p(s)$ | 3 | 47.59 | 0 | 0.68 | -19.8 | 0 |
| | | $\psi(R_v)\ p(s)$ | 4 | 49.92 | 2.33 | 0.21 | -19.14 | 0.09 |
| | | $\psi(NIR_v)\ p(s)$ | 4 | 51.24 | 3.64 | 0.11 | -19.8 | 0 |
| | 200ha | $\psi(.)\ p(s)$ | 3 | 83.5 | 0 | 0.55 | -37.66 | 0 |
| | | $\psi(R_v)\ p(s)$ | 4 | 84.33 | 0.83 | 0.36 | -36.16 | 0.18 |
| | | $\psi(NIR_v)\ p(s)$ | 4 | 87.07 | 3.57 | 0.09 | -37.54 | 0.02 |
| | 300ha | $\psi(.)\ p(s)$ | 3 | 84.77 | 0 | 0.75 | -38.39 | 0 |
| | | $\psi(R_v)\ p(s)$ | 4 | 86.95 | 2.18 | 0.25 | -37.66 | 0.09 |
| ***P. tajacu*** | 400ha | $\psi(R_v)\ p(s)$ | 4 | 82.75 | 0 | 0.7 | -35.56 | 0.3 |
| | | $\psi(.)\ p(s)$ | 3 | 84.77 | 2.02 | 0.26 | -38.39 | 0 |
| | | $\psi(NIR_v)\ p(s)$ | 4 | 88.4 | 5.65 | 0.04 | -38.38 | 0 |
| | 500ha | $\psi(R_v)\ p(s)$ | 4 | 84.73 | 0 | 0.46 | -36.55 | 0.21 |
| | | $\psi(.)\ p(s)$ | 3 | 84.77 | 0.04 | 0.45 | -38.39 | 0 |
| | | $\psi(NIR_v)\ p(s)$ | 4 | 87.93 | 3.2 | 0.09 | -38.15 | 0.03 |

The covariates are resistance distances derived from the textural variance of the red ($R_v$), and near-infrared ($NIR_v$) spectral bands. The null model does not include a covariate (.). The models' number of parameters (K), Akaike Information Criterion for small samples (AICc), Akaike differences (ΔAICc), Akaike weights ($w_i$), log-likelihood (LL), and Nagelkerke's $R^2$ index of ($R^2$) are shown.

**Table S6. Model selection analysis for occupancy (*ψ*) covariates for four terrestrial mammals in the Lacandona rainforest, Mexico.**

| Specie | Metric | Model | *LL* | *AICc* | $\Delta_i$ | $w_i$ | $R^2$ | $\chi^2$ | *P* | $\hat{c}$ |
|---|---|---|---|---|---|---|---|---|---|---|
| *O. virginianus* | FC | **$\psi(FC_{300})p(s)$** | **-22.59** | **56.82** | **0** | **0.33** | **0.47** | **92.92** | **0.3** | **0.89** |
| | | $\psi(FC_{200})p(s)$ | -22.74 | 57.11 | 0.29 | 0.29 | 0.46 | 84.27 | 0.4 | 1.05 |
| | | $\psi(FC_{400})p(s)$ | -22.8 | 57.24 | 0.42 | 0.27 | 0.46 | 90.73 | 0.28 | 0.67 |
| | | $\psi(FC_{500})p(s)$ | -23.85 | 59.33 | 2.52 | 0.09 | 0.38 | 99.02 | 0.17 | 1.39 |
| | | $\Psi(.)p(.)$ | -27.47 | 62.94 | 6.13 | 0.02 | 0 | 84.18 | 0.37 | 1.19 |
| | PD | **$\psi(PD_{400})p(s)$** | **-25.37** | **62.38** | **0** | **0.34** | **0.24** | **84.21** | **0.42** | **1.07** |
| | | $\psi(PD_{500})p(s)$ | -25.51 | 62.65 | 0.27 | 0.3 | 0.23 | 84.21 | 0.37 | 1.13 |
| | | $\Psi(.)p(.)$ | -27.47 | 62.94 | 0.57 | 0.26 | 0 | 84.18 | 0.34 | 1.14 |
| | | $\psi(PD_{200})p(s)$ | -27.23 | 66.1 | 3.72 | 0.05 | 0.03 | 84.18 | 0.36 | 1.14 |
| | | $\psi(PD_{300})p(s)$ | -27.37 | 66.37 | 3.99 | 0.05 | 0.01 | 84.19 | 0.4 | 1.28 |
| | MH | **$\psi(MH_{300})p(s)$** | **-22.85** | **57.33** | **0** | **0.63** | **0.45** | **91.14** | **0.27** | **1.23** |
| | | $\psi(MH_{400})p(s)$ | -24.13 | 59.9 | 2.57 | 0.17 | 0.35 | 81.13 | 0.4 | 1.15 |
| | | $\psi(MH_{200})p(s)$ | -24.33 | 60.29 | 2.96 | 0.14 | 0.34 | 84.69 | 0.36 | 1.15 |
| | | $\Psi(.)p(.)$ | -27.47 | 62.94 | 5.62 | 0.04 | 0 | 84.18 | 0.34 | 1.17 |
| | | $\psi(MH_{500})p(s)$ | -26.72 | 65.08 | 7.75 | 0.01 | 0.09 | 84.24 | 0.37 | 1.05 |
| | MR | $\Psi(.)p(.)$ | -27.47 | 62.94 | 0 | 0.57 | 0 | 84.18 | 0.4 | 1 |
| | | **$\psi(MR_{200})p(s)$** | **-27.29** | **66.21** | **3.27** | **0.11** | **0.02** | **84.18** | **0.43** | **1.16** |
| | | $\psi(MR_{500})p(s)$ | -27.29 | 66.22 | 3.28 | 0.11 | 0.02 | 84.18 | 0.33 | 1.34 |

| | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | $\psi(MR_{300})p(s)$ | -27.32 | 66.27 | 3.32 | 0.11 | 0.02 | 84.18 | 0.39 | 1.01 |
| | | $\psi(MR_{400})p(s)$ | -27.39 | 66.41 | 3.47 | 0.1 | 0.01 | 84.18 | 0.41 | 1.05 |
| *P. tajacu* | FC | **$\psi(FC_{500})p(.)$** | **-23.26** | **54.53** | **0** | **0.26** | **0.44** | **121.66** | **0.45** | **0.92** |
| | | $\psi(FC_{400})p(.)$ | -23.33 | 54.67 | 0.14 | 0.25 | 0.43 | 116.38 | 0.5 | 0.83 |
| | | $\psi(FC_{300})p(.)$ | -23.7 | 55.4 | 0.87 | 0.17 | 0.4 | 115.47 | 0.61 | 0.7 |
| | | $\psi(FC_{200})p(.)$ | -24.03 | 56.05 | 1.52 | 0.12 | 0.38 | 117.44 | 0.79 | 0.65 |
| | | $\psi(FC_{400})p(f)$ | -22.97 | 57.58 | 3.05 | 0.06 | 0.46 | 117.34 | 0.55 | 0.78 |
| | | $\psi(FC_{300})p(f)$ | -23.11 | 57.86 | 3.33 | 0.05 | 0.45 | 115.46 | 0.81 | 0.64 |
| | | $\psi(FC_{500})p(f)$ | -23.12 | 57.88 | 3.35 | 0.05 | 0.45 | 119.79 | 0.57 | 0.79 |
| | | $\psi(FC_{200})p(f)$ | -23.87 | 59.38 | 4.85 | 0.02 | 0.39 | 120.79 | 0.7 | 0.66 |
| | | $\Psi(.)p(.)$ | -27.67 | 60.26 | 5.73 | 0.01 | 0 | 116.61 | 0.76 | 0.68 |
| | | $\psi(.)p(f)$ | -27.51 | 63.02 | 8.5 | 0 | 0.02 | 126.81 | 0.69 | 0.77 |
| | PD | $\Psi(.)p(.)$ | -27.67 | 60.26 | 0 | 0.3 | 0 | 116.61 | 0.73 | 0.62 |
| | | **$\psi(PD_{400})p(.)$** | **-26.37** | **60.74** | **0.49** | **0.24** | **0.15** | **117.15** | **0.77** | **0.63** |
| | | $\psi(PD_{500})p(.)$ | -27.15 | 62.31 | 2.05 | 0.11 | 0.06 | 116.49 | 0.7 | 0.68 |
| | | $\psi(PD_{200})p(.)$ | -27.22 | 62.44 | 2.18 | 0.1 | 0.06 | 116.8 | 0.65 | 0.73 |
| | | $\psi(PD_{300})p(.)$ | -27.44 | 62.88 | 2.62 | 0.08 | 0.03 | 116.49 | 0.77 | 0.64 |
| | | $\psi(.)p(f)$ | -27.51 | 63.02 | 2.77 | 0.08 | 0.02 | 126.81 | 0.68 | 0.79 |
| | | $\psi(PD_{400})p(f)$ | -26.23 | 64.09 | 3.83 | 0.04 | 0.17 | 130.85 | 0.61 | 0.87 |
| | | $\psi(PD_{200})p(f)$ | -27.09 | 65.82 | 5.56 | 0.02 | 0.07 | 123.55 | 0.62 | 0.81 |

| | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | $\psi(PD_{500})p(f)$ | -27.09 | 65.82 | 5.56 | 0.02 | 0.07 | 120.15 | 0.65 | 0.87 |
| | $\psi(PD_{300})p(f)$ | -27.31 | 66.26 | 6 | 0.01 | 0.04 | 125.5 | 0.59 | 0.8 |
| MH | **$\psi(MH_{400})p(.)$** | **-23.78** | **55.57** | **0** | **0.46** | **0.4** | **117.34** | **0.51** | **0.78** |
| | $\psi(MH_{300})p(.)$ | -24.86 | 57.72 | 2.15 | 0.16 | 0.31 | 116.27 | 0.51 | 0.79 |
| | $\psi(MH_{500})p(.)$ | -25.38 | 58.75 | 3.18 | 0.09 | 0.26 | 138.24 | 0.3 | 0.97 |
| | $\psi(MH_{400})p(f)$ | -23.77 | 59.17 | 3.6 | 0.08 | 0.4 | 111.91 | 0.67 | 0.66 |
| | $\psi(MH_{200})p(.)$ | -26.01 | 60.02 | 4.45 | 0.05 | 0.19 | 115.93 | 0.73 | 0.69 |
| | $\psi(MH_{500})p(f)$ | -24.24 | 60.11 | 4.54 | 0.05 | 0.36 | 132.1 | 0.39 | 0.96 |
| | $\Psi(.)p(.)$ | -27.67 | 60.26 | 4.69 | 0.04 | 0 | 116.61 | 0.71 | 0.63 |
| | $\psi(MH_{300})p(f)$ | -24.32 | 60.27 | 4.7 | 0.04 | 0.35 | 117.05 | 0.72 | 0.72 |
| | $\psi(.)p(f)$ | -27.51 | 63.02 | 7.46 | 0.01 | 0.02 | 126.81 | 0.64 | 0.82 |
| | $\psi(MH_{200})p(f)$ | -25.77 | 63.17 | 7.6 | 0.01 | 0.22 | 125.37 | 0.55 | 0.82 |
| MR | $\Psi(.)p(.)$ | -27.67 | 60.26 | 0 | 0.38 | 0 | 116.61 | 0.69 | 0.69 |
| | **$\psi(MR_{500})p(.)$** | **-27.01** | **62.02** | **1.76** | **0.16** | **0.08** | **116.82** | **0.74** | **0.67** |
| | $\psi(MR_{200})p(.)$ | -27.3 | 62.61 | 2.35 | 0.12 | 0.05 | 116.51 | 0.63 | 0.71 |
| | $\psi(.)p(f)$ | -27.51 | 63.02 | 2.77 | 0.1 | 0.02 | 126.81 | 0.56 | 0.86 |
| | $\psi(MR_{400})p(.)$ | -27.58 | 63.17 | 2.91 | 0.09 | 0.01 | 116.55 | 0.73 | 0.64 |
| | $\psi(MR_{300})p(.)$ | -27.67 | 63.33 | 3.08 | 0.08 | 0 | 116.62 | 0.74 | 0.62 |
| | $\psi(MR_{500})p(f)$ | -26.94 | 65.51 | 5.25 | 0.03 | 0.09 | 120.07 | 0.66 | 0.77 |
| | $\psi(MR_{200})p(f)$ | -27.18 | 66 | 5.74 | 0.02 | 0.06 | 123.51 | 0.61 | 0.79 |

| | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | $\psi(MR_{400})p(f)$ | -27.47 | 66.58 | 6.32 | 0.02 | 0.03 | 123.71 | 0.74 | 0.7 |
| | | $\psi(MR_{300})p(f)$ | -27.51 | 66.66 | 6.4 | 0.02 | 0.02 | 127.15 | 0.63 | 0.8 |
| *L. pardalis* | FC | $\boldsymbol{\psi(FC_{300})p(s)}$ | **-28.67** | **68.98** | **0** | **0.42** | **0.61** | **102.62** | **0.51** | **0.73** |
| | | $\psi(FC_{400})p(s)$ | -28.85 | 69.33 | 0.36 | 0.35 | 0.6 | 103.65 | 0.65 | 0.6 |
| | | $\psi(FC_{500})p(s)$ | -29.56 | 70.76 | 1.78 | 0.17 | 0.56 | 102.45 | 0.61 | 0.65 |
| | | $\psi(FC_{200})p(s)$ | -30.59 | 72.82 | 3.84 | 0.06 | 0.5 | 103.71 | 0.53 | 0.73 |
| | | $\Psi(.)p(.)$ | -36.02 | 80.03 | 11.05 | 0 | 0 | 101.15 | 0.63 | 0.71 |
| | PD | $\boldsymbol{\psi(PD_{400})p(s)}$ | **-33.48** | **78.59** | **0** | **0.44** | **0.27** | **101.18** | **0.56** | **0.71** |
| | | $\psi(PD_{500})p(s)$ | -34.15 | 79.94 | 1.35 | 0.22 | 0.21 | 101.22 | 0.59 | 0.64 |
| | | $\Psi(.)p(.)$ | -36.02 | 80.03 | 1.44 | 0.21 | 0 | 101.15 | 0.63 | 0.63 |
| | | $\psi(PD_{300})p(s)$ | -35.33 | 82.3 | 3.71 | 0.07 | 0.08 | 101.04 | 0.57 | 0.57 |
| | | $\psi(PD_{200})p(s)$ | -35.41 | 82.45 | 3.86 | 0.06 | 0.07 | 101.17 | 0.67 | 0.65 |
| | MH | $\boldsymbol{\psi(MH_{300})p(s)}$ | **-28.75** | **69.14** | **0** | **0.7** | **0.6** | **101.79** | **0.52** | **0.63** |
| | | $\psi(MH_{400})p(s)$ | -29.72 | 71.08 | 1.93 | 0.27 | 0.55 | 106.2 | 0.48 | 0.63 |
| | | $\psi(MH_{200})p(s)$ | -32.55 | 76.73 | 7.59 | 0.02 | 0.36 | 103.24 | 0.48 | 0.64 |
| | | $\psi(MH_{500})p(s)$ | -33.22 | 78.07 | 8.92 | 0.01 | 0.3 | 103.97 | 0.46 | 0.66 |
| | | $\Psi(.)p(.)$ | -36.02 | 80.03 | 10.89 | 0 | 0 | 101.15 | 0.56 | 0.6 |
| | MR | $\Psi(.)p(.)$ | -36.02 | 80.03 | 0 | 0.52 | 0 | 101.15 | 0.54 | 0.8 |
| | | $\boldsymbol{\psi(MR_{500})p(s)}$ | **-35.46** | **82.55** | **2.52** | **0.15** | **0.07** | **101.25** | **0.66** | **0.59** |
| | | $\psi(MR_{200})p(s)$ | -35.6 | 82.84 | 2.8 | 0.13 | 0.05 | 101.1 | 0.49 | 0.6 |

| | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | $\psi(MR_{400})p(s)$ | -35.65 | 82.93 | 2.9 | 0.12 | 0.05 | 101.07 | 0.54 | 0.57 |
| | | $\psi(MR_{300})p(s)$ | -35.98 | 83.6 | 3.56 | 0.09 | 0 | 101.14 | 0.58 | 0.59 |
| *P. onca* | FC | **$\psi(FC_{400})p(s)$** | **-15.89** | **43.41** | **0** | **0.37** | **0.42** | **11.35** | **0.63** | **0.84** |
| | | $\psi(FC_{200})p(s)$ | -16.13 | 43.89 | 0.48 | 0.29 | 0.4 | 10.98 | 0.65 | 0.87 |
| | | $\psi(FC_{300})p(s)$ | -16.27 | 44.17 | 0.76 | 0.25 | 0.39 | 10.59 | 0.6 | 0.84 |
| | | $\Psi(.)p(.)$ | -19.8 | 47.59 | 4.18 | 0.05 | 0 | 10.91 | 0.55 | 0.89 |
| | | $\psi(FC_{500})p(s)$ | -18.12 | 47.88 | 4.46 | 0.04 | 0.21 | 10.69 | 0.74 | 0.82 |
| | PD | $\Psi(.)p(.)$ | -19.8 | 47.59 | 0 | 0.43 | 0 | 10.91 | 0.58 | 0.95 |
| | | **$\psi(PD_{400})p(s)$** | **-18.48** | **48.6** | **1.01** | **0.26** | **0.17** | **10.95** | **0.67** | **0.9** |
| | | $\psi(PD_{500})p(s)$ | -19.29 | 50.21 | 2.62 | 0.12 | 0.07 | 10.89 | 0.66 | 0.82 |
| | | $\psi(PD_{200})p(s)$ | -19.34 | 50.32 | 2.72 | 0.11 | 0.06 | 10.9 | 0.64 | 0.88 |
| | | $\psi(PD_{300})p(s)$ | -19.57 | 50.78 | 3.19 | 0.09 | 0.03 | 10.87 | 0.62 | 0.87 |
| | MH | **$\psi(MH_{400})p(s)$** | **-16** | **43.64** | **0** | **0.65** | **0.41** | **11.31** | **0.64** | **0.81** |
| | | $\psi(MH_{300})p(s)$ | -17.48 | 46.6 | 2.95 | 0.15 | 0.27 | 10.69 | 0.64 | 0.79 |
| | | $\Psi(.)p(.)$ | -19.8 | 47.59 | 3.95 | 0.09 | 0 | 10.91 | 0.71 | 0.84 |
| | | $\psi(MH_{200})p(s)$ | -18.16 | 47.96 | 4.32 | 0.07 | 0.2 | 10.84 | 0.61 | 0.87 |
| | | $\psi(MH_{500})p(s)$ | -18.85 | 49.33 | 5.69 | 0.04 | 0.12 | 10.76 | 0.71 | 0.86 |
| | MR | $\Psi(.)p(.)$ | -19.8 | 47.59 | 0 | 0.53 | 0 | 10.91 | 0.68 | 0.87 |
| | | **$\psi(MR_{500})p(s)$** | **-19.13** | **49.9** | **2.31** | **0.17** | **0.09** | **10.92** | **0.64** | **0.89** |
| | | $\psi(MR_{200})p(s)$ | -19.44 | 50.51 | 2.92 | 0.12 | 0.05 | 10.89 | 0.65 | 0.91 |

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| $\psi(MR_{400})p(s)$ | -19.72 | 51.07 | 3.48 | 0.09 | 0.01 | 10.92 | 0.63 | 0.88 |
| $\psi(MR_{300})p(s)$ | -19.8 | 51.23 | 3.64 | 0.09 | 0 | 10.91 | 0.58 | 0.91 |

The covariates are the percentage of forest cover (FC), patch density (PD), the percentage of habitat from matrix (MH) and matrix resistance (MR). The subscript numbers indicate the buffer size (in hectares) of each covariate. The null model does not include a covariate (.). The models' log-likelihood (LL), Akaike Information Criterion (AIC), Akaike differences ($\Delta_i$), Akaike weights ($w_i$), the Nagelkerke's $R^2$ ($R^2$), the models' Pearson chi-square ($\chi^2$), significance ($P$) and overdispersion parameter ($\hat{c}$) of each model are shown. The selected models (and therefore, the scale of effect of each metric) for further analysis are in bold.

# CAPÍTULO V. DISCUSIÓN Y CONCLUSIONES GENERALES

Conservar la diversidad de plántulas y mantener los factores que la promueven son cruciales para la regeneración de los bosques tropicales húmedos. Es por ello que en esta tesis identificamos y evaluamos qué factores de las estructuras del fragmento y el paisaje mantienen la diversidad de la comunidad de plántulas y la presencia de mamíferos terrestres en un bosque tropical húmedo hiper fragmentado en la Selva Lacandona.

A pesar de que esta región aún tiene un alto porcentaje de bosque remanente (Arasa-Gisbert et al., 2021; San-José et al., 2019), la deforestación se concentra en los bosques de terraza aluvial adyacentes al río Lacantún, donde la mayor parte de la cobertura arbórea ha sido eliminada para la expansión de pastizales ganaderos y cultivos temporales y agroindustriales (Berget et al., 2021; Carabias et al., 2015). El bosque primario de estas zonas está reducido a pocos fragmentos de tamaños menores a las 100 ha y la intensificación de las actividades agrícolas y ganaderas limitan su regeneración a partir de bosques secundarios (M. Lohbeck et al., 2022). Considerando que los bosques tropicales húmedos hiper fragmentados (aquellos con una cobertura de bosque primario < 30%, dominados por matrices agropecuarias  fragmentos menores a las 50 ha; Oliveira et al., 2008; Tabarelli et al., 2012) serán dominantes en el mediano y largo plazo (Taubert et al., 2018), los paisajes analizados en nuestro sitio son representativos de las condiciones actuales y futuras de los PMH tropicales, así como idóneos para determinar los factores que a actúan a múltiples escalas sobre la regeneración del bosque primario dentro de fragmentos.

Tomando en cuenta la baja cobertura de bosque primario remanente en el sitio de estudio (< 20%) y de acuerdo con la hipótesis del umbral de fragmentación (Andren, 1994), hipotetizamos que la diversidad de plántulas y la presencia de mamíferos terrestres se encuentran fuertemente influenciadas por factores a escala de fragmento (i.e., tamaño, estructura/diversidad del bosque y nivel de disturbio), la matriz circundante (i.e., porcentaje de bosques secundarios y sus efectos sobre la complementación/conectividad del paisaje en mamíferos) y la configuración del paisaje (i.e., densidad, agregación y asilamiento de los fragmentos, así como su contraste de borde con las matrices adyacentes).

### *El área basal tiene efectos en cascada sobre la composición y la diversidad β de plántulas*

A escala local, encontramos que la composición y la diversidad β de especies comunes y dominantes de plántulas fueron favorecidas por la reducción en la abundancia de plántulas demandantes de luz en fragmentos con una alta área basal. También observamos que la diversidad α de todas las especies de plántulas (riqueza) está determinada por la abundancia de plántulas tolerantes a la sombra, las cuales fueron afectadas negativamente en fragmentos con una alta abundancia de plántulas demandantes de luz y dentro de paisajes con una baja agregación de fragmentos.

El área basal influencia la abundancia y composición de plántulas a través de la producción de frutos (Chapman et al., 1992), la disponibilidad de luz, agua y nutrientes en el suelo (J S Denslow, 1987; Madelon Lohbeck et al., 2015; Martinez-Ramos & Soto-Castro, 1993; Turner, 2004) y la mortalidad conespecífica de plántulas (Wright, 2002). En nuestro estudio, el área basal solamente afectó la abundancia de plántulas demandantes de luz, sugiriendo que fragmentos perturbados (menor abundancia de árboles grandes) promueven el establecimiento y sobrevivencia de estas especies al incrementar la disponibilidad de luz (J S Denslow, 1987; Julie S. Denslow, 1996). Estas condiciones promueven el establecimiento de un subconjunto de especies que son ecológicamente redundantes, que carecen de relación filogenética y que dan lugar a ensambles de especies empobrecidos y dominados por pocas especies con altas abundancias (Oliveira et al., 2008; Tabarelli et al., 2012). Estos ensambles indican un proceso de homogenización biótica, caracterizado por una baja composición de la comunidad (i.e., menor disimilitud entre comunidades), como una reducción en la diversidad β (i.e., menor recambio de especies) a escala local y de paisaje (Olden & Rooney, 2006; Solar et al., 2015; Tabarelli et al., 2012).

Lo anterior es congruente con nuestras observaciones, donde una mayor abundancia de plántulas demandantes de luz redujo tanto la composición de plántulas, como la diversidad β de especies típicas y dominantes, variables sensibles a las fluctuaciones de abundancias (Jost, 2007; Roden et al., 2018). Además, la ausencia de efectos directos por parte de la estructura del paisaje, respaldan las hipótesis que establecen que las especies generalistas y las poblaciones con una alta densidad de individuos son principalmente afectadas por factores a escalas pequeñas (Miguet et al., 2016). Esto apoya los efectos en cascada de la estructura del paisaje sobre la abundancia de una palma competidora de luz, la cual representó el factor local tuvo el mayor impacto sobre respuestas biológicas afectadas a escalas pequeñas, tales como la densidad de especies e individuos (Hernández-Ruedas et al., 2018).

Por el contrario, la abundancia de plántulas tolerantes a la sombra fue mayormente explicada por la agregación de fragmentos en el paisaje, lo cual respalda las hipótesis de Miguet et al. (2016) arriba mencionadas. Las plántulas tolerantes a la sombra tienen una especialización de hábitat mayor que las especies demandantes de luz, así como una menor densidad de población (Julie S. Denslow, 1996; Turner, 2004). Además, sus abundancias son reguladas por la mortalidad conespecífica de plántulas y el forrajeo de frutos, semillas y plántulas por mamíferos terrestres (Camargo-Sanabria et al., 2014; Comita et al., 2007, 2010; Dirzo & Miranda, 1990). Lo anterior sugiere que la estructura del paisaje afecta la abundancia de las plántulas tolerantes a la sombra al facilitar o limitar la llegada de dispersoras de semillas y de depredadores de semillas/plántulas.

Este supuesto está respaldado por estudios previos que encontraron una contribución significativa del porcentaje de bosque primario en el paisaje sobre la riqueza y abundancia de la lluvia de semillas y los brinzales de especies de árboles especialistas de dispersión biótica (Arasa-Gisbert et al., 2021; San-José et al., 2019). Estos estudios concluyeron que la pérdida de especies tolerantes a la sombra es resultado de la falta de dispersión de semillas en paisajes cuya baja cobertura de bosque limita el movimiento de fauna, la cual dispersa el 90% de las especies de árboles de bosques tropicales (Jordano, 2000). No obstante, el tamaño del ámbito hogareño de la fauna puede variar en función de la agregación de fragmentos en paisajes con bajo porcentaje de hábitat (Gardiner et al., 2019; Hodgson et al., 2012; Radford et al., 2005), aminorando el efecto de la pérdida de hábitat sobre el movimiento de fauna.

En este trabajo, encontramos que la abundancia de plántulas tolerantes a la sombra aumentó en paisajes con una alta agregación de fragmentos, lo que sugiere que este patrón configuracional promueve la llegada de dispersores de semillas y de depredadores de semillas y plántulas. Las funciones de dispersión y depredación, aunadas a la mortalidad conespecífica de plántulas que promueven su diversidad (Comita et al., 2010; Harms et al., 2000; Wright, 2002) explican el efecto positivo que la abundancia de plántulas tolerantes a la sombra tiene sobre la diversidad α de todas las especies de plántulas. Resulta interesante que la abundancia de plántulas tolerantes a la sombra fuera afectada por la abundancia de plántulas demandantes de luz, lo cual sugiere que las segundas ejercen una presión competitiva por recursos. La exclusión competitiva puede jugar un papel importante en la reducción de la diversidad α dentro de bosques con una alta disponibilidad de luz y una menor presión por herbívoros (Wright, 2002). Esto respalda el efecto indirecto que observamos de la abundancia de plántulas demandantes de luz sobre la riqueza de especies.

### *La diversidad α y β responden a distintos componentes de la estructura del paisaje*

A su vez, la diversidad α y β de las plántulas fueron afectadas por la composición y configuración del paisaje, respectivamente. Por un lado, la α disminuyó en paisajes dominados por bosques secundarios. Por otro lado, la diversidad β de especies comunes y dominantes fue promovida en paisajes con una alta densidad de fragmentos, mientras que la diversidad β que considera a todas las especies (incluyendo aquellas especies raras con bajas abundancias) disminuyó en paisajes con un alto contraste de borde.

En la sección anterior quedó establecido que el incremento en la riqueza de plántulas en paisajes con una mayor agregación de fragmentos está asociado con una mayor llegada de dispersores de semillas y de mamíferos terrestres que promueven su diversidad. Esto resalta el papel que tiene la configuración del paisaje para promover la dispersión de semillas y la persistencia de funciones ecológicas en paisajes muy fragmentados (Fahrig, 2017; Haan et al., 2020).

Por el contrario, el efecto negativo del porcentaje de bosques secundarios sobre los tres órdenes de diversidad α sugieren la llegada de un grupo de especies reducido en la lluvia de semillas. La composición de la vegetación secundaria puede ejercer una fuerte influencia en la diversidad de especies que se establecen en los bordes y claros de los fragmentos (Laurance et al., 2006, 2007; Nascimento et al., 2006). A su vez, esta composición es resultado de la historia de uso de suelo y la intensidad, duración y frecuencia de la perturbación previa al crecimiento de la vegetación secundaria (Laurance et al., 2007; Zermeño-Hernández et al., 2015).

En la región de estudio, las comunidades de plántulas que se establecen en coberturas con suelos fuertemente compactados, afectados por incendios severos y/o frecuentes presentan una menor densidad de individuos y especies, así como bajos valores de diversidad (Zermeño-Hernández et al., 2015). La cobertura asociada a este tipo de manejo son los pastizales ganaderos, los cuales son dominantes en los bosques de planicies aluviales (Berget et al., 2021; Carabias et al., 2015; Zermeño-Hernández et al., 2015). Por lo tanto, los bosques secundarios que se desarrollan en estas condiciones presentan una estructura y diversidad menores que en bosques secundarios establecidos en usos de suelo con una menor severidad de disturbio como los sitios que fueron utiliuzados en este trabajo, reduciendo su potencial de regeneración (Chazdon, 2014).

Estos bosques a su vez, tienen una fuerte influencia en la trayectoria de regeneración de la vegetación dentro de fragmentos, las cuales divergen en función de la composición de especies de los bosques adyacentes (Laurance et al., 2007). A esto hay que agregar la influencia de las coberturas dominantes en el paisaje circundante, debido a que la diversidad arbórea está fuertemente afectada por la dominancia de coberturas de uso de suelo con un alto grado de perturbación (Tenius Ribeiro et al., 2019; Zermeño-Hernández et al., 2016). Como resultado, se espera que la dominancia de pastizales ganaderos y sus bosques secundarios derivados tengan un efecto negativo sobre la diversidad α de las plántulas.

El incremento de la diversidad β de las plántulas en paisajes con bajos contrastes de borde y una mayor densidad de fragmentos podría sugerir que la heterogeneidad espacial de las especies de plántulas es promovida ya sea por sea la llegada de especies desde fragmentos con distintos ensambles de árboles, la reducción de los efectos de borde o la llegada de dispersores de semillas y mamíferos terrestres que contribuyen a mantener su diversidad.

La alta heterogeneidad de hábitats y condiciones ambientales entre fragmentos promueven el establecimiento de comunidades de árboles con composiciones muy diferentes entre sí, lo que aumenta la diversidad β a escala regional (Arroyo-Rodríguez et al., 2013; Bennett & Gilbert, 2016; Hernández-Ruedas et al., 2014). Además, se espera que la dispersión de semillas se incremente en paisajes con un mayor número de fragmentos, los cuales tienen un efecto positivo sobre la lluvia de semillas (San-José et al., 2019). Por lo tanto, la densidad de parches puede incrementar la diversidad β de las plántulas al facilitar la llegada de semillas de fragmentos con ensambles de árboles heterogéneos. Los resultados de los capítulos II y III nos muestran que la diversidad β de especies típicas y dominantes es afectada por el área basal del fragmento a través de la fluctuación de abundancias de plántulas demandantes de luz y por la configuración del paisaje que facilita la llegada de especies nuevas.

Finalmente, el efecto negativo del contraste de borde sobre la diversidad β de todas las especies (incluyendo aquellas con bajas abundancias), puede estar asociado a una mayor exposición a los efectos de borde o a una barrera que impide la llegada de mamíferos terrestres. La homogenización del paisaje está fuertemente vinculada con la magnitud de los efectos de borde, los cuales promueven la dominancia de pocas especies tolerantes a la perturbación (Oliveira et al., 2008; Tabarelli et al., 2010). Los efectos de borde incrementan la mortalidad de plántulas tolerantes a la sombra y desplazan a las especies raras, al mismo tiempo que promueven el recambio de especies demandantes de luz (Benítez-Malvido et al., 2018; Krishnadas et al., 2018). Por lo tanto, la diversidad β de plántulas raras puede mantenerse en fragmentos donde los efectos de borde son aminorados a través de un bajo contraste de borde.

Sin embargo, se esperaría que estos efectos ocurrieran a una escala espacial menor a la observada en nuestro trabajo (200 ha). La escala del efecto registrada para el contraste de borde fue similar a la observada para la proporción de matrices abiertas sobre la riqueza y diversidad de especies de brinzales especialistas en paisajes hiper fragmentados (Arasa-Gisbert et al., 2021). En este estudio, se plantea que la apertura de matrices incrementa el aislamiento de los fragmentos al limitar el movimiento de dispersores de semillas, dando como resultado una menor abundancia y riqueza (Galán-Acedo et al., 2019; San-José et al., 2019).

Además la riqueza y similitud de la comunidad de mamíferos terrestres entre fragmentos está fuertemente vinculada con la dominancia de matrices estructuralmente similares a la vegetación del fragmento (Arce-Peña et al., 2022; Garmendia et al., 2013), lo que sugiere que las matrices con cobertura arbórea facilitan el movimiento de fauna entre fragmentos (Arroyo-Rodríguez et al., 2020). La actividad de estos mamíferos regula la abundancia y distribución espacial de especies de plántulas dominantes, lo que promueve la diversidad β y la persistencia de especies raras (Bleher & Böhning-Gaese, 2001; Fragoso et al., 2003; Paine & Beck, 2007; Villar et al., 2019). Corroborar este argumento requerirá de analizar los efectos en cascada del porcentaje de matrices abiertas/permeables o del porcentaje bordes contrastantes en el paisaje sobre la diversidad β a través de la ocupación, abundancia o índice de defaunación del fragmento.

### *El papel de la densidad de fragmentos y la resistencia de la matriz sobre la conectividad del paisaje en mamíferos terrestres*

Finalmente, la presencia de mamíferos terrestres -cuyos patrones de actividad y forrajeo promueven la diversidad de plántulas- fue favorecida tanto por la densidad de fragmentos, como por la conectividad proporcionada por la matriz circundante. En este caso, encontramos que la probabilidad de ocupación de los fragmentos para tres de las cuatro especies de mamíferos evaluadas aumentó en los paisajes que tuvieron una menor resistencia al movimiento a través de la matriz.

Cabe destacar que los la escala de los efectos de la matriz sobre la disponibilidad de hábitat fue menor respecto a los efectos que tuvo sobre la resistencia al movimiento de fauna. Esto respalda la predicción de Miguet et al. (2016) planteando que la escala del efecto en variables que afectan el éxito reproductivo/forrajeo es menor que aquellas variables que influencian la dispersión. Este resultado muestra que la matriz afecta la presencia de mamíferos a través de procesos que operan a distintas escalas de manera simultánea.

## Literatura citada

Andren, H. (1994). Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. *Oikos*, *71*, 355–366. https://doi.org/10.2307/3545823

Arasa-Gisbert, R., Arroyo-Rodríguez, V., Galán-Acedo, C., Meave, J. A., & Martínez-Ramos, M. (2021). Tree recruitment failure in old-growth forest patches across human-modified rainforests. *Journal of Ecology*, *March*, 1–13. https://doi.org/10.1111/1365-2745.13643

Arce-Peña, N. P., Arroyo-Rodríguez, V., Avila-Cabadilla, L. D., Moreno, C. E., & Andresen, E. (2022). Homogenization of terrestrial mammals in fragmented rainforests: the loss of species turnover and its landscape drivers. *Ecological Applications*, *32*(1). https://doi.org/10.1002/eap.2476

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., … Tscharntke, T. (2020). Designing optimal human-modified landscapes for forest biodiversity conservation. *Ecology Letters*. https://doi.org/10.1111/ele.13535

Arroyo-Rodríguez, V., Rös, M., Escobar, F., Melo, F. P. L., Santos, B. A., Tabarelli, M., & Chazdon, R. (2013). Plant β-diversity in fragmented rain forests: Testing floristic homogenization and differentiation hypotheses. *Journal of Ecology*, *101*(6), 1449–1458. https://doi.org/10.1111/1365-2745.12153

Benítez-Malvido, J., Lázaro, A., & Ferraz, I. D. K. (2018). Effect of distance to edge and edge interaction on seedling regeneration and biotic damage in tropical rainforest fragments: A long-term experiment. *Journal of Ecology*, *106*(6), 2204–2217. https://doi.org/10.1111/1365-2745.13003

Bennett, J. R., & Gilbert, B. (2016). Contrasting beta diversity among regions: how do classical and multivariate approaches compare? *Global Ecology and Biogeography*, *25*(3), 368–377. https://doi.org/10.1111/geb.12413

Berget, C., Verschoor, G., García-Frapolli, E., Mondragón-Vázquez, E., & Bongers, F. (2021). Landscapes on the move: Land-use change history in a mexican agroforest frontier. *Land*, *10*(10). https://doi.org/10.3390/land10101066

Bleher, B., & Böhning-Gaese, K. (2001). Consequences of frugivore diversity for seed dispersal, seedling establishment and the spatial pattern of seedlings and trees. *Oecologia*, *129*(3), 385–394. https://doi.org/10.1007/s004420100747

Camargo-Sanabria, A. A., Mendoza, E., Guevara, R., Martínez-Rmos, M., & Dirzo, R. (2014). Experimental defaunation of terrestrial mammalian herbivores alters tropical rainforest understorey diversity. *Proceedings of the Royal Society B: Biological Sciences*, *282*(1800). https://doi.org/10.1098/rspb.2014.2580

Carabias, J., De la Maza, J., & Cadena, R. (2015). *Conservación y desarrollo sustentable en la Selva Lacandona: 25 años de actividades y experiencia*. Natura y Ecosistemas Mexicanos.

Chapman, C. A., Chapman, L. J., Wangham, R., Hunt, K., Gebo, D., & Gardner, L. (1992).

Estimators of Fruit Abundance of Tropical Trees. *Biotropica*, *24*(4), 527–531. https://doi.org/10.2307/2389015

Chazdon, R. L. (2014). *Second Growth: The Promise of Tropical Forest Regeneration in an Age of Deforestation*. University of Chicago Press. https://doi.org/doi:10.7208/9780226118109

Comita, L. S., Aguilar, S., Pérez, R., Lao, S., & Hubbell, S. P. (2007). Patterns of woody plant species abundance and diversity in the seedling layer of a tropical forest. *Journal of Vegetation Science*, *18*(2), 163. https://doi.org/10.1658/1100-9233(2007)18[163:powpsa]2.0.co;2

Comita, L. S., Muller-Landau, H. C., Aguilar, S., & Hubbell, S. P. (2010). Asymmetrie density dependence shapes species abundances in a tropical tree community. *Science*, *329*(5989), 330–332. https://doi.org/10.1126/science.1190772

Denslow, J S. (1987). Tropical Rainforest Gaps and Tree Species Diversity. *Annual Review of Ecology and Systematics*, *18*(1), 431–451. https://doi.org/10.1146/annurev.es.18.110187.002243

Denslow, Julie S. (1996). Functional Group Diversity and Responses to Disturbance. In *Biodiversity and Ecosystem Processes in Tropical Forests* (Vol. 122, pp. 127–151). Springer, Berlin, Heidelberg. https://doi.org/10.1007/978-3-642-79755-2_7

Dirzo, R., & Miranda, A. (1990). Contemporary Neotropical Defaunation and Forest Structure, Function, and Diversity-A Sequel to John Terborgh*. *Conservation Biology*, *4*(4), 444–447. https://doi.org/10.1111/j.1523-1739.1990.tb00320.x

Fahrig, L. (2017). Ecological Responses to Habitat Fragmentation Per Se. *Annual Review of Ecology, Evolution, and Systematics*, *48*(1), 1–23. https://doi.org/10.1146/annurev-ecolsys-110316-022612

Fragoso, J. M. V, Silvius, K. M., & Correa, J. A. (2003). Long-distance sees dispersal by tapirs increase seed survival and aggregates tropical trees. *Ecology*, *84*(8), 1998–2006. https://doi.org/10.1890/01-0621

Galán-Acedo, C., Arroyo-Rodríguez, V., Estrada, A., & Ramos-Fernández, G. (2019). Forest cover and matrix functionality drive the abundance and reproductive success of an endangered primate in two fragmented rainforests. *Landscape Ecology*, *34*(1), 147–158. https://doi.org/10.1007/s10980-018-0753-6

Gardiner, R., Proft, K., Comte, S., Jones, M., & Johnson, C. N. (2019). Home range size scales to habitat amount and increasing fragmentation in a mobile woodland specialist. *Ecology and Evolution*, *9*(24), 14005–14014. https://doi.org/10.1002/ece3.5837

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*(4), 331–344. https://doi.org/10.1017/S0266467413000370

Haan, N. L., Zhang, Y., & Landis, D. A. (2020). Predicting Landscape Configuration Effects on Agricultural Pest Suppression. *Trends in Ecology and Evolution*, *35*(2), 175–186. https://doi.org/10.1016/j.tree.2019.10.003

Harms, K. E. E., Wright, S. J. J., Calderón, O., Hernández, A., & Herre, E. A. a. (2000). Pervasive density-dependent recruitment enhances seedling diversity in a tropical forest. *Nature*, *404*(6777), 493–495. https://doi.org/10.1038/35006630

Hernández-Ruedas, M. A., Arroyo-Rodríguez, V., Meave, J. A., Martínez-Ramos, M., Ibarra-Manríquez, G., Martínez, E., Jamangapé, G., Melo, F. P. L., & Santos, B. A. (2014). Conserving tropical tree diversity and forest structure: The value of small rainforest patches in moderately-managed landscapes. *PLoS ONE*, *9*(6), e98931. https://doi.org/10.1371/journal.pone.0098931

Hernández-Ruedas, M. A., Arroyo-Rodríguez, V., Morante-Filho, J. C., Meave, J. A., & Martínez-Ramos, M. (2018). Fragmentation and matrix contrast favor understory plants through negative cascading effects on a strong competitor palm. *Ecological Applications*, *28*(6), 1546–1553. https://doi.org/10.1002/eap.1740

Hodgson, J. A., Thomas, C. D., Dytham, C., Travis, J. M. J., & Cornell, S. J. (2012). The Speed of Range Shifts in Fragmented Landscapes. *PLOS ONE*, *7*(10), e47141. https://doi.org/10.1371/journal.pone.0047141

Jordano, P. (2000). Fruits and frugivory. In M. Fenner (Ed.), *Seeds: the ecology of regeneration in plant communities* (2nd ed., pp. 125–166). CABI Publishing.

Jost, L. (2007). Partitioning diversity into independent alpha and beta components. *Ecology*, *88*(10), 2427–2439. https://doi.org/10.1890/06-1736.1

Krishnadas, M., Bagchi, R., Sridhara, S., & Comita, L. S. (2018). Weaker plant-enemy interactions decrease tree seedling diversity with edge-effects in a fragmented tropical forest. *Nature Communications*, *9*(1). https://doi.org/10.1038/S41467-018-06997-2

Laurance, W. F., Nascimento, H. E. M., Laurance, S. G., Andrade, A. C., Fearnside, P. M., Ribeiro, J. E. L., & Capretz, R. L. (2006). Rain forest fragmentation and the proliferation of successional trees. *Ecology*, *87*(2), 469–482. https://doi.org/10.1890/05-0064

Laurance, W. F., Nascimento, H. E. M. M., Laurance, S. G., Andrade, A., Ewers, R. M., Harms, K. E., Luizão, R. C. C. C., & Ribeiro, J. E. (2007). Habitat fragmentation, variable edge effects, and the landscape-divergence hypothesis. *PLoS ONE*, *2*(10), e1017. https://doi.org/10.1371/journal.pone.0001017

Lohbeck, M., DeVries, B., Bongers, F., Martínez-Ramos, M., Navarrete-Segueda, A., Nicasio-Arzeta, S., Siebe, C., Pingarroni, A., Wies, G., & Decuyper, M. (2022). Mexican agricultural frontier communities differ in forest dynamics with consequences for conservation and restoration. *Remote Sensing in Ecology and Conservation*, *37*(2), 10–14. https://doi.org/10.1002/RSE2.262

Lohbeck, Madelon, Poorter, L., Martínez-Ramos, M., Bongers, F., Martinez-Ramos, M., Bongers, F., & Craft, N. J. B. (2015). Biomass is the main driver of changes in ecosystem process rates during tropical forest succession. *Ecology*, *96*(5), 1242–1252. https://doi.org/10.1890/14-0472.1

Martinez-Ramos, M., & Soto-Castro, A. (1993). Seed rain and advanced regeneration in a tropical rain forest. *Vegetatio*, *107*, 299–318. https://doi.org/10.1007/BF00052231

Miguet, P., Jackson, H. B., Jackson, N. D., Martin, A. E., & Fahrig, L. (2016). What determines the spatial extent of landscape effects on species? *Landscape Ecology*, *31*(6), 1177–1194. https://doi.org/10.1007/s10980-015-0314-1

Nascimento, H. E. M., Andrade, A. C. S., Camargo, J. L. C., Laurance, W. F., Laurance, S. G., & Ribeiro, J. E. L. (2006). Effects of the Surrounding Matrix on Tree Recruitment in Amazonian Forest Fragments. *Conservation Biology*, *20*(3), 853–860.

https://doi.org/10.1111/j.1523-1739.2006.00344.x

Olden, J. D., & Rooney, T. P. (2006). On defining and quantifying biotic homogenization. *Global Ecology and Biogeography*, *15*(2), 113–120. https://doi.org/10.1111/j.1466-822X.2006.00214.x

Oliveira, M. A., Santos, A. M. M., & Tabarelli, M. (2008). Profound impoverishment of the large-tree stand in a hyper-fragmented landscape of the Atlantic forest. *Forest Ecology and Management*, *256*(11), 1910–1917. https://doi.org/10.1016/j.foreco.2008.07.014

Paine, C. E. T., & Beck, H. (2007). Seed predation by neotropical rain forest mammals increases diversity in seedling recruitment. *Ecology*, *88*(12), 3076–3087. https://doi.org/10.1890/06-1835.1

Radford, J. Q., Bennett, A. F., & Cheers, G. J. (2005). Landscape-level thresholds of habitat cover for woodland-dependent birds. *Biological Conservation*, *124*(3), 317–337. https://doi.org/10.1016/j.biocon.2005.01.039

Roden, V. J., Kocsis, Á. T., Zuschin, M., & Kiessling, W. (2018). Reliable estimates of beta diversity with incomplete sampling. *Ecology*, *99*(5), 1051–1062. https://doi.org/10.1002/ecy.2201

San-José, M., Arroyo-Rodríguez, V., Jordano, P., Meave, J. A., & Martínez-Ramos, M. (2019). The scale of landscape effect on seed dispersal depends on both response variables and landscape predictor. *Landscape Ecology*, 1–12. https://doi.org/10.1007/s10980-019-00821-y

San-José, M., Arroyo-Rodríguez, V., & Meave, J. A. (2019). Regional context and dispersal mode drive the impact of landscape structure on seed dispersal. *Ecological Applications*, *0*(0), eap.2033. https://doi.org/10.1002/eap.2033

Solar, R. R., 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., 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*(10), 1108–1118. https://doi.org/10.1111/ele.12494

Tabarelli, M., Aguiar, A. V., Girão, L. C., Peres, C. A., & Lopes, A. V. (2010). Effects of pioneer tree species hyperabundance on forest fragments in Northeastern Brazil. *Conservation Biology*, *24*(6), 1654–1663. https://doi.org/10.1111/j.1523-1739.2010.01529.x

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. https://doi.org/10.1016/j.biocon.2012.06.020

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*(7693), 519–522. https://doi.org/10.1038/nature25508

Tenius Ribeiro, J. C., Nunes-Freitas, A. F., Fidalgo, E. C. C., & Uzêda, M. C. (2019). Forest fragmentation and impacts of intensive agriculture: Responses from different tree functional groups. *PLoS ONE*, *14*(8). https://doi.org/10.1371/journal.pone.0212725

Turner, I. M. (2004). *The Ecology of Trees in the Tropical Rain Forest* (P. S. Ashton, S. P. Hubbell, D. H. Janzen, P. H. Raven, & P. B. Tomilson (Eds.)). Cambridge University Press.

Villar, N., Siqueira, T., Zipparro, V. B., Farah, F., Schmaedecke, G., Hortenci, L., Brocardo, C. R., Jordano, P., & Galetti, M. (2019). The cryptic regulation of diversity by functionally complementary large tropical forest herbivores. *Journal of Ecology*, 1365-2745.13257. https://doi.org/10.1111/1365-2745.13257

Wright, S. J. (2002). Plant diversity in tropical forests: A review of mechanisms of species coexistence. *Oecologia*, *130*(1), 1–14. https://doi.org/10.1007/s004420100809

Zermeño-Hernández, I., Méndez-Toribio, M., Siebe, C., Benítez-Malvido, J., & Martínez-Ramos, M. (2015). Ecological disturbance regimes caused by agricultural land uses and their effects on tropical forest regeneration. *Applied Vegetation Science*, *18*(3), 443–455. https://doi.org/10.1111/avsc.12161

Zermeño-Hernández, I., Pingarroni, A., & Martínez-Ramos, M. (2016). Agricultural land-use diversity and forest regeneration potential in human- modified tropical landscapes. *Agriculture, Ecosystems and Environment*, *230*, 210–220. https://doi.org/10.1016/j.agee.2016.06.007