El Colegio de la Frontera Sur

Conectividad del paisaje para crácidos dependientes de bosques en el Corredor Biológico Mesoamericano Sierra Madre del Sur

Tesis

presentada como requisito parcial para optar al grado de
Doctora en Ciencias en Ecología y Desarrollo Sustentable
Con orientación en Ciencias de la Sustentabilidad

Por

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2020

Anexo 13

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El Colegio de la Frontera Sur

San Cristóbal de las Casas, Chiapas, 29 de Mayo de 2020.

Las personas abajo firmantes, miembros del jurado examinador de:

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“Conectividad del paisaje para crácidos dependientes de bosques en el Corredor Biológico Mesoamericano Sierra Madre del Sur”

para obtener el grado de **Doctor (a) en Ciencias en Ecología y Desarrollo Sustentable**

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DEDICATORIA

Dedico esta tesis a mi familia, por su apoyo y amor incondicional, que hacen tan plena mi vida. A mi hija Itzel Jimena, a mi madre, Angelina Ocampo; a mi esposo Efraín Hernández, a todos mis hermanos y hermanas, cuñados y cuñadas, sobrinos y sobrinas, los amo enormemente. También a mi padre Rito Escobar y a mi hermana Udy, que aunque ya no están físicamente para vivir este acontecimiento, sin duda compartirían con mucha alegría y orgullo esta nueva meta lograda.

AGRADECIMIENTOS

Al Consejo Nacional de Ciencia y Tecnología por haberme otorgado la beca No. 396685 para realizar los estudios de doctorado. Al proyecto Innovación socio-ambiental GIEZCA por el apoyo financiero para la primera fase del trabajo de campo, a Ecometrica LTD por el financiamiento en la segunda fase de campo y UK Space Agency, a través del proyecto Forest2020 por el apoyo para la producción de mapas de alta resolución y para la publicación de ambos artículos científicos.

Agradezco a cada uno de los miembros de mi consejo tutelar por su apoyo, interés y valiosas aportaciones en la tesis y artículos científicos: A Miguel Ángel Castillo Santiago, por su invaluable apoyo metodológico, logístico y financiero, por su paciencia y por su constante inducción para realizar y concluir este proceso. A Nicole Sibelet, por su gran calidad humana, por su aporte en el aspecto social de la investigación, por su apoyo para gestionar la estancia académica y por su hospitalidad en el CIRAD, Montpellier, Francia. A Susana Ochoa Gaona, por su cálida amistad, por su esencial asesoría y por su apoyo financiero para la publicación del primer artículo. A Paula Lidia Enríquez Rocha, por su orientación, sus valiosos aportes sobre ecología de las especies y por las bases de datos de crácidos de El Triunfo.

A Claudia María Monzón Alvarado, por su asesoría inicial para definir el diseño del proyecto. A todos los académicos de los cursos de Ciencias de la Sustentabilidad y Ecología del paisaje, por las interesantes reflexiones en clases. A Coral Jazvel Pacheco Figueroa, Juan de Dios Valdez Leal, Eduardo Jorge Naranjo Piñera, Esteban Pineda Diez de Bonilla, Rafael Calderón Contreras, Darío Navarrete Gutiérrez, Raúl Vaca Genuit y Sergio Cortina Villar, que en la revisión final, en el examen predoctoral y en la evaluación de protocolo aportaron recomendaciones para mejorar la investigación.

Al Laboratorio de Análisis Geográfico (LAIGE-ECOSUR), en particular a Darío Navarrete, Roberto Domínguez, Rocío Espinosa, Rafael García, Edith Mondragón y Rosa Elena Escobar por su apoyo y asesoría en la clasificación de imágenes de satélite y uso de SIG. A Delfino Méndez y al programa Ermex de la Secretaria de Marina por las facilidades prestadas para la adquisición de las imágenes SPOT. A Julio César Llanes y Marta Trejo, por su apoyo en la gestión

administrativa de gastos de campo. A Israel Cárdenas, por su entusiasta apoyo y su alegre compañía en la primera fase de campo.

A Guillermo Velasco Barajas por su apoyo logístico durante el diseño de este proyecto, por facilitarme el vínculo con otras organizaciones relacionadas con el área de estudio y por la información proporcionada sobre la misma, infinitas gracias. A la Cooperativa AMBIO, por su pronto y oportuno apoyo de vinculación con las comunidades que asesoran, por su invaluable apoyo logístico en la primera fase de campo: Sotero Quechulpa, Marcela Delgadillo, Israel Cárdenas y Luis Alberto Mendoza. Mil gracias.

Al director y personal técnico de La Frailescana: Raúl Díaz, Manuela Morales y a los integrantes de las brigadas comunitarias que me brindaron su hospitalidad, su apoyo como guías de campo y con el muestreo de sitios en Piedras Negras, Francisco Murguía, Nueva Reforma Agraria, Plan de Ayala y San Juan de los Ángeles (Villa Corzo).

A los directores y personal técnico de El Triunfo, por su respaldo y apoyo logístico en campo: Juan Carlos Castro, Alekser Vázquez, Jannete González y Rossana Megchun. A los guardaparques por su apoyo logístico y en el trabajo de campo: Adolfo y Arsenio Carbajal, Edilberto Galvez, Abilevi López y su hermano Abiligam López.

Al Fondo de Conservación El Triunfo (FONCET), particularmente a Andrómeda Rivera, Carolina Guzmán y Carlos Estrada, por su invaluable apoyo logístico para coincidir con sus viajes a las localidades de estudio, por su apoyo en el trabajo de campo, por la información geográfica y documental del trabajo que ahí realizan, así como por la vinculación con las brigadas comunitarias de Loma Bonita, Santa Rosa Las Nubes (Mapastepec) y Puerto Rico (Montecristo de Guerrero) que nos dieron alojamiento y/o nos brindaron apoyo en el trabajo de campo. A don Héctor Pérez y Hugo Ventura, de Loma Bonita, por su apoyo también en la segunda etapa del trabajo de campo, les estoy muy agradecida.

A la organización cafetalera CESMACH y Rigoberto Hernández, por la información proporcionada en bases de datos y por facilitarnos la llegada a las comunidades Rancho Bonito, Santa Isabel Ziján y La Lagunita (municipio de Capitán Luis A. Vidal), por su hospitalidad, muchas gracias.

A la Secretaría de Medio Ambiente e Historia Natural, particularmente a la Dirección de Áreas Naturales y Vida Silvestre, por las bases de datos proporcionadas. A Pronatura Sur, A.C., por la información geográfica y documental proporcionada, por permitirme participar en un evento con monitores de aves de la sierra madre. A la Comon Yaj Noptic por su colaboración en campo. Al Grupo intercomunitario de acción territorial de la microcuenca La Suiza, y la Asociación Regional de Silvicultores Sierra Motozintla A.C. por su colaboración y apoyo logístico. A las autoridades y habitantes de los ejidos y comunidades; por permitir la realización del trabajo de campo.

Agradezco también al personal de ECOSUR San Cristóbal, que en distintos momentos me brindaron su amable apoyo: Hermilo Cruz, Germán Hernández, Mercedes Guadarrama, Nancy Zamora y Mario Zúñiga de la biblioteca, a las secretarias Olga Jardón y Carla Gasca, a las auxiliares de servicios escolares: Mercedes Castro, Aurora Bautista, Alma Moreno, Susana Carpio, Agnes Jiménez, Eréndira Alor y Yareni López. A Laura Rubio, mi querida amiga, por su amistad y hospitalidad durante los períodos de clases.

A mi esposo y colega Efraín Hernández, por las múltiples revisiones de redacción a mis documentos en diferentes fases del proyecto de tesis. A mis compañeros con los que compartí clases y actividades: Matilde, Raisa, Romeo, Hakna, Manuela y Juan Carlos. A Verenice Escamilla, por sus valiosos comentarios y asesoría para la preparación del examen predoctoral y para la gestión de la beca mixta. A mis grandes amigas de otras generaciones: Alma Liz Vargas y Laura Ponce, por los momentos de aprendizaje compartidos.

Contenido

Resumen

El manejo de los recursos naturales requiere una visión integrada del funcionamiento del paisaje, muchos procesos ecológicos son determinados por la forma en que se usa y maneja la tierra. En este trabajo se estudiaron las relaciones y factores socioambientales que moldean la fragmentación y la conectividad de los bosques en la porción Sierra Madre del Sur del Corredor Biológico Mesoamericano (CBSMS). Con datos de campo, imágenes satelitales e información ecológica de tres especies de crácidos, se analizó el grado de fragmentación, conectividad funcional, usos del suelo y condición ecológica de los bosques del CBSMS. También se realizó un análisis a nivel de terreno con información de 106 entrevistas, sobre los factores causales del cambio de uso del suelo en las zonas cafetaleras, que abarcan una amplia extensión de la región estudiada. En general, los hábitats de las tres especies estuvieron adecuadamente conectados, excepto en tres zonas de la periferia del área de estudio, las cuales presentaron alta fragmentación y bajos valores de conectividad. Este último atributo, la conectividad del paisaje, depende en gran medida de fragmentos que presentaron una condición ecológica intermedia y baja (debido a la presencia de bosques secundarios y sistemas agroforestales de café). La superficie forestal y agroforestal modificada en el período fue de 2631 ha. El 93% de esos cambios correspondieron a la pérdida y degradación del hábitat. Los factores causales predominantes de los cambios en sistemas agroforestales de café fueron: la incidencia de plagas y enfermedades, la baja rentabilidad y la frecuencia de deslaves en las parcelas. La volatilidad del precio del café, los efectos del cambio climático, y la reducción de apoyos gubernamentales amenazan la persistencia de los cultivos de café bajo sombra y la biodiversidad en esta región, por lo que las medidas de adaptación que se planifiquen en los próximos años serán decisivas para continuar apoyando los objetivos de este corredor biológico.

Palabras clave: Conectividad del paisaje, Corredor biológico, Fragmentación de hábitat, Cambios en el paisaje, Causas de cambio, Paisaje funcional

Capítulo 1. Introducción general

1. Introducción

Pérdida, degradación y fragmentación del hábitat

La creciente pérdida, degradación y fragmentación de hábitat, junto con la intensificación del uso del suelo, se reconocen ampliamente como las principales amenazas para la conservación de la biodiversidad y de los servicios ecosistémicos asociados (Saunders et al. 1991; Vitousek et al. 1997). Los impactos en la biodiversidad dependerán de factores, como la calidad, cantidad y configuración de los fragmentos remanentes, las características de las coberturas o usos de suelo predominantes (matriz) y de la cercanía, forma y tamaño de los fragmentos de bosque (Walter et al. 2017), además de otros factores socioeconómicos.

La fragmentación del paisaje es el proceso por el cual un fragmento contiguo de hábitat es transformado en varios pequeños, complejos o simples y sin conexión entre ellos (Fahrig 1997; Wang et al. 2014). Este proceso tiene dos efectos principales, que son: la alteración del microclima dentro y alrededor del remanente y el aislamiento de cada área de otros fragmentos remanentes en el paisaje circundante (Saunders et al. 1991). Estos cambios afectan la dinámica de los procesos ecológicos y sus interacciones, que en consecuencia, alteran la forma en que los animales utilizan los hábitats remanentes y puede poner en riesgo la capacidad de algunas especies para moverse entre los fragmentos (Tylianakis et al. 2008; Anderson et al. 2015). La fragmentación del hábitat puede conducir al aislamiento de las poblaciones, y poner en riesgo la persistencia en el largo plazo de especies especializadas en hábitats particulares (Khimoun et al. 2016).

Las implicaciones de la fragmentación de hábitats se han abordado desde diferentes perspectivas, particularmente a través de la teoría de la biogeografía de islas, la ecología de metapoblaciones y los efectos de borde (McArthur and Wilson 1967; Hanski and Ovaskainen 2003; Franklin and Lindenmayer 2009). El número de especies en paisajes fragmentados depende del tamaño del fragmento y de su grado de aislamiento, por lo que los fragmentos más grandes y más cercanos tendrían mayor número y diversidad de especies, debido a una mayor tasa de colonización y a una menor tasa de extinción (McArthur and Wilson 1967). Por otra parte, el ambiente de un organismo se describe como un conjunto de fragmentos de hábitat dentro de una matriz inhóspita, en el que una población de una especie puede estar ocurriendo, formada por varias subpoblaciones separadas en fragmentos discretos de hábitat adecuado, con la capacidad de migrar de un sitio a otro (Hanski 1999). El conjunto de todas estas subpoblaciones se denomina "metapoblación" (Opdam 1991; Hanski and Ovaskainen 2003).

Hábitat y distribución de especies

El hábitat de una especie es determinado por la suma de todos los recursos específicos que necesitan los organismos para sobrevivir, implica más que la vegetación y su estructura, su tamaño en gran medida depende de las áreas de reproducción y los corredores de migración y dispersión que los animales ocupan durante la temporada no reproductiva (Hall et al. 1997). Para las especies dependientes de bosques conservados, el área de hábitats adecuados disminuye conforme se incrementan las áreas de uso humano (Jordán 2000).

La distribución de las especies está determinada por la interacción entre el grado de asociación que tiene cada especie con la proporción y distribución de los diferentes hábitats en el paisaje (Cushman et al. 2010). Los modelos de presencia se usan para estimar el hábitat potencial basado sólo en datos de presencia de las especies, además de variables predictoras biológicamente significativas para la especie. Los modelos obtenidos pueden ser usados para identificar áreas adicionales con condiciones ambientales similares que podrían ser hábitat para las especies objeto de estudio. (Bender and Fahrig 2005).

Permeabilidad de la matriz y de los bordes de hábitat

Al moverse a través de diferentes tipos de hábitat, los animales pueden experimentar alta variación en el riesgo de mortalidad, la permeabilidad de la matriz, por lo tanto, es muy variable (Hein et al. 2003; Ovaskainen 2004; Suter et al. 2007). La permeabilidad de los bordes de hábitat, se ha definido como la capacidad que tienen de funcionar como filtros que impiden o facilitan el flujo de materia, energía y organismos; lo que depende de la percepción y respuesta de las especies, por ejemplo, si son generalistas o especialistas de hábitat (Laurance and Williamson 2001; López-Barrera et al. 2005). La matriz, es decir, las áreas que rodean los fragmentos de hábitat, puede tener diferentes grados de permeabilidad para las especies especialistas del hábitat, dependiendo de las características estructurales y de composición de la vegetación. Los animales pueden percibir el nivel de calidad de la matriz y modifican su comportamiento de movilidad, su permanencia y su distribución espacial para minimizar los riesgos y maximizar los beneficios en cada ambiente (Cornelius et al. 2017). En paisajes forestales, las matrices abiertas representan un alto riesgo de depredación para las especies del bosque, por lo que actúan como barreras completas o semipermeables para el movimiento de estas especies entre los fragmentos. Si la matriz tiene una cobertura forestal más alta y densa y el riesgo de depredación es bajo, las especies pueden permanecer más tiempo, por lo que la matriz funciona como un complemento del hábitat y contribuye a la persistencia de las poblaciones (Driscoll et al. 2013; Biz et al. 2017).

Conectividad del paisaje

La conectividad del paisaje ha sido señalada como "el grado en que se facilita o se impide el movimiento de organismos entre los fragmentos del paisaje" (Taylor et al. 1993; Tischendorf and Fahrig 2000); Se puede estudiar de dos formas: por el tamaño, forma y configuración de los fragmentos (conectividad estructural), o bien, con base en la respuesta de los organismos a elementos individuales del paisaje y su capacidad para moverse entre ellos (conectividad funcional). La última depende de la conducta y percepción de cada especie sobre la estructura del paisaje, por lo tanto, varía entre especies (Baguette and Van Dyck 2007; Ziółkowska et al. 2014). El mantenimiento de conectividad de los paisajes permite a las especies minimizar los efectos de la pérdida y fragmentación del hábitat, así también mejorar el flujo de genes, la dispersión de la fauna, la viabilidad de la población y de los servicios ecosistémicos (Galpern et al. 2011; Crouzeilles et al. 2013). El mantenimiento o mejora de la conectividad es un proceso clave para el funcionamiento y la persistencia de poblaciones estructuradas en paisajes fragmentados (Bergerot et al. 2013).

Corredor Biológico Mesoamericano Sierra Madre del Sur

Los corredores biológicos surgen como una estrategia para mitigar los efectos de la fragmentación, éstos tienen el objetivo de facilitar el movimiento de organismos para impulsar el intercambio genético entre los individuos de una metapoblación, la conservación de las vías migratorias y hábitats de descanso, proporcionar conectividad en todos los biomas y en última instancia, reducir el riesgo de extinción de las especies (Hilty et al. 2006; LaPoint et al. 2013). El Corredor Biológico Mesoamericano (CBM) es una iniciativa de cooperación entre los siete países centroamericanos y México, firmada en 1996. Esta iniciativa se enfoca en concertar de forma coordinada, un conjunto de actividades dirigidas a la conservación de la diversidad biológica y la promoción del desarrollo humano sostenible en sus territorios. Particularmente en Chiapas, el CBM ha tenido la misión de mantener y propiciar la conectividad de las especies de flora y fauna en zonas con alto valor biológico, mediante el apoyo a las prácticas de conservación y el fomento de actividades productivas sustentables (CONABIO 2013). El CBM se ubica en un área de alta diversidad y endemismos de especies de flora y fauna, razón por la cual es reconocido como uno de los "hotspots" (puntos calientes) de biodiversidad más importantes del mundo (Myers et al. 2000; Brooks et al. 2002).

Especies indicadoras

Algunas especies pueden funcionar como indicadores ecológicos de ciertas comunidades o hábitats, de condiciones o de cambios ambientales (De Cáceres et al. 2010). Estas especies suelen tener requerimientos específicos de hábitat y respuestas determinadas a los cambios ambientales, los cuales pueden ser extrapolados a especies que comparten requerimientos de hábitat y características de dispersión similares (Closset-Kopp et al. 2016). Las especies indicadoras se determinan mediante un análisis de la relación entre dos elementos, la especie y grupos de sitios, a través de valores de presencia o abundancia de las especies observadas en un conjunto de sitios muestreados, lo que permite obtener información sobre cualquiera de ellos o sobre ambos (De Cáceres et al. 2010).

Los crácidos son una familia de aves de América Tropical, que son útiles como especies indicadoras de la conectividad de los bosques, ya que habitan preferentemente los bosques tropicales, sus hábitos de movimiento son predominantemente arbóreos y responden negativamente a la fragmentación de hábitat. La familia *Cracidae* está integrada por 50 especies que son endémicas (de distribución exclusiva) en las áreas boscosas tropicales y subtropicales del continente americano. Estas especies de aves son importantes depredadores y dispersores de semillas, además de que representan una fuente importante de proteína para las comunidades rurales (White 2001; Rivas Romero et al. 2003). No obstante, existen diferencias marcadas entre las especies en la respuesta a las perturbaciones antrópicas en su hábitat. Los hocofaisanes (género *Crax*) y las pavas (*Penelopina, Penelope, Oreophasis*) dependen de los bosques primarios y responden negativamente al aprovechamiento forestal intensivo, así como a la conversión de su hábitat a campos de cultivo, en tanto que las chachalacas (género *Ortalis*) se adaptan rápidamente a los disturbios y tienen mayor resistencia a la presión por cacería. Entre las pavas y hocofaisanes también hay diferencias en cuanto a su uso o selección de hábitat, las pavas son principalmente arborícolas, en tanto que los hocofaisanes son mayormente terrestres (López et al. 2014).

Para este estudio, las especies que se incluyeron bajo el criterio "dependientes de bosques" fueron: el pavón (*Oreophasis derbianus*), el pajuil (*Penelopina nigra*) y la pava (*Penelope purpurascens*). Estas especies son relevantes como indicadoras de conectividad forestal, ya que tienen hábitos arborícolas, son habitantes de bosques maduros y secundarios, responden negativamente a la fragmentación de hábitat y a las prácticas de cacería, debido a la dependencia de su movimiento a través de los árboles y a su baja capacidad de reproducción (Thornton et al. 2012; Kattan et al. 2016). Con base en la lista de especies nativas en riesgo de la Norma Oficial Mexicana, el pajuil y el pavón son especies que se encuentran en “Peligro de Extinción”, en tanto que la pava cojolita está “Amenazada” (SEMARNAT 2010).

Factores causales y dinámica de cambio de uso de suelo

El cambio de uso del suelo tiene un impacto en la estructura y funciones del paisaje, afecta la calidad de los hábitats y, por tanto, la biodiversidad del paisaje (Fohrer et al. 2002; Parcerisas et al. 2012). La comprensión de las relaciones entre los grupos humanos que habitan en las regiones de alta biodiversidad y su medio ambiente son necesarias para diseñar estrategias de conservación destinadas a reducir los impactos y preservar algunas características de los paisajes (Álvarez Martínez et al. 2011).

Los factores causales del cambio en el uso y cobertura del suelo son el resultado de una interconexión compleja de procesos socioeconómicos y ambientales, los cuales afectan directa o indirectamente la forma en la que los propietarios deciden sobre el uso de la tierra. Los factores causales del cambio de uso de suelo pueden dividirse en dos categorías: los próximos (directos o locales) y los subyacentes (indirectos o profundos). Los primeros son las acciones inmediatas a nivel local, que tienen impacto directo en la cobertura forestal y los procesos de los ecosistemas, mientras que los factores causales subyacentes explican un contexto más amplio, externo a las comunidades locales que manejan la tierra, por lo que generalmente son incontrolables a nivel local, pero explican las causas que respaldan estas acciones locales, a las cuales afectan (Geist and Lambin 2002; Lambin and Helmut 2007).

Los cambios en el uso del suelo pueden implicar la pérdida de cobertura forestal, como la expansión agrícola o de infraestructura; o en sentido contrario, preservar y fomentar la cobertura forestal, por ejemplo, las prácticas de manejo forestal o agroforestal sostenible, la protección de bosques o el turismo ecológico. En el estudio del cambio de uso del suelo se pueden distinguir los actores y los factores causales. Los actores (individuos e instituciones) son los agentes de toma de decisiones y de mediación, actúan en consecuencia e influyen en otros actores y en el ambiente con sus acciones; en tanto que los factores causales son la expresión materializada de estas decisiones o acciones (Schneeberger et al. 2007; Hersperger et al. 2010).

Para el estudio de los factores causales, algunos autores sugieren considerar dos aspectos relevantes: a) la escala espacial en la que se abordará y la escala temporal adecuada, b) los factores causales deben agregarse en un nivel adecuado de detalle, procurando un equilibrio entre precisión y generalización (Bürgi et al. 2005; Schneeberger et al. 2007). Los estudios de caso suelen proporcionar información sobre los actores y sus características (van Vliet et al. 2015). La selección de las variables que se deben incluir para explicar los cambios en el paisaje es específica del contexto y depende de la pregunta planteada, de la escala y de los límites del sistema analizado (Parcerisas et al. 2012).

2. Justificación

Este estudio se abordó desde el marco teórico de la ecología del paisaje, que es una ciencia interdisciplinaria que concibe al paisaje como resultado de la interacción de las sociedades humanas con el medio en que habitan, de las dinámicas del pasado, que son determinantes para entender su estado y función actual, y el estudio de su evolución futura (Urquijo Torres and Barrera Bassols 2009). Evaluar las áreas de conectividad funcional en un corredor biológico es esencial para verificar si efectivamente están cumpliendo su papel en la conservación de la biodiversidad en el largo plazo, pero los posibles resultados dependen de las características propias de la especie o grupo de especies bajo estudio y de las relaciones que éstas tienen con elementos de los sistemas ecológicos y sociales de su entorno, las cuales son complejas. La información resultante de este tipo de estudios es crítica para la formulación adecuada de estrategias de conservación, manejo y de restauración en zonas muy degradadas. Estos estudios permiten contribuir a mejorar las condiciones estructurales del paisaje para una especie o grupos de especies de interés (Poiani et al. 2000).

En la Sierra Madre de Chiapas, algunos autores (Castillo-Santiago et al. 2010; Cortina-Villar et al. 2012) han cuantificado la pérdida de la cobertura vegetal a diferentes escalas. Además, De la Torre et al. (2018) han elaborado modelos de hábitat adecuado para complementarlo con corredores críticos de conectividad para tapir (*Tapirus bairdii*) en la Sierra Madre de Chiapas. Estos estudios revelan importantes esfuerzos de conservación y manejo del paisaje, a partir del establecimiento de las ANP en esta zona, que han frenado las tasas de deforestación previas. Sin embargo, los impactos registrados hasta ahora en el paisaje del CBSMS tienen repercusiones en las especies más sensibles, cuyas poblaciones quedan expuestas al deterioro de la calidad de su hábitat y a interferencias con los elementos de los hábitats periféricos (Saunders et al. 1991; Fahrig 2003; Santos and Tellería 2006). Se han realizado diversos estudios sobre distribución y abundancia de especies (Tejeda Cruz 2009; Bonilla-Sánchez et al. 2010; Pineda Diez de Bonilla 2012), pero hasta ahora no se han realizado estudios sobre los efectos de los cambios en la configuración del hábitat sobre la distribución de especies dependientes de bosques, considerando elementos como la conectividad entre fragmentos y la calidad de la matriz. Actualmente, una de las principales amenazas para la biodiversidad en esta área se relaciona con la pérdida de hábitat por la intensificación de uso de suelo de cafetales bajo sombra y su conversión a sistemas con nula o reducida cobertura arbórea, que representan matrices inhóspitas para las especies adaptadas a bosques (Williams-Guillén and Perfecto 2010; Libert Amico 2016). A través de este estudio se plantea analizar los factores causales relacionados con esta problemática y la manera en que afectan la conectividad del hábitat de los crácidos dependientes de bosques.

3. Objetivos

Objetivo General

Evaluar la conectividad del paisaje y su dinámica de cambio a través del hábitat de crácidos dependientes de bosques en el Corredor Biológico Mesoamericano Sierra Madre del Sur.

Objetivos específicos

1) Identificar los factores ambientales asociados con la distribución de crácidos dependientes de bosques en el CBSMS
2) Estimar la conectividad estructural y funcional del paisaje del CBSMS para las especies indicadoras evaluadas.
3) Analizar el impacto de los factores causales del cambio de uso del suelo en la estructura y conectividad del paisaje.

4. Preguntas de investigación

Pregunta principal: ¿Cómo los cambios en el paisaje han afectado la conectividad para los crácidos dependientes de bosques y cómo influyen los factores que los causan en la integridad ecológica y específicamente en la pérdida, fragmentación y/o la conectividad de hábitat para estas especies?

Pregunta secundaria 1. ¿Qué variables ambientales están asociadas con el hábitat y distribución de los crácidos dependientes de bosques?

Pregunta secundaria 2. ¿Cuál es el grado de fragmentación del paisaje y cómo afecta a la conectividad de las especies indicadoras evaluadas?

Pregunta secundaria 3. ¿Qué factores causales directos o indirectos producen el cambio de uso de suelo y en qué áreas del CBSMS?

5. Hipótesis de investigación

Hipótesis 1: Las variables ambientales de altitud, la precipitación y la temperatura influyen el hábitat y distribución de las tres especies de crácidos estudiados.

Hipótesis 2. Se espera una mayor área de distribución y mayor conectividad para la pava cojolita y la menor área de distribución y menor conectividad estructural y funcional para el pavón.

Hipótesis 3. La degradación de los sistemas agroforestales amenaza la conectividad de crácidos dependientes de bosques en el CBSMS.

6. Estructura de la tesis

La tesis es no monográfica y está estructurada en cuatro capítulos, incluido el capítulo de introducción general. En el segundo capítulo se abordaron los objetivos 1 y 2, en donde se identificaron los factores ambientales relacionados con la distribución de tres especies de crácidos: la pava (*Penelope purpurascens*), el pajuil (*Penelopina nigra*) y el pavón (*Oreophasis derbianus*) y se estimó la conectividad estructural y funcional para estas especies. Para ello, se elaboraron modelos de distribución potencial (Maxent) y mapas de hábitat de cada uno de ellos. Asimismo, se evaluó la calidad de hábitat mediante un índice de condición ecológica aplicado a datos de campo de 75 parcelas de muestreo, se evaluó el nivel de fragmentación y la conectividad funcional mediante un análisis espacialmente explícito. En el capítulo tres se evaluó el cambio de uso de suelo en el período 2005-2015 y se analizaron los factores que influyen en la estructura y conectividad del paisaje, para lo cual se elaboró un mapa de cambio de uso del suelo con base en imágenes de satélite de alta resolución y se aplicaron 106 encuestas en cuatro localidades, para evaluar los factores causales de los cambios en los sistemas agroforestales de café. Finalmente, en el capítulo 4 se presenta la discusión general y las principales conclusiones de cada capítulo y del documento integrado.

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Capítulo 2. Assessment of Habitat Quality and Landscape Connectivity for Forest-Dependent Cracids in the Sierra Madre del Sur Mesoamerican Biological Corridor, México

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Primer artículo de investigación publicado el 30 de septiembre de 2019

https://doi.org/10.1177/1940082919878827

Información del artículo:

Revista Tropical Conservation Sciences, volumen 12, páginas 1–16.

Assessment of Habitat Quality and Landscape Connectivity for Forest-Dependent Cracids in the Sierra Madre del Sur Mesoamerican Biological Corridor, México

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First Published September 30, 2019 Research Article
https://doi.org/10.1177/1940082919878827
A correction has been published:
Corrigendum to Assessment of Habitat Quality and Landscape Connectivity for Forest-Dependent Cracids in the Sierra Madre del Sur Mesoamerican Biological Corridor, México

Abstract

Assessing landscape connectivity allows us to identify critical areas that impede or facilitate the movement of organisms and their genes and to plan their conservation and management. In this article, we assessed landscape connectivity and ecological condition of the habitat patches of a highly biodiverse region in Chiapas, Mexico. We employed data of three cracid species with different characteristics in habitat use and mobility. The habitat map of each species was derived from a spatial intersection of the models of potential distribution and a high-resolution map of current land cover and land use. The ecological condition of vegetation types was evaluated using 75 field plots. Structure of landscape was estimated by fragmentation metrics, while functional connectivity was assessed using spatially explicit graph analysis. The extent of suitable habitat for *Oreophasis derbianus*, *Penelopina nigra*, and *Penelope purpurascens* correspond to 25%, 46%, and 55% of the study area (5,185.6 km^2), respectively. Although the pine-oak forests were the most fragmented vegetation type, habitats of the three species were well connected, and only 4% to 9% of the fragments located on the periphery of the corridor had low connectivity. Landscape connectivity depends mainly on land uses with an intermediate and lower ecological condition (secondary forests and coffee agroforestry systems). Therefore, we suggest that in addition to promoting the improvement in connectivity in fragmented forests, conservation efforts should be aimed at preventing the conversion of mature forests into agricultural uses and maintaining agroforestry systems.

Keywords potential distribution, habitat quality, forest fragmentation, agroforestry systems, functional connectivity

Introduction

The persistence of species in a fragmented landscape has been the subject of study of island biogeography and metapopulation dynamics and can be interpreted as the result of the equilibrium of extinction and colonization processes (McArthur & Wilson, 1967). On this basis, species populations are more likely to occur in larger and well-connected habitat fragments than in small and isolated fragments (Dupré & Ehrlén, 2002; Hanski, 1998). However, recent research has shown evidence that this also depends on the patch context: the spatial heterogeneity, on permeability of the matrix (surface surrounding the habitat), and the behavior of each species in response to the landscape structure. If the matrix surrounding habitat fragments is not completely hostile, if it has usable resources for the species, island biogeography has limited application (Sekercioglu, Loarie, Oviedo Brenes, Ehrlich, & Daily, 2007; Tscharntke et al., 2012). The matrix can have variable levels of quality for species due to their structural and composition, resulting in different levels of permeability that provide wide-ranging risks and survival benefits for the animals that cross it. In this way, the matrix functions as a complete or a semipermeable barrier that can contribute to animal movement or as a habitat complement (Biz, Cornelius, & Metzger, 2017; Driscoll, Banks, Barton, Lindenmayer, & Smith, 2013).

Besides, species with different ecological needs and dispersal capacities may respond differently to habitat fragmentation, which may be determinant in ensuring the survival of the population (Liao, Bearup, & Blasius, 2017). Landscape connectivity can be explained as the physical arrangement of the vegetation structure in the landscape or by an organism's response to that structure (functional connectivity; Tischendorf & Fahrig, 2000; Xun, Yu, & Wang, 2017). Different approaches have been applied to assess connectivity, including structural metrics and the network approach or graph theory. Structural metrics quantify heterogeneity, levels of fragmentation, and habitat isolation at different scales (Botequilha Leitão & Ahern, 2002). In addition, by using spatially explicit graph analysis, it is possible to estimate functional connectivity and model the possibilities of species movement in a network of habitat fragments spatially isolated in heterogeneous landscapes (Saura & Rubio, 2010; Urban & Keitt, 2001). According to this approach, habitat fragments are represented by nodes in a graph and the distance between them is represented by links, which in turn represent the dispersal possibilities of a species between two patches (Bodin & Saura, 2010; Saura & Rubio, 2010). Consequently, the results of the functional connectivity analysis will depend on the ecological requirements and the mobility capacity of the species studied.

Members of the Cracidae bird family are useful as an indicator species for forest connectivity since they inhabit tropical forests, their movement habits are predominantly arboreal, and they respond negatively to habitat fragmentation. They also play a vital role in the regeneration of tropical forests because they are seed dispersers (Thornton, Branch, & Sunquist, 2012). In this bird family, guans (genera *Penelopina*, *Penelope*, and *Oreophasis*) are the species with arboreal habits that are most sensitive to the conversion of forested landscapes to agriculture and to continuous hunting pressure, due to their low reproductive capacity (López et al., 2014)..

Landscape connectivity analysis represents a valuable tool for planning landscape conservation and management actions and allows the identification and prioritization of critical areas for conservation; the identification of these areas is particularly necessary for biodiverse landscapes affected by high anthropic pressure, such as biological corridors that connect net of natural protected areas. Even though the goal of biological corridors is to facilitate the animal movement between fragments, thereby increasing gene flow, and eventually ensure the viability of populations (Evans, Levey, & Tewksbury, 2013; Simberloff, Farr, Cox, & Mehlman, 1992), few works have analyzed their degree of functional connectivity and ecological quality of their forest fragments.

In this article, we applied a landscape connectivity analysis to identify the critical areas for maintaining forest connectivity in a biological corridor of southeast Mexico. Species-distribution models, high-resolution land-cover maps, and the ecological requirements of the three cracids species (*Penelope purpurascens*, *Penelopina nigra*, and *Oreophasis derbianus*) were employed to elaborate habitat maps. Spatially graph analysis was carried out to calculate their functional connectivity; moreover, an ecological condition index of the habitats fragments was calculated using field data.

Methods

Study Area

The study area corresponds to the Sierra Madre del Sur Mesoamerican Biological Corridor (SMSMBC), a subsystem of the Mesoamerican Biological Corridor, which is an international initiative to coordinate and implement conservation and sustainable human development actions (Miller, Chang, & Johnson, 2001). SMSMBC is recognized as one of the world's most important biodiversity hotspots due to host high richness and endemism of the species (Brooks et al., 2002; Myers, Mittermeier, Mittermeier, da Fonseca, & Kent, 2000). It covers an area of 5,185.6 km^2 and it is located in southern Mexico, in the physiographic region of Sierra Madre de Chiapas (Müllerried, 1982); the relief of this area forms a mountainous landscape with hillside exposures facing the Pacific Ocean and the Central Chiapas Depression, with an altitudinal gradient ranging from sea level to 3,000 m asl (Instituto Nacional de Estadística y Geografía, 2017; Müllerried, 1982). Ten vegetation types were recorded, including one of the largest areas of cloud forest in Mexico (Challenger, 1998). Within the corridor, there are three Protected Natural Areas—El Triunfo (biosphere reserve), La Frailescana (natural resource protection area), and Cordón Pico El Loro Paxtal (state reserve)—and the remaining area is without specific protection. Productive human activities are not allowed in the El Triunfo core zones so the best conserved forests are found there. The buffer zone also includes areas with good conservation status but low-impact productive activities are practiced in this area (Figure 1).

Habitat Maps

Three sources of information were employed to elaborate the current habitat maps of the species: (a) potential species-distribution models derived from presence-only records, (b) a high-resolution map of the vegetation types and current land use (scale 1:40,000) elaborated for this study, and (c) reviews of the literature and field data to identify the ecological requirements of the three species. Once all the maps were ready, a spatial intersection operation was applied to obtain the current distribution areas. After that, a filter was applied to select only the vegetation types, and land uses reported in the ecological requirements review.

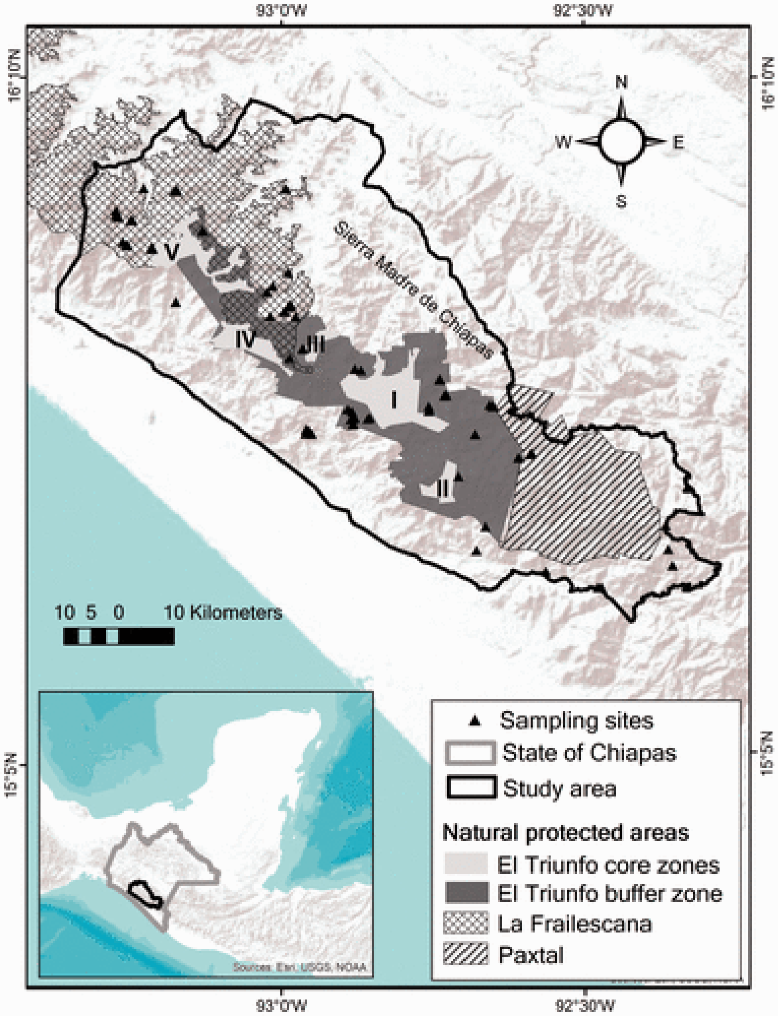


Figure 1. Protected natural areas and management zones of the El Triunfo Biosphere Reserve located in the Sierra Madre del Sur Mesoamerican Biological Corridor in the state of Chiapas, Mexico. El Triunfo core zone is subdivided into five polygons: I (El Triunfo), II (Ovando), III (Custepec), IV (El Venado), and V (La Angostura). The black triangles represent the location of the 75 sampling sites in this study.

Potential species-distribution model

The maximum entropy method was used to model species distributions with presence-only data and environmental layers. In this study, we obtained 137 visual and vocal records or other evidence such as feathers, nests, or eggs. Complementary records (4,145) of the three species in Chiapas were obtained from the following:

1. Biological information platforms (scientific collections) such as The Global Biodiversity Information Facility (GBIF.org, 2016) and CONABIO's National Biodiversity Information System (Enríquez, Rangel-Salazar, Vázquez Pérez, & Partida Lara, 2014);
2. Species monitoring records (visual, auditory and camera traps): from the Secretariat of Environment and Natural History (Secretaría de Medio Ambiente e Historia Natural, 2017), the community monitoring coordination of La Frailescana (Bioconciencia, 2015, 2016), the Network of Community Monitors of the Sierra Madre and Coast of Chiapas (Pronatura Sur, 2017), the Campesinos Ecológicos de la Sierra Madre de Chiapas organization (Campesinos Ecológicos de la Sierra Madre de Chiapas, 2017), and PRONATURA Sur A.C. (Pronatura Sur, 2014).

To minimize doubtful georeferencing data in the potential distribution map, we eliminated duplicate records (records within the same grid cell, res of 100 m^2) and only employed records from the period 2010 to 2017. The performance of the model was evaluated using the ROC statistic (Phillips, Anderson, & Schapire, 2006), a data set of 203 records *of P. purpurascens*, 740 of *P. nigra*, and 32 records of *O. derbianus* were used, of which 75% was used to calibrate the model of each species and 25% for validation. The variables used in the models were as follows: minimum and maximum temperature, precipitation (Fick & Hijmans, 2017), elevation (Instituto Nacional de Estadística y Geografía, 2017), and potential vegetation (Rzedowski, 1990). Potential vegetation has been described as “the natural vegetation that would exist in a given place if land use had never existed” (Levavasseur, Vrac, Roche, Paillard, & Guiot, 2013). The potential vegetation map was used to define the potential distribution area based on existing environmental conditions, regardless of changes in land cover and land use. The correlation between the predictor variables was calculated using Pearson’s correlation coefficient, using R’s packages (R Core Team, 2018). Data modeling was done on Maxent version 3.3.3k (Phillips, 2016).

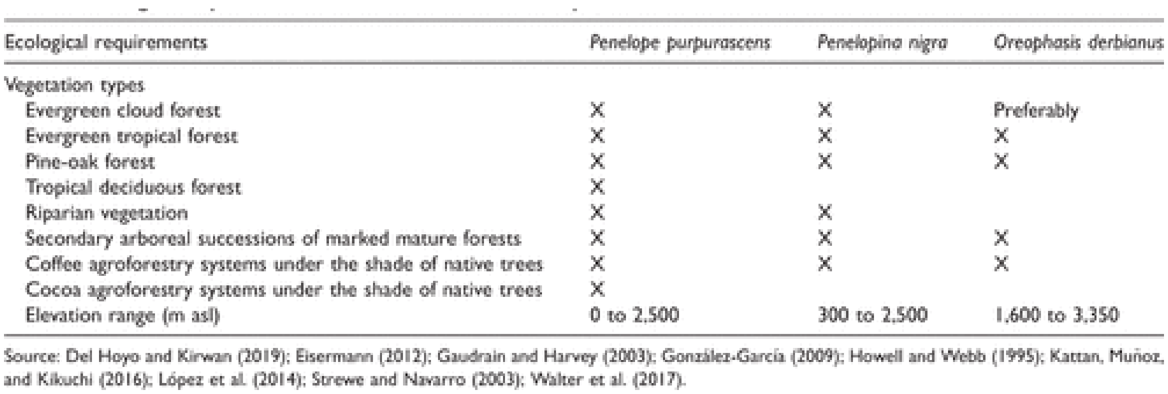
High-resolution land-cover/land-use maps

Using high-resolution satellite images SPOTs 6 and 7 (Secretaría de Marina, 2008), a map of vegetation types and land use in the study area was drawn up. All scenes included panchromatic (spatial resolution of 1.5 m) and multispectral (four bands with spatial resolution of 6 m) bands dated January 25, 2015, February 8, 2015, and February 14, 2014 (SPOT 6) and January 31, 2015, February 21, 2015, and February 26, 2015 (SPOT 7). The images were classified with an object-oriented approach, using the random forest algorithm (Breiman, 2001). Training samples were derived from information obtained in the field and from other sources such as the National Forest Inventory (Ricker, Villela, & Espinosa, 2019), coffee plantation census (COMCAFE, 2008), and the georeferenced records of woody species from the ECOSUR herbarium (ECO-CH-H). In addition to the spectral data of the satellite images, environmental data available in the following layers were used: digital elevation model, with spatial resolution of 30 m; exposure, slope, and solar radiation (derived from the digital elevation model); and precipitation and annual mean temperature generated from bioclimatic data from the State of Chiapas (Fick & Hijmans, 2017). At a later stage, errors in the automated classification were detected and corrected by visual inspection of the map. All satellite image processing was performed using the open software Python and QGIS (Clewley et al., 2014; QGIS Development Team, 2017).

Ecological requirements

The cracid species have different ecological niche widths but very similar requirements in their arboreal habits, the types of fruit in their diet, and the need to migrate altitudinally, following the fructification of the arboreal species, so they partially share habitat in some altitudinal ranges and types of vegetation (Table 1).

Table 1. Ecological Requirements of the Three Studied Cracids Species.



Ecological requirements	*Penelope purpurascens*	*Penelopina nigra*	*Oreophasis derbianus*
Vegetation types			
Evergreen cloud forest	X	X	Preferably
Evergreen tropical forest	X	X	X
Pine-oak forest	X	X	X
Tropical deciduous forest	X		
Riparian vegetation	X	X	
Secondary arboreal successions of marked mature forests	X	X	X
Coffee agroforestry systems under the shade of native trees	X	X	X
Cocoa agroforestry systems under the shade of native trees	X		
Elevation range (m asl)	0 to 2,500	300 to 2,500	1,600 to 3,350

Source: Del Hoyo and Kirwan (2019); Eisermann (2012); Gaudrain and Harvey (2003); González-García (2009); Howell and Webb (1995); Kattan, Muñoz, and Kikuchi (2016); López et al. (2014); Strewe and Navarro (2003); Walter et al. (2017).

Of the three species, *O. derbianus* is heavily dependent on the evergreen cloud forest and has a restricted geographic distribution and is endemic to Mesoamerica. Based on the International Union for Conservation of Nature categories, *O. derbianus* is classified as "Endangered" (EN), criterion C2a(i), while *P. nigra* is Vulnerable (VU), and *P. purpurascens* is classified as Least Concern (LC) (Birdlife International, 2016a, 2016b, 2016c).

Ecological Condition Index

From April to August 2017, 14 field trips were conducted to measure 75 sampling sites in nine municipalities (Figure 1). At each site, a circular plot of 1,000 m^2 was established, and a set of indicator variables were recorded including vegetation type, canopy height, basal area of dominant tree species, and tree species richness. Forest disturbance factors were also recorded such as grazing and trampling, firewood and wood extraction, damages for fire, trails, and logging evidence. Disturbance qualitative data were classified into three classes depending on their intensity or frequency: absent or low, medium, and high. Finally, the qualitative and quantitative values assigned to the variables were processed to construct a multicriteria ecological condition index (Ochoa-Gaona et al., 2010), which range from 0 (*worst condition*) to 1 (*best condition*).

Landscape Fragmentation

Metrics of landscape fragmentation were calculated using raster format of habitat maps and the software Fragstats v. 4.3 (McGarigal & Marks, 1995). The metrics used to measure composition and structure at class and landscape level were as follows: percentage of landscape or percentage of habitat (PLAND), patch density (PD), largest patch index (LPI), mean patch size (Area_MN), interspersion and juxtaposition index (IJI), and contagion (CONTAG) (McGarigal & Marks, 1995; Vila, Vargas, Llausàs, & Ribas, 2006). Only the four-cell neighborhood criterion was used to calculate the above metrics.

Functional Connectivity

Statistics derived from spatial graph analysis

The functional connectivity of habitat fragments was evaluated using statistics derived from the analysis of spatial graphs. Two derived indices were used in the Conefor 2.6 program (Saura & Torné, 2009): the integral connectivity index (IIC) and the probability of connectivity (PC). The first is based on a binary connection model and is recommended for analyzing the structure and general pattern of long-term functional connectivity, while the second uses a probabilistic connection model and is useful for studying the flow of organisms regardless of their origin (Qi, Fan, Nam, Wang, & Xie, 2017). To calculate both indices, Conefor requires information on the node attribute, distances between them, and dispersion distances. As an indicator of node attribute, the size of the fragment was used, as well as the Euclidean distance between the edges of each fragment and the dispersal distances defined for each species (see next subsection).

Once the indices were calculated, their values were grouped into two categories according to their contribution to landscape connectivity, using the natural break method, which better groups similar values between classes that have considerable differences in data values (Smith, Goodchild, & Longley, 2018). The dIIC index corresponds to the ranking of each patch according to the proportion by which the value of the IIC decreases when this patch is removed (Decout, Manel, Miaud, &

Luque, 2012). In the same way, dPC represents percentage of the variation in PC caused by the removal of each individual element from the landscape (Saura & Rubio, 2010). dIIC is divided into three fractions that indicate different aspects of connectivity (Crouzeilles, Lorini, Grelle, Lucia, & Eduardo, 2013):

1. dIICintra estimates available habitat based on the area provided by the patch;
2. dIICconnect values critical patches that facilitate the flow of species between two other patches within the shortest path, and this fraction is used as a criterion for selecting priority stepping stones or corridors; and
3. dIICflux evaluates fragments based on area-weighted dispersal flow and is used as a substitute for how well one fragment connects to another when it is the final or starting point of flow.

Dispersal distance

Based on the literature reviewed, no data were found on the specific range of action of the three species, so dispersal distances data from species of the same family or taxonomic genus with similar habits were used as a reference and experts were also consulted. For *P. purpurascens*, a range of 10 to 15 km for maximum dispersion distance was estimated; this range was based on the reported dispersion distances of another species of the same genus, the white-winged guan (*Penelope albipennis*), with similar body structure and habits, which moves a maximum of 13 km during an annual period to where food is more readily available (Pratolongo, 2004). For *P. nigra*, a range of 3 to 8 km was defined because it moves at a slower speed than *P. purpurascens* (Eisermann, 2012). For *O. derbianus*, a range of 0.5 to 1.5 km was estimated because it is a sedentary species and is no ability to fly, as it is a glider (González-García, 2011, 2012).

Results

Habitat Map

Potential distribution models

Potential distribution values were high for the three species, for *O. derbianus* was 90.6%, for *P. nigra* 90%, and for *P. purpurascens* was 83.4%. These values were acceptable because they were higher than 0.5 of a random model (Figure 2). Different environmental variables were related to the distribution of the three species. Precipitation was negatively related to the occurrence of *P. purpurascens* and *P. nigra,* elevation was also a positively related to *P. nigra* and *O. derbianus*, and minimum temperature was positively associated with *O. derbianus.*

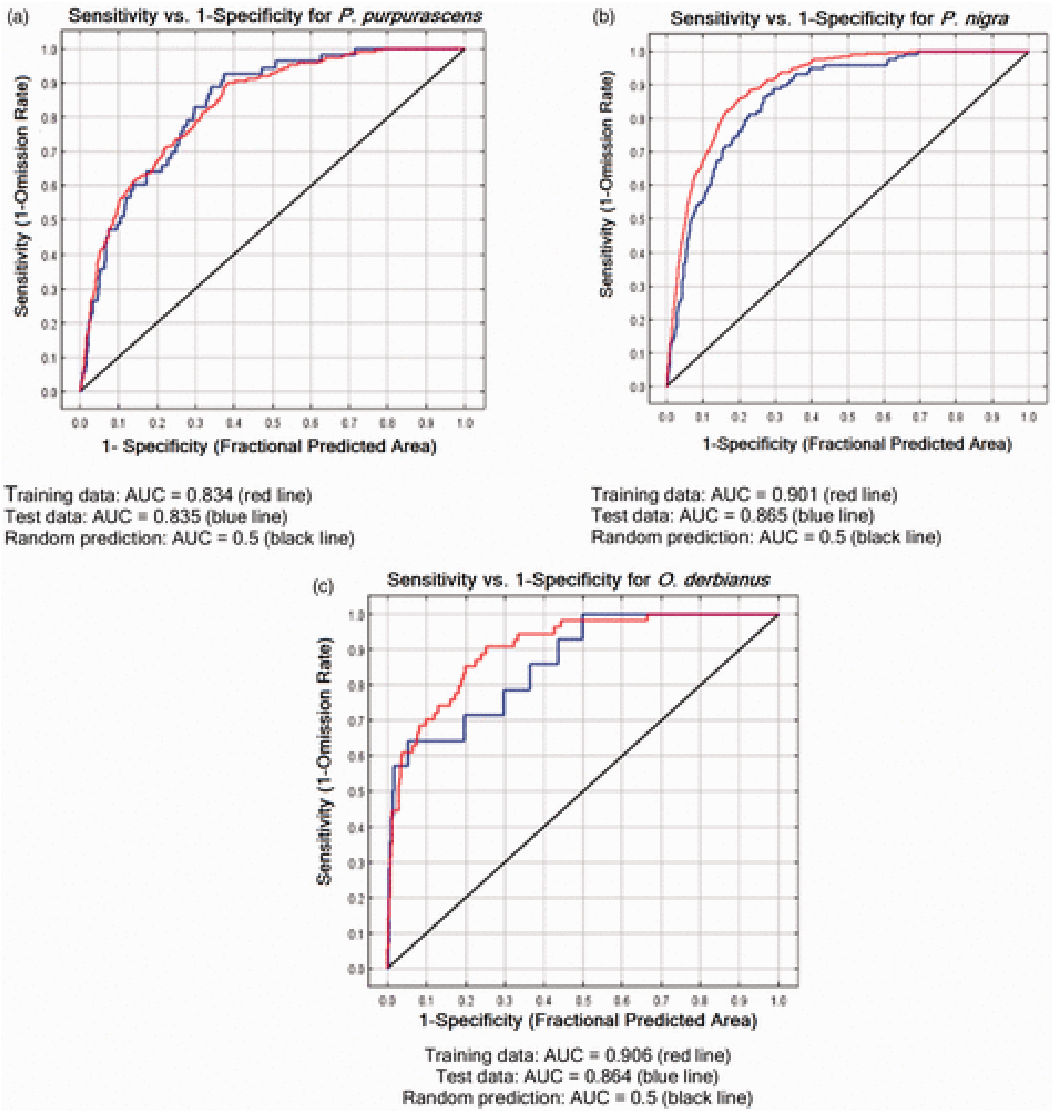


Figure 2. Área under the receiver operating characteristic curve (AUC) to evaluate model performance for (a) *P. purpurascens*, (b) *P. nigra*, and (c) *O. derbianus*). The value of AUC ranges from 0 to 1. An AUC value of 0.50 indicates that model did not perform better than random, whereas a value of 1.0 indicates perfect discrimination.

We found a high correlation ($r \geq |.5|$) between elevation and maximum and minimum temperatures, also between maximum and minimum temperatures. The other variables have a low correlation with each other ($|0.1| < r \leq |.3|$). Despite of this correlation, these variables were used as predictors of the model, based on Braunisch et al. (2013) that it is preferable to include correlated variables, but potentially relevant to the current distribution model, when the “true” predictor of a set of correlated variables cannot be identified.

High-resolution land-cover/land-use maps

We identified 11 forest land-cover types that account for 66.5% of the study area, of which 3 correspond to mature forests (89,150 ha), 6 secondary or disturbed forests (178,641 ha), and 2 agroforestry systems of coffee and cocoa (77,584 ha) (Figure 3). Six land uses were also identified, including different types of agriculture, human settlements, areas without vegetation, and water bodies, which account for 174,094 ha (33.5% of the study area).

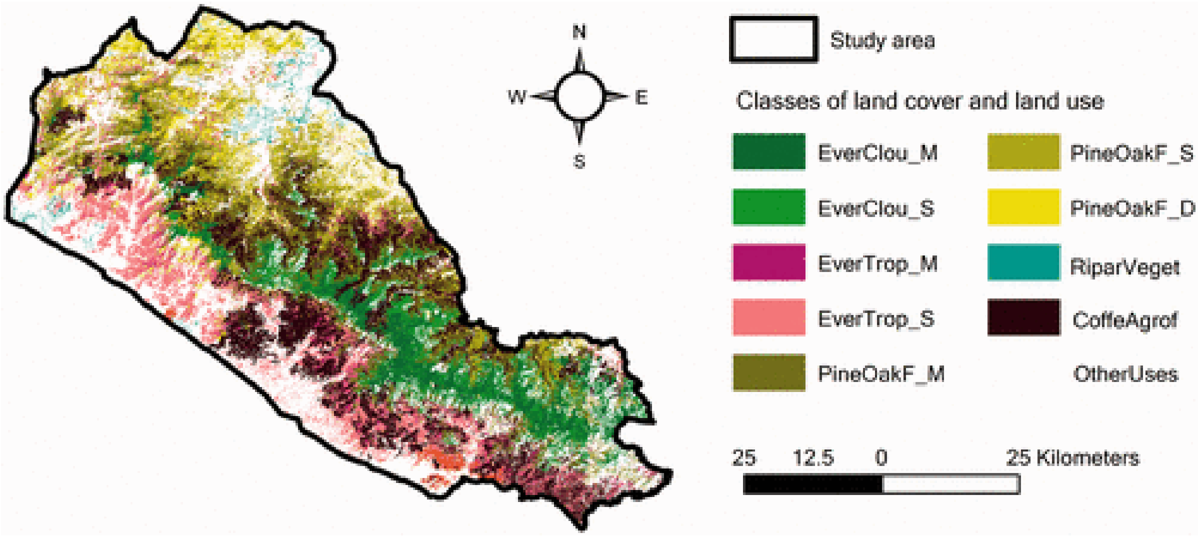


Figure 3. High-resolution map showing the most important vegetation types and land uses in the study area. Vegetation types covering less than 1% of the study area are not included. EverClou_M = mature evergreen cloud forest; EverClou_S = secondary evergreen cloud forest; EverTrop_M = mature evergreen tropical forest; EverTrop_S = secondary evergreen tropical forest; PineOakF_M = mature pine-oak forest; PineOakF_S = secondary pine-oak forest; PineOakF_D = disturbed pine-oak forest; RiparVeget = riparian vegetation; CoffeAgro = coffee agroforestry systems.

Habitat map

The current habitat for the indicator species was a mixture of mature and disturbed forests and agroforestry systems (Figure 4). The habitat of *P. purpurascens* occupied 282,893 ha (55% of the study area), *P. nigra* occupied 238,435 ha (46%), and *O. derbianus* only 127,233 ha (25%). The coffee agroforestry system, mature pine-oak forest, and secondary evergreen cloud forest conformed the habitat of the three species mainly. In the habitat of *O. derbianus,* the mature evergreen cloud forest was also one of the largest (Figure 5). In terms of protection levels, a high proportion of the habitats of *P. nigra* and *P. purpurascens* were out of the protected natural areas, with a low level of legal protection (Figure 6).

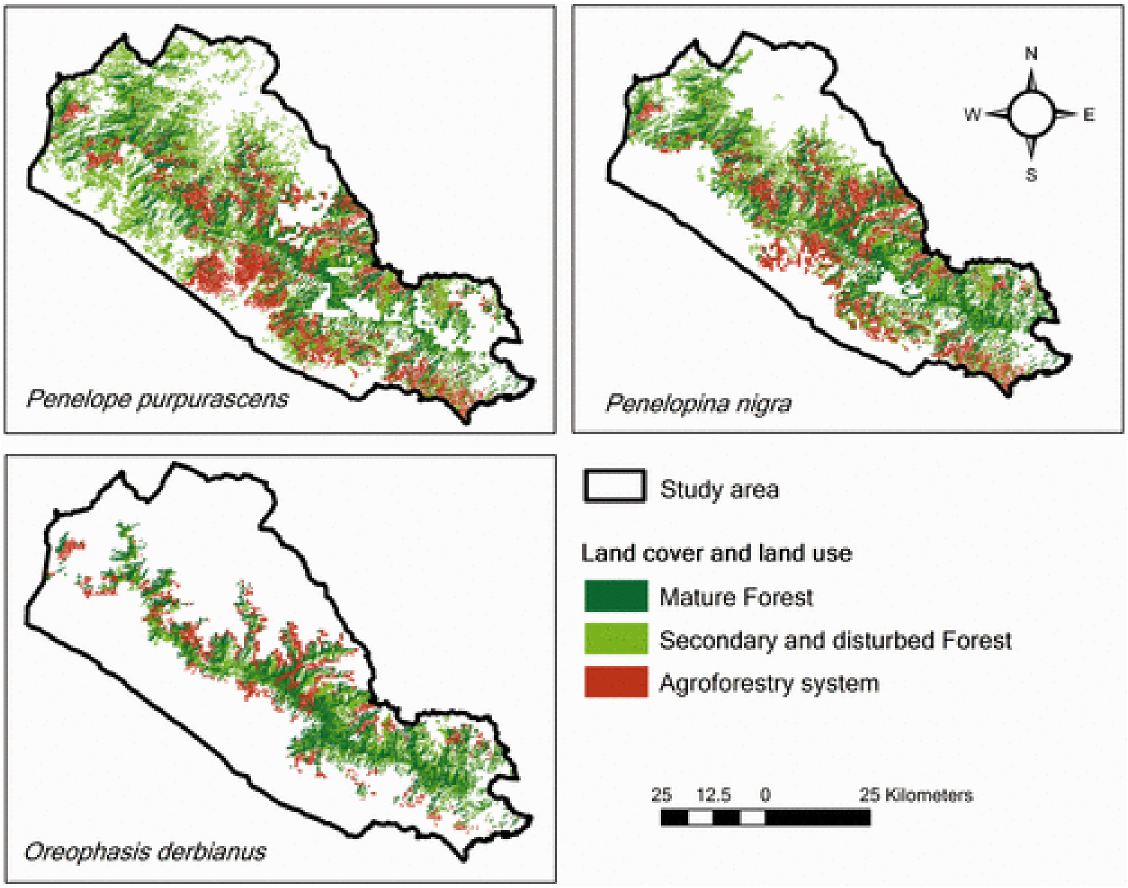


Figure 4. Distribution of forests and agroforestry systems in the current habitat of the three cracid species in the study area.

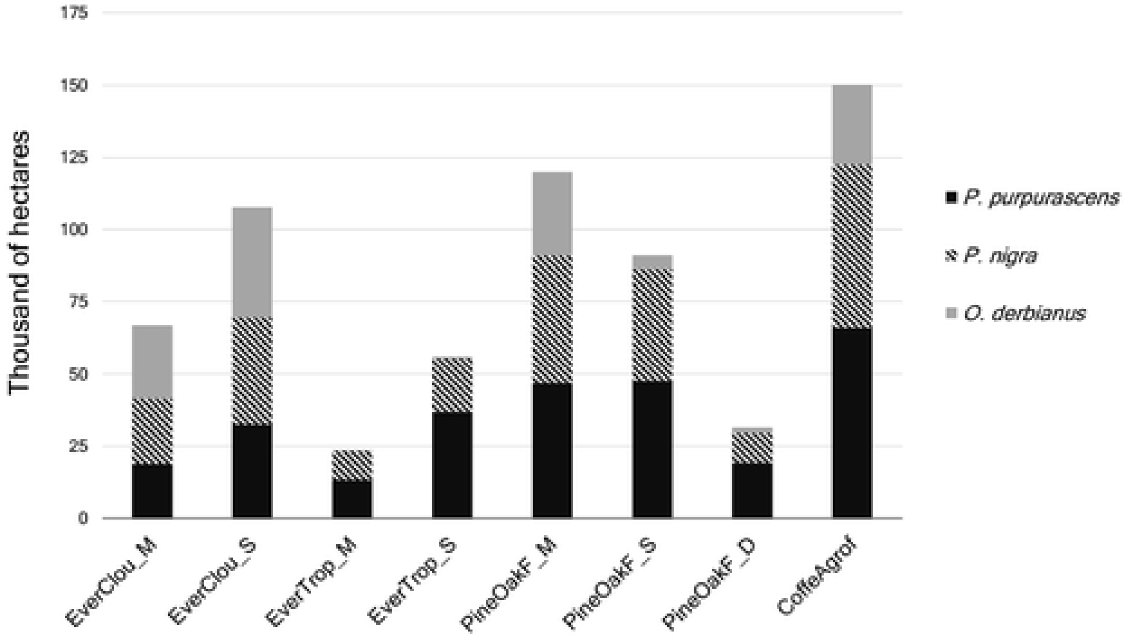


Figure 5. Main vegetation types and land uses in the habitats of the three cracid species. Land cover and land uses of less than 1% of the study area were not included. EverClou_M = mature evergreen cloud forest; EverClou_S = secondary evergreen cloud forest; EverTrop_M = mature evergreen tropical forest; EverTrop_S = secondary evergreen tropical forest; PineOakF_M = mature pine-oak forest; PineOakF_S = secondary pine-oak forest; PineOakF_D = disturbed pine-oak forest; CoffeAgrof = coffee agroforestry systems.

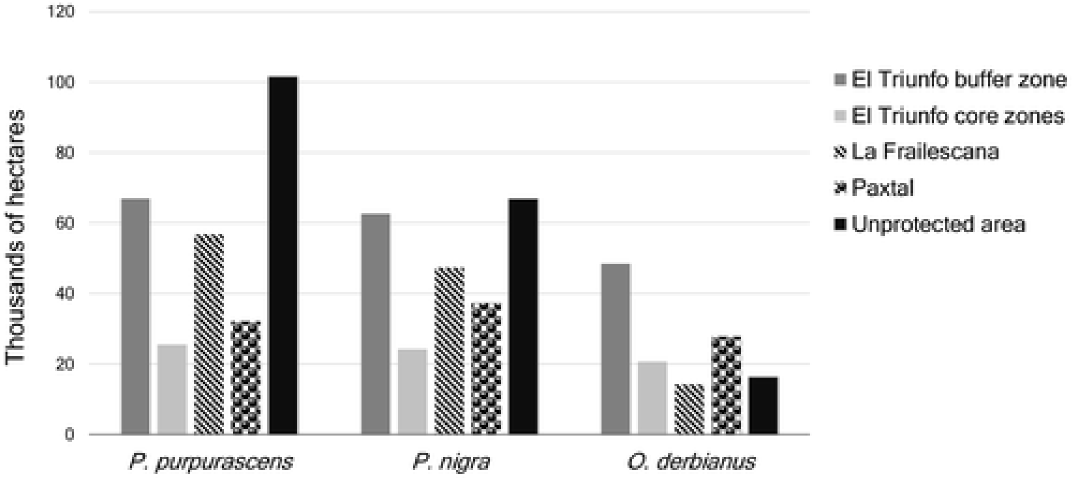


Figure 6. Surface area occupied by the three cracid species in each protection or management zones in the study area.

Ecological Condition Index

The ecological condition index showed that mature forests provided the highest richness of tree species, the most significant vertical and horizontal structure, lowest levels of disturbance, and, in general, best habitat quality, while agroforestry systems presented the most considerable disturbance and lowest quality of habitat (Figure 7).

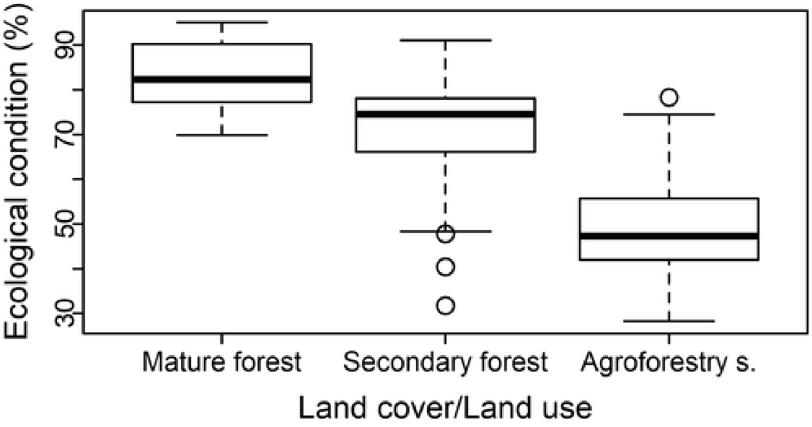
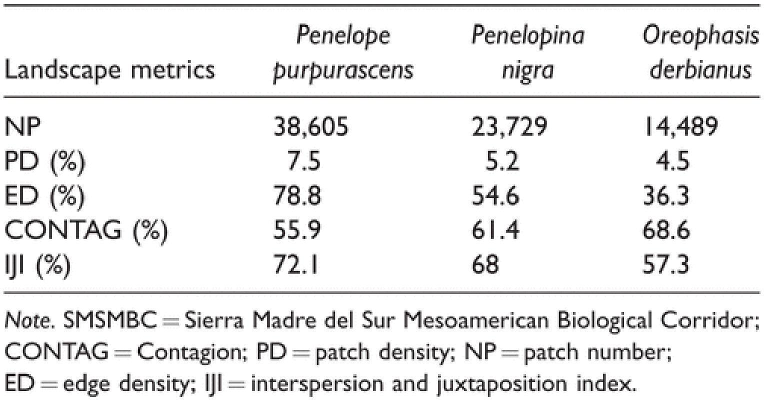


Figure 7. Index of the ecological condition of the sites grouped by land-cover/land-use type. 733 × 388mm (120 × 120 DPI).

Landscape Fragmentation

According to the fragmentation indexes, the structural connectivity of the habitat of the three species is still at an intermediate level; for example, in all cases, the contagion index was higher than 50% (Table 2). At the class level, mature evergreen cloud forest was the least fragmented, while mature, secondary, and disturbed pine-oak forests and secondary evergreen cloud forest were the highest fragmented classes, consistently both IJI and PD had higher values (Table 3).

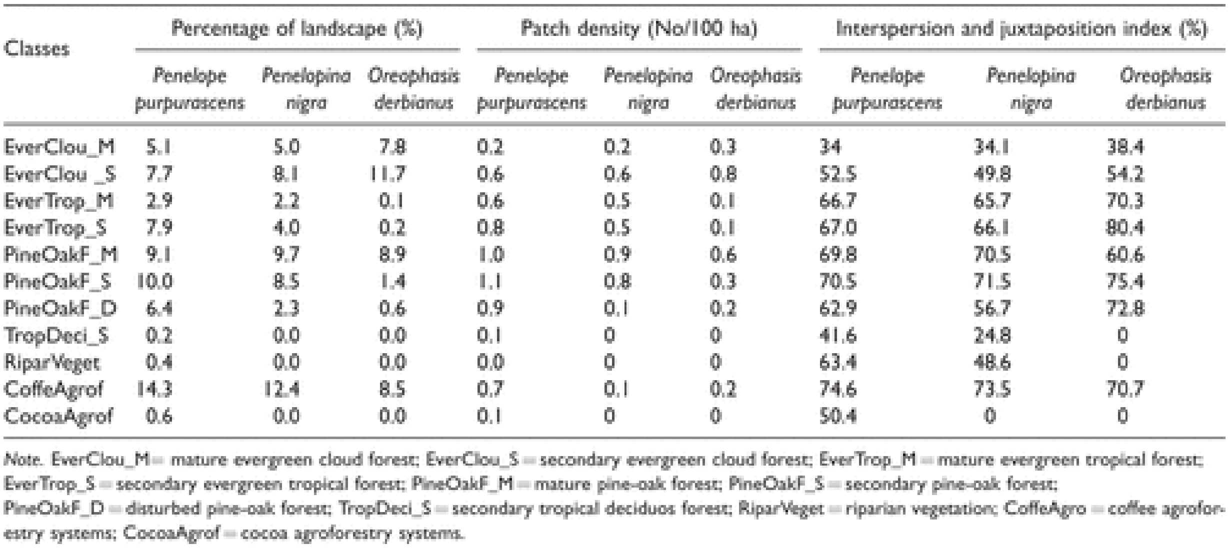
Table 2. Landscape-level metrics for three cracid species in the SMSMBC.



Landscape metrics	*Penelope purpurascens*	*Penelopina nigra*	*Oreophasis derbianus*
NP	38,605	23,729	14,489
PD (%)	7.5	5.2	4.5
ED (%)	78.8	54.6	36.3
CONTAG (%)	55.9	61.4	68.6
IJI (%)	72.1	68	57.3

Note. SMSMBC = Sierra Madre del Sur Mesoamerican Biological Corridor; CONTAG = Contagion; PD = patch density; NP = patch number; ED = edge density; IJI = interspersion and juxtaposition index.

Table 3. Structural Class-Level Metrics for the Habitat of the Three Cracid Species in the Study Area.



Classes	Percentage of landscape (%)			Patch density (No/100 ha)			Interspersion and juxtaposition index (%)		
	Penelope purpurascens	*Penelopina nigra*	*Oreophasis derbianus*	*Penelope purpurascens*	*Penelopina nigra*	*Oreophasis derbianus*	*Penelope purpurascens*	*Penelopina nigra*	*Oreophasis derbianus*
EverClou_M	5.1	5.0	7.8	0.2	0.2	0.3	34	34.1	38.4
EverClou _S	7.7	8.1	11.7	0.6	0.6	0.8	52.5	49.8	54.2
EverTrop_M	2.9	2.2	0.1	0.6	0.5	0.1	66.7	65.7	70.3
EverTrop_S	7.9	4.0	0.2	0.8	0.5	0.1	67.0	66.1	80.4
PineOakF_M	9.1	9.7	8.9	1.0	0.9	0.6	69.8	70.5	60.6
PineOakF_S	10.0	8.5	1.4	1.1	0.8	0.3	70.5	71.5	75.4
PineOakF_D	6.4	2.3	0.6	0.9	0.1	0.2	62.9	56.7	72.8
TropDeci_S	0.2	0.0	0.0	0.1	0	0	41.6	24.8	0
RiparVeget	0.4	0.0	0.0	0.0	0	0	63.4	48.6	0
CoffeAgrof	14.3	12.4	8.5	0.7	0.1	0.2	74.6	73.5	70.7
CocoaAgrof	0.6	0.0	0.0	0.1	0	0	50.4	0	0

Note. EverClou_M = mature evergreen cloud forest; EverClou_S = secondary evergreen cloud forest; EverTrop_M = mature evergreen tropical forest; EverTrop_S = secondary evergreen tropical forest; PineOakF_M = mature pine-oak forest; PineOakF_S = secondary pine-oak forest; PineOakF_D = disturbed pine-oak forest; TropDeci_S = secondary tropical deciduos forest; RiparVeget = riparian vegetation; CoffeAgro = coffee agroforestry systems; CocoaAgrof = cocoa agroforestry systems.

Coffee agroforestry systems had the largest fragment size (LPI) in the habitat of *P. purpurascens* (6,211 ha) and *P. nigra* (4,271 ha). The mature evergreen cloud forest for *O. derbianus* had the largest continuous forest fragment size (LPI = 6,072 ha). For the *P. purpurascens* habitat, the main land cover were coffee agroforestry system, mature and secondary pine-oak forest. Mature evergreen cloud forest and coffee agroforestry systems had the largest mean patch size (Area_MN = 24 ha and 22 ha, respectively), which represented habitat availability for this species (Table 3).

In the *P. nigra* habitat, mature and secondary pine-oak forests and secondary evergreen cloud forests were widespread but very fragmented, the coffee agroforestry systems presented a more compact area and the largest mean patch size (85 ha). In *O. derbianus* habitat, mature evergreen cloud forest, secondary pine-oak forest, and coffee agroforestry systems were predominant. The latter presented the largest mean patch size (35.5 ha), indicating opportunities for movement and resources but also a lower quality habitat for this species, which is dependent on specific cloud forest conditions. Mature evergreen cloud forest had the second largest mean patch size (24 ha) and the largest continuous forest patch size (6,072 ha), this implies availability of habitat that is suitable for this species (Figure 3).

Functional Connectivity

The habitat of the three species was connected through a single node or patch that almost occupied the entire area. In the *P. purpurascens* habitat, the central node (243,703 ha) corresponded 50% to 35% of the dIIC and 95% to 93% of the dPC for dispersal distances of 10 to 15 km. The main contribution of this node was as a flow facilitator and as a priority corridor (Figure 8). In addition, three zones with low values of dIIC were identified (Figure 8, Zones a to c). Zone a in Figure 8 is composed of 24 patches (ranging from 20 to 1,149 ha) that function as flow facilitators; the largest node in this zone also acts as a stepping stones connecting the north of the study area. Finally, Zones h and i in Figure 8 are composed of patches ranging from 21 to 171 ha and 20 to 1,059 ha, respectively, function as flow facilitators. These zones and patches with less connectivity as a whole comprise an area of 20,557 ha, composed by secondary tropical forest (37%), secondary pine-oak forest (16%), disturbed pine-oak forest (13%), coffee agroforestry systems (8%), and other forest types (26%).

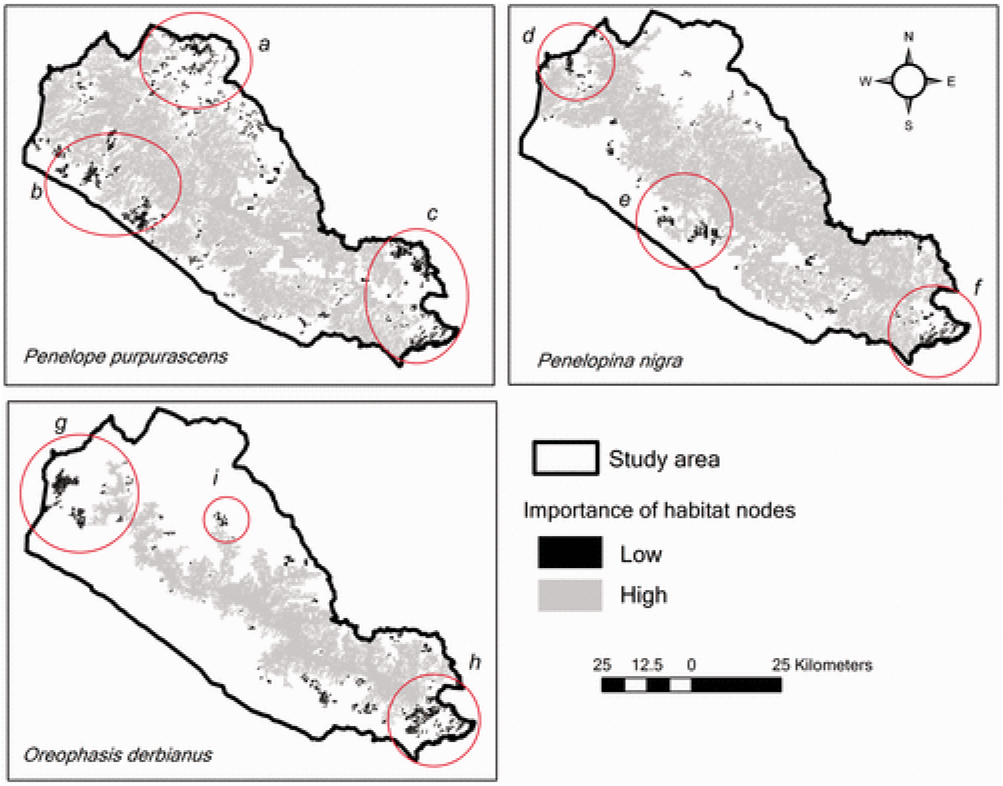


Figure 8. Connectivity level (dIIC) of habitat nodes for functional connectivity of *P. purpurascens*, *P. nigra*, and *O. derbianus*, based on three dispersion distances for each species. The red circle indicates the areas with lower functional connectivity for each species.

In the *P. nigra* habitat, one single node (229,923 ha) represented 99.9% of the dIIC and dPC in the network. This node contributes as a habitat provider (dIICintra) and as a priority corridor for this network (dIICconnect). Besides, three main zones with low connectivity values (dIIC) were identified (Figure 8, Zones d to f). Zone d in Figure 8 is composed of nodes (ranging from 41 to 572 ha) that function as flow facilitating elements. Zone e in Figure 8 functions as flow facilitator and it is made of four nodes (128 to 517 ha) with abandoned coffee-growing areas now under regeneration process due to the inhabitants being relocated to other areas after they were affected by Hurricane Stan. Zone f in Figure 8 had nodes (58 to 493 ha) that function as connectors to the south of the Sierra Madre de Chiapas. The nodes of lowest connectivity values occupy a total area of 8,510 ha and area composed mainly by secondary tropical forest (23%), coffee agroforestry systems (23%), secondary pine-oak forest (16%), disturbed pine-oak forests (10%), and, to a lesser extent, other types of forests (27%).

In the *O. derbianus* habitat, a single node of 115,702 ha represented connectivity value higher than 99% for dispersion distances of 0.5 to 1.5 km (Figure 8). The main roles of the nodes were as habitat providers (dIICintra) and as facilitators of the flow of the species between fragments (dIICflux). Besides, three zones with less connectivity were identified (Zones g to i in Figure 8); Zone g in Figure 8 functions as flow facilitators toward La Frailescana and the north of the Sierra Madre. Zone h in Figure 8 functions as a stepping stones (dIICconnect) to the south of the Sierra Madres; this zone was made up for one larger node and several smaller, isolated, and heterogeneous patches. Small patches without connection compose Zone i in Figure 8. The nodes with the least connectivity occupy a total of 11,529 ha and are composed mainly of coffee agroforestry systems (40%), mature pine-oak forest (27%), secondary evergreen cloud forest (14%), and, to a lesser extent, other types of forest (19% overall).

Discussion

Habitat Map and Ecological Condition

Analysis of the ecological condition data showed that mature forests presented the best habitat quality, because of their higher structural complexity, higher tree species richness, and lower levels of disturbance. Coffee agroforestry systems presented higher levels of anthropic disturbance. In the study area, although forest cover occupied between 41% and 86% of the potential distribution areas of the species studied, only 11% to 15% of this coverage corresponds to mature forest; disturbed forests, and agroforestry systems occupy the rest. The ecological condition will have a differentiated impact on the species studied.

O. derbianus is recognized as being dependent on evergreen cloud forest and sensitive to disturbance (González-García, 2012), but most of the information is restricted to the breeding season (González-García, 2017). Nevertheless, in this study, we include other types of forests and coffee agroforestry systems in their habitat due to recent evidence of their presence in these forests and land use in El Triunfo and La Frailescana (Ciro Mejía Martínez, personal comm., June 29, 2017; Francisco Murguía Community Monitoring Brigade, June 21, 2018). In La

Frailescana, *O. derbianus* has been recorded in lower elevations of its altitudinal range (900 m asl), which still requires further investigation (Bioconciencia, 2016).

Factors causing a decline in *O. derbianus* populations in addition to those mentioned earlier include the establishment of new coffee plantations and the effects of climate change (González-García, 2017; Peterson et al., 2001). Our results indicated that only 20% of its habitat remains as mature evergreen cloud forest, other types of forests with different degrees of fragmentation and disturbance and coffee agroforestry systems occupy the rest. However, these alternative forms of land use conserve relative permeability of movement between fragments of mature forest, which could be buffering the habitat as a whole, mitigating disturbance and improving connectivity (Cayuela, Golicher, & Rey-Benayas, 2006). Nevertheless, more studies are needed to define the impact that the lower quality of resources provided by these fragments could have on the health of populations of this species.

On the other hand, *P. nigra* can be considered as the species with the most optimal habitat conditions because it has the higher tolerance for disturbed forests and shaded coffee agroforestry systems of native trees, some of which produce the fruits on which this species feeds. In El Triunfo, it has been reported as common in moderate-sized populations, but it is recognized that in some sites these birds require adequate protection against hunting and deforestation (González-García, 2009; López et al., 2014). *P. purpurascens* prefers mature or slightly disturbed forests with a high proportion of vegetation cover in which it is rare (González-García & Martínez-Morales, 2010).

Habitat Connectivity

The study area presents an intermediate level of connectivity (Contag ≥55.9 and ≤68.6, IJI ≥ 57.3 ≤ 72.1%) for the three species. In particular, the mature, secondary, and disturbed pine-oak forests; the secondary evergreen cloud forest; and the mature and secondary evergreen tropical forests present the highest degree of fragmentation. On the other hand, functional connectivity analysis showed that habitats are connected for all three species through a main node, due to the large proportion of coffee agroforestry systems that connect forests in the middle and high elevations of the Sierra Madre de Chiapas. The patches with less functional connectivity are located toward the periphery of the habitat of each species and are immersed in an inhospitable matrix of agricultural land use and occupy a large area: For *P. purpurascens*, this was 20,557 ha (Figure 8, Zones a to c), for *P. nigra* of 8,510 ha (Figure 8, Zones d to f) and for *O. derbianus* of 11,529 ha (Figure 8, Zones g to h), occupied by mosaics of forests and agroforestry systems. It is important to conserve these fragments insofar as they connect with other larger areas and for the value of their coverage for the conservation of each species, so it would be advisable to apply restoration strategies that maintain the connectivity of the species to these habitat remnants.

An improvement in the structural connectivity of these species would require establishing stepping stones patches with tree species that produce the fruits on which this species feed and other types of links between the areas of remaining tropical forests in social (ejidos) and private properties in the lower parts of both slopes of the Sierra Madre. On the other hand, since these are landscapes managed by humans, fruit trees can be maintained or augmented in these systems to ensure the long-term survival of these frugivorous species (Sekercioglu et al., 2007). This can only be achieved by creating agreements with local landowners and stakeholders through land-use policies and conservation incentive schemes (Sibelet, Chamayou, Newing, & Montes, 2017).

Implications for Conservation

The landscape mosaic is predominantly connected by a matrix of coffee agroforestry systems in which the habitat fragments of the three species are immersed, so the maintenance of the connectivity of the species depends to a great extent on improvement in the structure of these systems. However, the incidence of pests and diseases in coffee plants have increased, and government policies have promoted rust-resistant varieties that do not require shadow of the canopy, as a strategy to counteract these problems. As a consequence, in recent decades, shaded coffee plantations (i.e., with a native tree coverage than regulate light quantity reaching coffee plants) in the Sierra Madre de Chiapas have been transforming to different management intensities, from monospecific leguminous shade trees (*Inga*), to industrial plantations with little or no shade (Dietsch, 2000; Williams-Guillén & Perfecto, 2010). With this trend, agroforestry systems could themselves be expanding the frontier of matrices hostile to forest-dependent species and also exerting intense pressure to change land use in adjacent areas to current connectivity. In that sense, it is essential that these kinds of agroforestry systems do not continue to increase at the expense of the primary and secondary forests.

Another threat to functional connectivity of these species is illegal hunting, because it reduces the efficiency of these areas to supporting wildlife movement, turning them into ecological traps that reduce the viability of the populations (Brodie et al., 2016). Illegal hunting is a common practice in the unprotected SMSMBC area and in Paxtal (where there is no staff to manage and prevent it) and to a lesser extent in all other SMSMBC protected areas (Figure 5). This situation is worrying because most of the habitat of *P. purpurascens* and *P. nigra* and a significant proportion of the habitat of *O. derbianus* are outside the protected natural areas. In some sites south of the SMSMBC, no individuals of these species have been observed for several years. Therefore, it may be necessary to establish environmental education strategies for the population living in these areas to ensure the management, survival, and flow of the populations of these species in their remaining habitats.

Additional threats include deforestation due to agricultural activities, poor management of forest exploitation, urban expansion, soil pollution by agrochemicals in the upper basin, and cattle expansion in unsuitable areas (Domínguez-Cervantes, 2009; Juan Pérez, 2017). Finally, it has been estimated that 13% of Mexico’s temperate forests, especially pine-oak forests, will be lost because of climate change. This is particularly significant for *O. derbianus* since it has been estimated that its distribution will be reduced due to fragmentation, loss of habitat, and effects of climate change (Peterson et al., 2001; Rojas-Soto, Sosa, & Ornelas, 2012; Villers, 1998).

Acknowledgments

The authors are grateful to the staff of the ECOSUR’s Geographic Analysis Laboratory for their support in the classification of satellite images. The authors also thank Guillermo Velasco Barajas for his logistical support during the design of this project, for his intermediation with other organizations, and for the information provided about the study area; the directors, technical, and operational staff of La Frailescana and El Triunfo for their collaboration and logistical support in the field; and the following institutions in the study area: CONABIO (Regional coordination in Chiapas and Tabasco, and Territorial analysis coordination), CentroGeo, and Secretaría de Medio Ambiente e Historia Natural for the databases and geographic information provided; Cooperative AMBIO, El Triunfo Conservation Fund (FONCET, from its designation in Spanish), Pronatura Sur, A.C., Comon Yaj Noptic, Intercommunity group of territorial action of micro-watershed La Suiza, the coffee organization CESMACH, and Regional Association of Silviculturists Sierra Motozintla A.C. for their collaboration and logistical support and for providing the databases and useful documentary and geographical information. The authors thank community monitoring brigades of the Piedras Negras, Plan de Ayala, Nuevo Reforma Agraria, San Juan de los Ángeles, Francisco Murguía, Loma Bonita and Santa Rosa Las Nubes for their support with the fieldwork; Israel Cárdenas Mayorga for the technical and logistical support during the fieldwork; the authorities and inhabitants of ejidos and communities; small and large landowners for allowing to carry out the tours and fieldwork. Finally, the two anonymous reviewers whose comments allowed us enhance this manuscript.

Declaration of Conflicting Interests

The author(s) declared no potential conflicts of interest with respect to the research, authorship, and/or publication of this article.

Funding

The author(s) disclosed receipt of the following financial support for the research, authorship, and/or publication of this article: Socio-environmental Innovation GIEZCA provided financial support for field data collection. Ecometrica and the British Space Agency provided the financial support through the Forests2020 project for the production of high-resolution maps and for the publication of this article. The National Council for Science and Technology, Mexico (CONACyT, from its designation in Spanish) granted a scholarship to the first author to pursue PhD studies.

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Capítulo 3. Driving Forces of Land Use Change in Agroforestry Landscapes in Southern Mexico

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Segundo artículo de investigación enviado a la revista **Journal of Environment & Development (JED)**

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Abstract

The causes of deforestation and forest degradation are complex and usually region-specific. In this paper, we deepen the analysis of the causes of land-use change of a high-biodiversity landscape in which shaded coffee systems allow the connectivity of several natural protected areas. We prepared maps of land-use change using high-resolution images; additionally, we conducted 106 semi-structured interviews to gather information about the causes of land-use change. Over ten years (2005 to 2015), the land-cover type of 2630 ha changed, 93 % of those changes correspond to habitat loss and degradation. In all cases, the predominant driving forces were the incidence of pests and diseases and the lack of profitability of coffee, which influenced the strategies available to each producer. The coffee price volatility, the government support decreases and the pests and diseases incidence, represent a serious threat to the conservation of shade coffee systems and biodiversity in this region.

Keywords: Agroforestry systems, Landscape change, Driving forces, Landscape connectivity, Biological corridor.

Introduction

The loss of tree cover affects the structure and functions of forest landscapes, degrading their capacity as habitats for wildlife species and providing ecosystem services (Hernández et al. 2015). Reduced ecosystem functioning can have negative effects on the well-being of human societies (Debolini et al. 2018); for example, at the local level increases the incidence of landslides and floods, and at the global level increases in greenhouse gases in the atmosphere.

Land use and land cover change are the result of a complex interconnection of socioeconomic and environmental processes called driving forces, which directly or indirectly affect the way in which landowners decide to the use their land. Driving forces can be divided into two categories: proximate (direct or local) and underlying (indirect or deep). The former are immediate actions at the local level that have direct impacts on forest cover and ecosystem processes, while the underlying causes explain the broader context and the fundamental forces behind these local actions (Geist and Lambin 2002; Lambin and Helmut 2007). Understanding how these forces operate is fundamental for designing nature conservation strategies, reducing negative impacts, and preserving some of the characteristics of natural landscapes (Álvarez Martínez et al. 2011; Kolb et al. 2013). This type of analysis is vitally important in regions of high biodiversity that are threatened by land use change.

In Mexico, one of the main strategies utilized to preserve its high species richness and endemism has been the establishment of natural protected areas (NPA) and biological corridors, the latter being proposed as a mechanism to maintain genetic exchange and to ensure the viability of wild species populations (Adams et al. 2004; Watson et al. 2014). In these regions of high biodiversity, the spaces dedicated to conservation have coexisted with low-impact production activities, such as agroforestry systems. This model has long been practiced in southeastern Mexico, where the coffee grown through agroforestry systems not only provides economic income to the owners but also frequently harbors high levels of tropical biodiversity, represents the habitat of a wide variety of species, provides invaluable ecosystem services, and even represents a fundamental element in ensuring the functional connectivity of the landscape (Escobar-Ocampo et al. 2019). However, this coexistence is not free of risks, since most coffee producers live in conditions of poverty and are highly vulnerable to variations in the price of the product, as well as to pests and crop diseases, among other factors.

Coffee has been an important commodity in the Mesoamerican region; hundreds of thousands of smallholder households depend on this crop for their livelihood (Eakin et al. 2011). In Mexico, approximately 3 million people work in the coffee sector; this population is highly vulnerable to serious economic stresses, such as market volatility, the spread of coffee pests and diseases, extreme weather events, and declining government support programs (Castellanos et al. 2012). Abrupt changes in socioeconomic and environmental conditions can represent disruptions to farmers' livelihoods and affect their ability to continue with cultivation practices (Tucker et al. 2010). In that sense, to develop better land use change scenarios, it is important to understand how farmers are responding to external factors and what the implications of their responses may be at the local and global levels (Eakin et al. 2011).

In this paper, our goal was to assess the magnitude of land use change in coffee agroforestry landscapes in a subregion of the Mesoamerican Biological Corridor in Mexico and to reach an in-depth understanding of the causes of these changes.

Methods

Study area

The study area is part of the Sierra Madre del Sur Mesoamerican Biological Corridor (SMSMBC). The SMSMBC is a subsystem of the Mesoamerican Biological Corridor, which is an international initiative to coordinate and implement conservation and sustainable human development actions (Miller et al. 2001). The SMSMBC is located at southern Mexico along the Sierra Madre de Chiapas and covers an area of 5,185.6 km^2 (Figure 1).

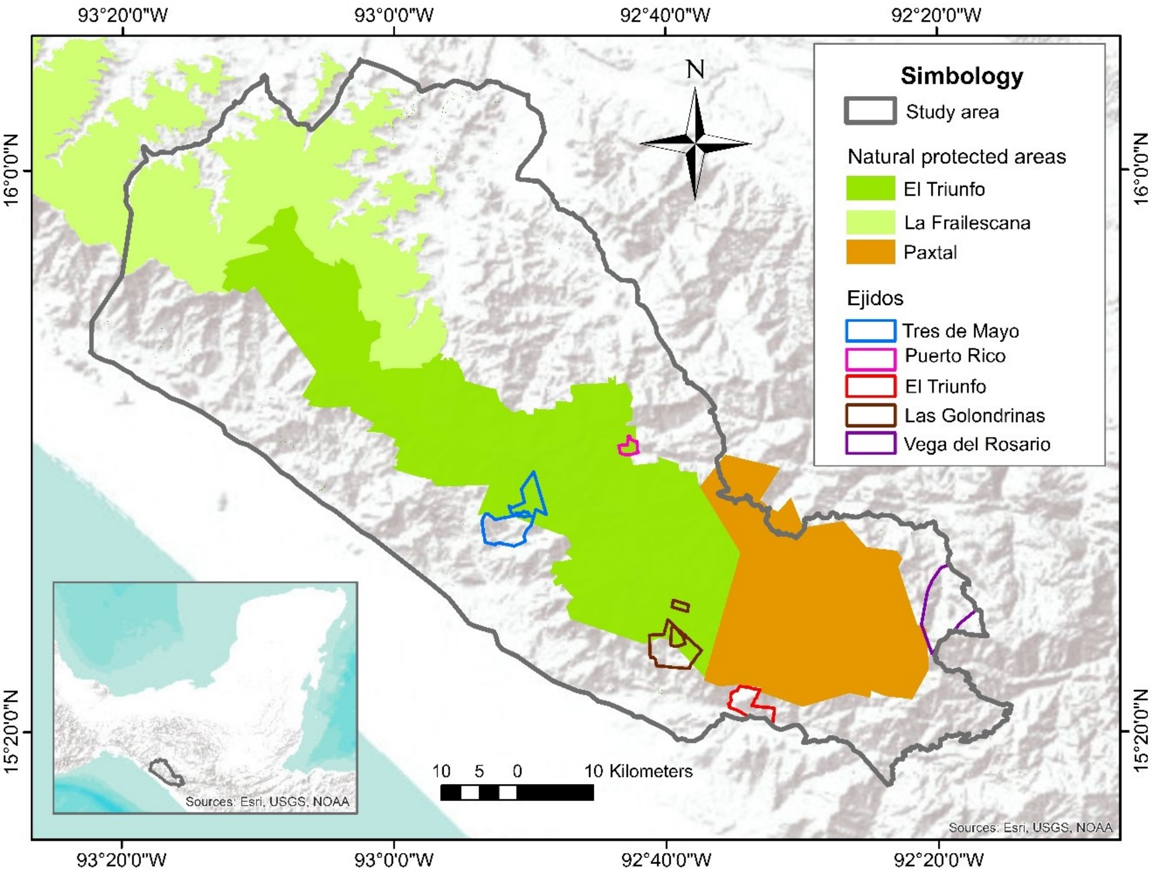

Figure 1. Protected and unprotected areas within the Sierra Madre del Sur Mesoamerican Biological Corridor and location of the ejidos in the case study.

This area is recognized as one of the most important biodiversity hotspots in the world; more than 2,000 species of vascular plants and at least 600 species of terrestrial vertebrates have been reported in this area. (Myers et al. 2000; Brooks et al. 2002). In addition to its biological importance, this area has also been recognized as an important provider of other environmental services, such as water capture and regulation, and carbon capture and storage

(Schroth et al. 2009; Cortina-Villar et al. 2012). Its relief is of a mountainous type, with an elevation gradient ranging from zero to 3,000 m asl (Müllerried 1982; INEGI 2017).

In terms of its area, the predominant land uses and vegetation types are seasonal agriculture and extensive livestock farming (21%), coffee agroforestry systems (14%) and secondary forests (34%) and to a lesser extent forests mature (17%) pine-oak forests, cloud forest, rainforests, and dry forests (Escobar-Ocampo et al. 2019). The shade coffee agroforestry system is usually managed through organic practices combined with agricultural and livestock activities. The production of basic crops (corn-beans) is carried out under the slash and burn system, with modifications and variations in crop management (Domínguez-Cervantes 2009).

Within the corridor, there are three natural protected areas: El Triunfo (biosphere reserve), a portion of La Frailescana (natural resources protection area) and Cordón Pico El Loro Paxtal (state reserve) (Figure 1). The registered population is 105,440 inhabitants, who are widely dispersed since only 9.4% of the inhabitants are distributed in 948 of the localities, while 95,468 inhabitants are concentrated in 337 of the localities (90% of the total population), which are located in the unprotected area (Domínguez-Cervantes 2009).

Evaluation of changes in land cover and land use

The assessment of the areas that had changes in forest cover during the 2005-2015 period was carried out through analysis of SPOT satellite images (10 m spatial resolution), and a combination of automated methods and photointerpretation was used to diminish the level of error of the maps. The sequence used to obtain the change maps is described below: a) the algebraic difference between the normalized SPOT images for 2005 and 2015 was calculated;

b) segments were created from the difference images; c) the segments with the highest probability of having experienced a change in coverage were detected using the *isolationforest* algorithm available in the SciKit-learn library (Pedregosa et al. 2011); d) through supervised classification, the segments that represented false changes were eliminated; and f) the rest of the segments were photointerpreted to assign the new landcover labels; the land use and coverage map for 2015 that was obtained from Escobar-Ocampo et al. (2019) was used as a reference. Satellite image processing was performed using Python and QGIS software (Clewley et al. 2014; QGIS Development Team 2017).

The types of change identified on the maps were defined as follows: a) habitat loss: occurs when former tree vegetation has completely changed to a land cover without tree vegetation; b) habitat degradation: reduction in tree density of a forest or agroforestry system; c) habitat gain: regeneration of shrub vegetation to tree vegetation or the conversion of agricultural systems to agroforestry systems; and d) habitat improvement: increased tree cover of an agroforestry system or change from open forest to secondary or mature forest. In this work, the habitat concept refers to the set of forest types and agroforestry systems used for three species of cracids, the horned guan (*Oreophasis derbianus*), the highland guan (*Penelopina nigra*) and the crested guan (*Penelope purpurascens*), more details are found in Escobar-Ocampo et al. (2019).

Additionally, change rates were calculated for the entire study area and its relationship with the protected and unprotected areas of the biological corridor.

Identification of the causes of land use change

Semistructured interviews

Information on the local causes of land use change was obtained through field trips and semistructured interviews (Sibelet et al. 2013) in farmer households. The field trips were conducted from April to August 2017, and interviews were conducted from July to August 2019. Five localities/ejidos located within the coffee growing zone of this biological corridor were selected: Tres de Mayo, Puerto Rico, El Triunfo, Las Golondrinas and Vega del Rosario (Figure 1, Table 1).

Table 1. Numbers of interviews applied and biophysical traits of the five locations selected as case studies

DATA	**Tres de Mayo**	**Puerto Rico**	**El Triunfo**	**Las Golondrinas**	**Vega del Rosario**
No. of interviews	22	21	20	22	21
Total area (ha)	3,330	362	2,193	2,501	6,025
Altitude range (m asl)	260-1380	1180-1720	260-1400	420-1860	1260-3080
Slope (degrees)	0-57	0-55	0-53	0-63	0-63
Precipitation of the driest month (mm)	Under 60	Under 40	Under 60	Greater than 40	Under 40
Average annual temperature (ºC)	Higher than 18	Higher than 18	Higher than 22	Higher than 18	12 to 18
Soil moisture (months)	7 to 9	8 to 9	7 to 9	8 to 10	9 to 11

Source: INEGI (2000), RAN (2019).

The criteria by which the study locations were selected were as follows:

a. Areas where changes in land cover were detected through image analysis (loss, degradation, gain and improvement of habitat)

b. Areas with distribution of the three cracid species (*O. derbianus, P. nigra* and *P. purpurascens*).
c. Areas with coffee production.

The data collected in the interview included socioeconomic and agricultural production data, land area and history of land cover and land use changes, problems related to land cover and land use changes, family organization for work and education, migration patterns, institutional support, importance of the forest for their activities and conservation actions. In addition, we explored the frequency with which incentive mechanisms, economic support, inputs and technical assistance were provided for different production systems at the municipal level through interviews with municipal officials and representatives of local production organizations. The variables obtained were classified as follows:

<u>Demographic</u>: age of the producer

<u>Economic</u>: low product price, lack of profitability, access to remittances

<u>Institutional</u>: access to rights as a partner in an organization, social incentives, production incentives and conservation incentives,

<u>Natural/Structural</u>: distance to the plot, landslides, elevation, slopes, incidence of pests and diseases (mainly coffee rust but also coffee berry borer and other pest insects), incidence of forest fires.

Technicians: access to technical assistance

The ejido is a territorial unit with a type of social tenure that consists of land, forest and water that are divided into individual plots, population centers and common use areas (Gutiérrez-Lacayo et al. 2003). The size of the selected ejidos varied from 362.5 ha to 6,025.58 ha; the areas had variable biophysical features, such as valleys and steep slopes (Table 1). The five ejidos were classified as highly marginalized (CONAPO 2012), and at the municipal level, 33% of the population lives in conditions of extreme poverty (CONEVAL 2015).

Results and Discussion

Changes in land cover

The overall accuracy of the land cover map was 87%; the highest uncertainty among the classes was in the identification between secondary forest and agroforestry systems. Due to the type of production activity in the region, it was more likely that several of the areas identified as secondary forest were agroforestry systems. On the other hand, all changes that implied loss or gain of forest cover were identified with high reliability (90%).

During the period from 2005-2015, changes in forest and agroforestry cover were recorded in an area of 2,631 ha, which represented approximately 0.5% of the study area. With respect to the modified area, the proportion of changes in the forest area in this period were as follows: loss (84%), degradation (9%), gain (7%) and improvement (1%). Secondary forest was the type of cover most affected by changes (Table 2).

The proportion of forest cover loss obtained in this study (2,631 ha, 0.5%) was considerably lower than that recorded by Cortina-Villar et al. (2012) for the Sierra Madre in the period from 1970-2000 (53,185 ha, 12%). These data suggest that the rate of deforestation has recently decreased, although this conclusion should also be taken with caution given that there were differences in the scales, methods, and the extent of the area studied. Most of the changes in land cover were concentrated outside the NPAs (Figure 2, Table 3).

Table 2. Changes in land cover and land use in the study area during the period from 2005-2015

Land cover/Land use 2005	Land cover/Land use 2015	Area (ha)	Process	%
Mature forest (428 ha)	Agricultural and livestock systems	347	Loss	14
	Shrubby vegetation	23		
	Human settlements	2		
	Secondary forest	30	Degradation	2.1
	Disturbed forest	24		
	Agroforestry systems	2		
Secondary forest (1792 ha)	Agricultural and livestock systems	1449	Loss	62
	Shrubby vegetation	170		
	Human settlements	15		
	Disturbed forest	112	Degradation	6
	Agroforestry systems	47		
Agroforestry systems (226 ha)	Agricultural and livestock systems	196	Loss	7.5
	Human settlements	1		
	Secondary forest	19	Improvement	1
	Disturbed forest	9	Degradation	0.4
Shrubby vegetation (185 ha)	Agroforestry systems	30	Gain	7
	Secondary forest	156		

In the protected areas, the greatest amount of habitat loss occurred in the buffer zone of El Triunfo and Paxtal Reserves. In La Frailescana, the changes were concentrated on the borders of the reserve, so it seems that the conservation mechanisms within the reserve have been working more actively. Outside of the NPAs, the changes were concentrated in the northwest and south of the study area, which was, in this case, due to the advance of the agricultural and extensive livestock frontiers. This was similar to the results of Cortina-Villar et al. (2012) for the Sierra Madre in the period from 1970-2000; in both studies, the secondary forests were the most affected by agricultural systems, especially in the lower and less steep valleys (Figure 2). The areas that experienced habitat loss partially coincided with the areas of least functional connectivity in the landscape according to Escobar-Ocampo et al. (2019), which was largely due to increased habitat fragmentation.

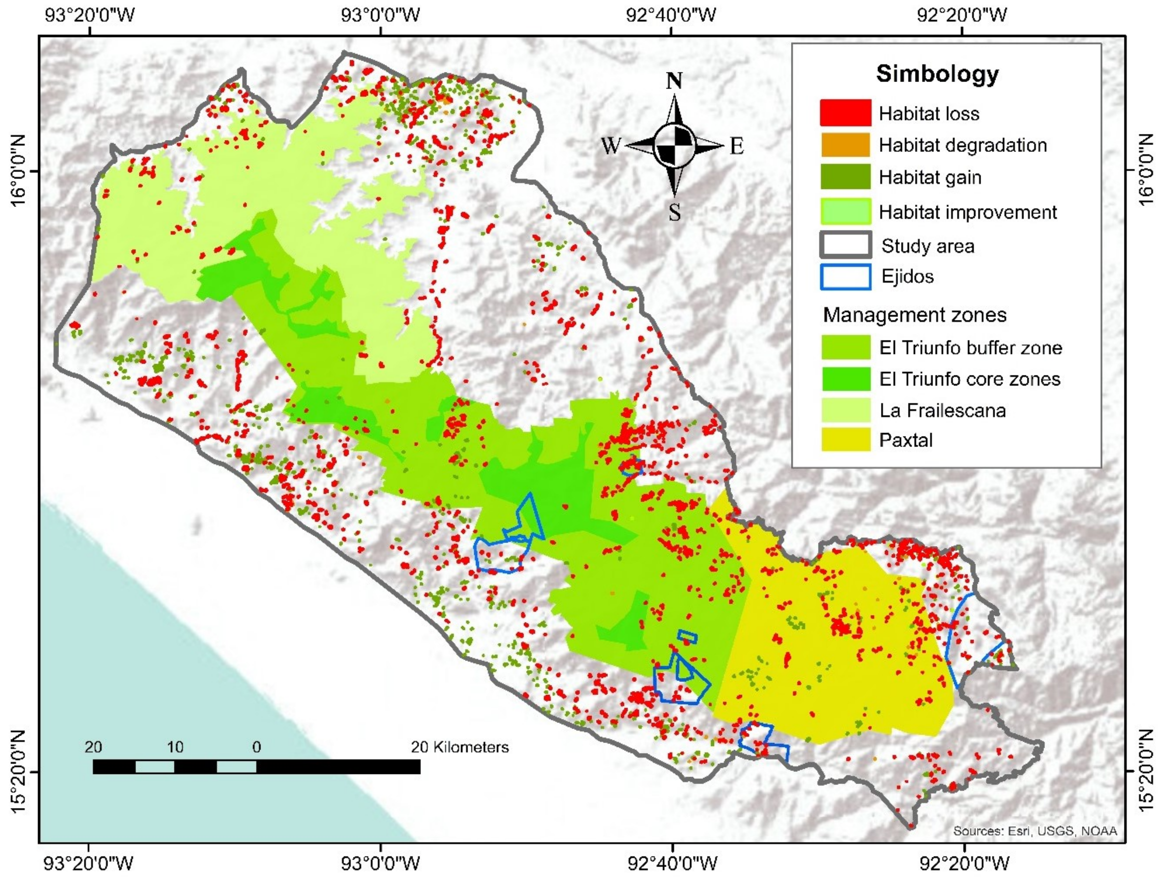

Figure 2. Types of land cover change during the period from 2005-2015 in the study area.

Table 3. Areas by type of habitat change in each management zone.

ZONE/RESERVE		Changes in habitat (ha)			
		Loss	**Degradation**	**Gain**	**Improvement**
Non-protected		1548	150	162	14
Paxtal		186	18	17	9
La Frailescana		106	13	4	0
El Triunfo	Buffer zone	347	23	7	12
	Core zone	17	2	1	0

Analysis of the causes of land use change in coffee agroforestry landscapes

The average surface area of coffee plantations declared by each interviewed producer fluctuated between 0 and 25 ha, with a median surface area of 3 ha. In Table 4, we systematize the main events that triggered land use change and the programs and institutions that have impacted the ejidos under study based on the information obtained in the field and the bibliographic review. These events were addressed by coffee producers through different strategies in each of the studied ejidos (Table 5).

Habitat loss was caused by the change in forest and agroforestry systems from coffee to shrub vegetation or agricultural and livestock systems. These changes were strongly related to the incidence of natural phenomena (landslides) and factors that motivated the abandonment or change of the agroforestry system, such as the distance to the plots, incidence of pests and diseases, advanced age of the producer, and low profitability. This process was more frequent in Puerto Rico and El Triunfo and to a lesser extent in Las Golondrinas (Figure 3).

Table 4. Events related to changes in the five ejidos (2005-2015)

Ejido	**Events**	**Incentives**			**Technical assistance**
		For conservation	**For production**	**Social programs**	
Tres de Mayo	Drop in coffee prices (1989) Coffee rust (1992)	CONAFOR PES (2010-2019)	PROCAMPO, PROCAFÉ, PROGAN	Oportunidades (2002-2014) Prospera (2014-2018)	CONAFOR, CONANP SAGARPA
Puerto Rico	Hurricane landslides (2005) Coffee rust (2012-2014) Pests in forests and shade trees (2012-2019)	FONCET-CONAFOR PES (2011-2020) Restoration/reforestation (2008)	PROCAMPO, PROCAFÉ, PROGAN, Stimulus/Prize/Credit (CESMACH, AMSA)	Oportunidades (2002-2014) Prospera (2014-2018)	CESMACH, AMSA, FONCET, GIAT, INIFAP, CONANP, SAGARPA
El Triunfo	Drop in coffee prices (1989) Coffee rust (2010-2014)	CONAFOR Restoration/reforestation (2012, 2015)	PROCAMPO, PROCAFÉ, PROGAN, Stimulus (GRAPOS, FEDECOS, UNORCAFÉ)	Oportunidades (2002-2014) Prospera (2014-2018)	UNORCAFÉ, GRAPOS, SAGARPA
Las Golondrinas	Hurricane landslides (2005) Coffee berry borer (2005) Coffee rust (2009-2015)	CONAFOR PES (2015-2019)	PROCAMPO, PROCAFÉ, PROGAN, Stimulus (ISMAM, Aguasanta, FIECH) Credit (California)	Oportunidades (2002-2014) Prospera (2014-2018)	CONAFOR, CONANP, ISMAM, Aguasanta, FIECH, SAGARPA
Vega del Rosario	Coffee rust (2009-2012)	CONAFOR PES (2013-2017)	PROCAMPO, PROCAFÉ, PROGAN, Stimulus/Prize/Credit (GRAPOS, ALLEGRO)	Oportunidades (2002-2014) Prospera (2014-2018)	GRAPOS, ALLEGRO, CONAFOR, SAGARPA

Abbreviations: Appendix A.

Table 5: Forest cover and strategies implemented to address the problem of coffee rust in the five ejidos (2005-2015)

Ejido	**% of forest and agroforestry area**		**Strategies in coffee AS**	**Change in coffee AS coverage (%)**	**Current production activities**
	Forest	**AS**			
Tres de Mayo	43	35	1, 3, 4, 6, 7, 8, 9	80-10	Livestock farming (cattle and sheep), pasture rent, basic grain cultivation and coffee growing
Puerto Rico	39	47	1, 3, 4, 5, 6, 7, 8, 9	80-30	Coffee farming, livestock farming, pasture rent
El Triunfo	22	57	1, 3, 4, 6, 8, 9	80-30	Coffee farming, coffee collection points, sale of roasted and ground coffee, livestock farming
Las Golondrinas	30	67	3, 4, 5, 6, 8, 9	80-10	Coffee growing (subsistence), basic grain cultivation and other self-consumption foods
Vega del Rosario	58	7	1, 2, 3, 4, 5, 7	50-10	Coffee growing, corn, beans and potatoes and livestock farming

Source: Author's own elaboration. Strategies: 1 - Plantation management (weeding, plant and shade pruning); 2 - Coffee pulp application at the base of the coffee plant; 3 Fungicides and/or foliar powder application; 4 - SAGARPA technical assistance; 5 - Technical assistance with organic production; 6 - Renewal of the coffee plantation with rust resistant but not shade tolerant coffee varieties; 7 - Mixed renewal with shade tolerant and non-shade tolerant varieties; 8 - Abandonment of coffee plantations and change to other agricultural or non-agricultural activities; 9 - Migration to northern Mexico or the USA.

AS: Coffee and/or cocoa agroforestry systems.

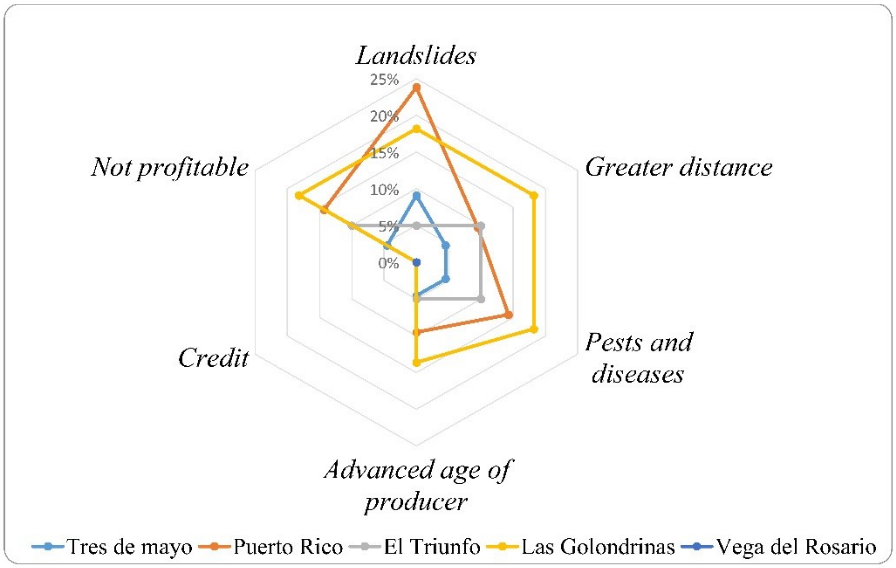

Figure 3. Driving forces associated with habitat loss in coffee agroforestry systems during the period from 2005-2015

The landslides and floods caused soil degradation in the coffee plantations, which made any crop unviable in these areas for several years. Eakin et al. (2012) reported that as a result of the greater impact of Hurricane Stan (2005) on farmers dependent on cash crops and due to the lack of credit and insurance against these losses, the percentage of households in which coffee cultivation was the main source of income fell from 82% before Stan to 18% in 2007. Difficulty in accessing plots (remoteness) and low economic profitability were some of the reasons why the land was sold or rented for agriculture. The agricultural systems that were installed in place of coffee were milpa (corn and beans) and pasture for livestock; the latter was installed only in areas with flat slopes.

Jurjonas et al. (2016) described another factor in forest cover loss: the children of farmers, who in some cases were more interested in migrating than working the inherited land, made it more likely that the land will be sold to others. On the other hand, market conditions drove the conversion of plots for self-consumption food production given the income restrictions faced by producers in buying food: "The profits from the coffee harvest are not enough to live on, just enough to help themselves and to invest; it takes a lot of work" (Independent and conventional coffee grower from Puerto Rico, translated to English by the first author).

Habitat degradation refers to the decline in shade trees and the shift from forests to agroforestry systems. Table 5 shows a decrease in coverage of agroforestry systems based on interviews. Degradation was one of the main consequences of the incidence of pests and diseases and was introduced as a strategy to reduce the presence of coffee rust in all ejidos; other frequently mentioned causes were low profitability and remoteness of the plots (Figure 4).

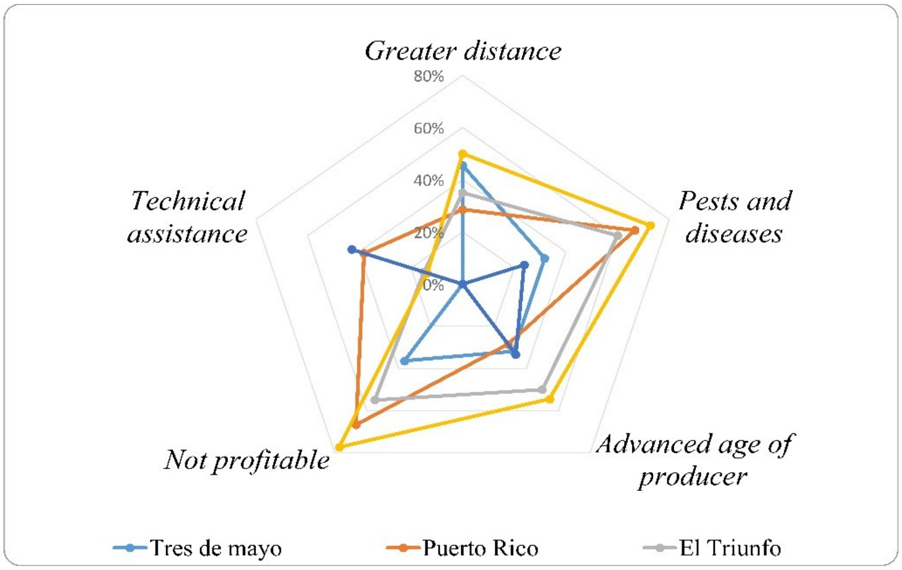

Figure 4. Driving forces associated with habitat degradation in coffee agroforestry systems during the period from 2005-2015

If, as stated in Jha et al. (2014), the development of coffee rust does not depend on the shade level but on local conditions of humidity, elevation, temperature and soil management, then there is still a risk that such shade reduction will be ineffective, but above all, that it will continue to generate a high ecological impact. In recent years, (2017), organizations that export organic coffee, such as Campesinos Ecológicos de la Sierra Madre de Chiapas (CESMACH) or the cooperative "Comon Yaj Noptic", have been testing different varieties that are resistant to coffee rust but tolerant of shade, which allows them to maintain greater shade coverage and maintain cup quality in their products. For example, CESMACH has produced and promoted among its partners the variety Rancho Bonito, also called Peñasco, which appears to be one of the sustainable alternatives that can maintaining coffee quality and forest cover in coffee agroforestry systems (CESMACH Technical advisor, personal comm., July 31, 2019).

Coffee cultivation has persisted due to access to family, institutional (social, productive and conservation) subsidies or additional income from other activities. Remittances in all cases did not stand out as a predominant driving force for change but remained a complementary factor to the family economy. This coincided with Eakin et al. (2012), who included remittances as an important variable for livelihoods and adaptation after a hurricane in three locations in Siltepec, Chiapas, but found no relationship between remittances and change in land use. These authors found that replacing coffee cultivation with alternative crops is a difficult decision because producers have already invested resources and time in coffee production, and the change would not be easy to reverse.

Habitat gain took two forms: the change from shrubby vegetation to secondary forest, as occurred in Las Golondrinas, and the change from agricultural systems to agroforestry systems, as occurred in Vega del Rosario (Figure 5). The first case implied the abandonment of the slash and burn agricultural systems due to the incidence of pests and diseases and the lack of profitability, which meant losses and economic crisis for these producers. In contrast, the coffee producers in Vega del Rosario changed from agricultural systems to agroforestry systems due to favorable conditions, such as having facilities as partners, access to technical assistance, social and production incentives.

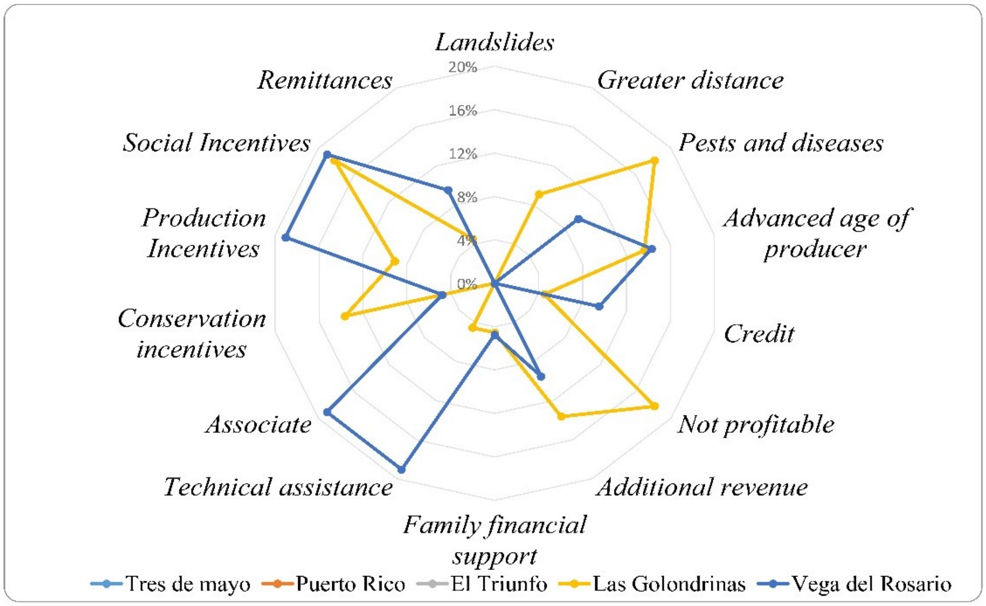

Figure 5. Driving forces associated with habitat gain in coffee agroforestry systems during the period from 2005-2015

In Las Golondrinas, the habitat gain has been a temporary change, as some farmers have obtained additional income from other activities, and as of 2019, they are being supported with the "Sembrando vida" program, so the coverage in these areas is being opened again to recover coffee cultivation. In Vega del Rosario, being associated with an organic production organization (GRAPOS) represents important economic differences in terms of the higher productivity of its coffee plantations with respect to those that are not associated and because of organic production stimuli. Because of this added value of the product, it is likely that more agricultural plots of these partners will continue to be converted into low-coverage coffee agroforestry systems.

The improvement in habitat occurred through the regeneration of coffee agroforestry systems when these were no longer productive for the farmers. The greatest frequency of habitat improvement was in Tres de Mayo and was related to natural (greater distance to the plot, pests and diseases in the coffee plants), demographic (age of the producer) and economic (lack of profitability) driving forces (Figure 6). This process was supported by economic (additional income from other productive activities) and institutional (access to social, conservation and production incentives) driving forces.

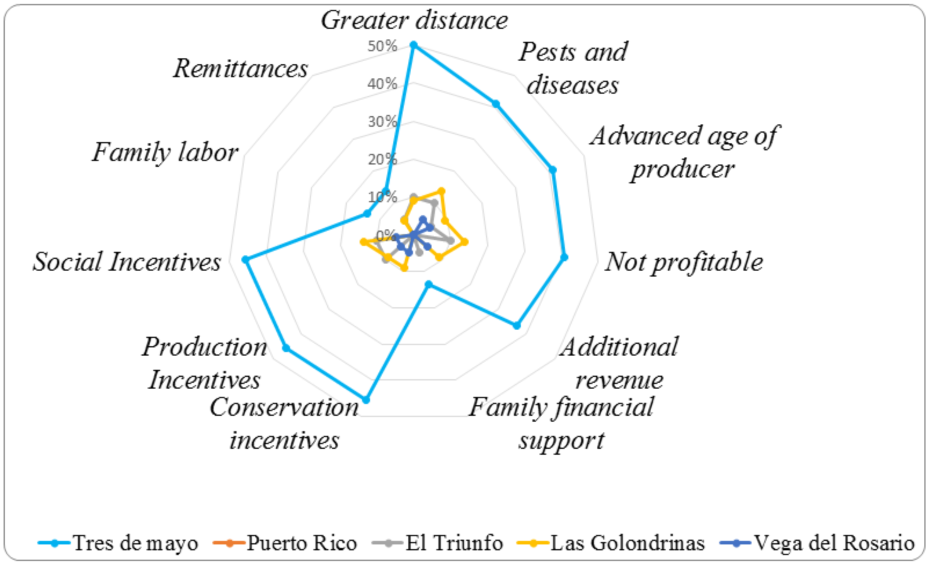

Figure 6. Driving forces associated with habitat improvement in coffee agroforestry systems during the period from 2005-2015

In Tres de Mayo, the location of the ejido within the core and buffer zone of El Triunfo Reserve, CONANP's institutional presence in the ejido, and the availability of land in the unprotected all had impacts. The coffee plantations located in the protected area were very far from the town, so when the price of coffee fell, it was no longer viable to move to maintain the crop, and these lands were abandoned. The landowners in this zone migrated and used resources from remittances to buy land in the unprotected zone, where they have established corn and bean crops, fruit plantations, coffee agroforestry systems, and mainly pastureland. These cultivation areas are spreading towards the east and south of the ejido. In this case, the migration of young people and the subsequent sending of remittances was an adaptation strategy for families in response to the coffee crisis, which was the main economic activity in the area. Tucker et al. (2010) reported that once people started migrating for long periods out of necessity, the relationships between households and the land were altered, which has implications for future production.

The general context of the ejidos studied was that the coffee plantations initially had high-quality varieties (Bourbon, Mundo Novo, Caturra and Marago) that tolerated up to 80% of native tree shade. In 1982, these varieties were affected by coffee rust (*Hemileia vastatrix*), but the farmers were supported by Mexican Coffee Institute (INMECAFE, by its Spanish acronym) to overcome the emergency. After the fall in coffee prices (1989), plantation management practices were abandoned due to lack of purchasing power, which may have been related to the subsequent reappearance of the disease. From 2010 to 2012, coffee rust reemerged with greater intensity, but the federal institutions that had supported production no longer existed, so a large portion of the coffee plantations became unproductive and others were abandoned because of their low productivity. Libert Amico (2016) pointed out that the strategy implemented by the government of the state of Chiapas and SAGARPA in response to the disease was the "crusade against coffee rust", which promoted the renovation of coffee plantations with varieties from the Catimor breeding line, which are resistant to coffee rust but require greater exposure to the sun. In addition, government institutions, coffee companies, and technicians recommended reducing shade cover to address the fungal epidemic, which led to the degradation of the cover of coffee systems or their conversion to agricultural fields (Libert Amico et al. 2019).

Due to low productivity and low prices, many farmers temporarily migrated or were dependent on conservation, social and productive incentives. Remittances were a source of resources for production activities in each of the studied ejidos. The most accessible labor in the best coffee period was obtained from day laborers who primarily came from Guatemala each harvest season, but the temporary migration of day laborers ceased with the depreciation of the Mexican peso against the quetzal and the crisis in the sector. The new generations of farmers were no longer adapted to intensive field work, and the labor force that still prevails is mostly elderly people (≥50 years). This condition did it difficult to sustain the activities required to maintain a healthy and productive coffee plantation.

Most producers have previously been associated with cooperatives or organic or conventional production organizations, but due to mistrust in the way resources were provided to members, more than half of the producers interviewed (62%) currently work independently and sell coffee fruit at different stages of processing, with intermediaries (coyotes) who offer very unstable and generally low prices. Eakin et al. (2006) pointed out that dependence on intermediaries is a factor in the sensitivity of coffee growers to the volatility of coffee prices. On the other hand, in some ejidos, membership in organic production organizations has shown advantages from economic incentives (social fair-trade award), benefits (economic credits and housing funds) and added value to their production.

Due to their location within the biological corridor and their forest cover, all the studied ejidos except El Triunfo have been beneficiaries of payment for environmental services (PES).

As a result, they have committed to several actions for example not to cut down trees in the conservation areas, not to burn their crops, not to hunt or use dogs inside the forest and to integrate a brigade for monitoring and surveillance of illicit activities such as those mentioned above. A certain abundance of wildlife species has also been observed in the El Triunfo ejido; however, due to its location outside of the protected areas, illegal hunting with firearms is common. This has created conflict with the owners of the land where hunting takes place because of the trespassing and the resulting collateral damage to the goods and resources within the properties. Vega del Rosario is also outside of the protected areas, but people in this locality have established an assembly agreement to not hunt animals, even after their PES period has expired. Violators of this agreement have been denounced by the ejido authorities to Federal Prosecutor's Office for Environmental Protection (PROFEPA, for its Spanish acronym).

Conclusions

The results in this study confirmed the strong interrelationship between forest conservation and the stability of agroforestry systems. The decline in government support, the migration of young people, and the incidence of pests and diseases represents a serious threat to biodiversity conservation in this region. Based on the socioeconomic situation of coffee producers in the case studies, there do not seem to be future scenarios that will maintain coffee plantations in the long term.

During the analyzed period, the driving forces that predominantly influenced the loss of habitat (84%) and the degradation of agroforestry systems (9%) were factors such as floods and landslides but especially the lack of profitability of the crop and its vulnerability to the incidence of pests and diseases. These factors resulted in intensified land use and land use change transformation from agroforestry systems to other agricultural uses. The degradation of coffee agroforestry systems was mainly related to the emergence of coffee rust and to institutional support, which required producers to reduce the area of canopy cover.

On the other hand, even though the loss of forest cover detected by remote sensors was relatively low (compared to that in other regions of the state), habitat degradation was a situation that was frequently encountered in the field work, so it was likely that the obtained maps underestimate the degradation of agroforestry systems.

Finally, the conservation mechanisms implemented in the protected areas seem to be working, since most of the area with habitat loss was located outside of the federal protected areas, although the loss and degradation of the vegetation in the buffer zone of the El Triunfo reserve is relatively worrying.

Acknowledgment

The authors are grateful to the UK Space Agency and Ecometrica LTD for the funding granted for the production of the maps. To the directors, technical and operational staff of La Frailescana and El Triunfo for their collaboration and logistical support in the field. To the institutions in the study area: El Triunfo Conservation Fund (FONCET, by its Spanish acronym), Pronatura Sur, A.C., Comon Yaj Noptic, Intercommunity group of territorial action of micro-watershed La Suiza, the coffee organization CESMACH, for their collaboration and logistical support, for providing us with databases and useful documentary and geographical information. To Walter López Báez, for the valuable information provided. To the authorities and inhabitants of ejidos and communities, to small and large landowners, for allowing us to carry out the tours and fieldwork.

Declaration of Conflicting Interests

The authors declared no potential conflicts of interest with respect to the research, authorship, and/or publication of this article.

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Appendix A

Acronym	Full name	Entity
Aguasanta	Organización Agua Santa San Marcos Evangelista Acacoyagua, Asociación Civil.	Local coffee organization
ALLEGRO	Allegro Café orgánico	Multinational coffee organization
AMSA	Agroindustrias Unidas de México, S.A. de C.V.	Multinational coffee organization
California	Beneficiadora de café California S.A.	Multinational coffee organization
CESMACH	Campesinos Ecológicos de la Sierra Madre de Chiapas	Local coffee organization
CONAFOR	Comisión Nacional Forestal	Federal government entity
CONANP	Comisión Nacional de Áreas Naturales Protegidas	Federal government entity
FEDECOS	Federación de Sociedades Cooperativas Cafetaleras, Costa Soconusco del Estado de Chiapas	Regional union of coffee cooperatives
FIECH	Federación Indígena Ecológica de Chiapas	Local coffee organization
FONCET	Fondo de Conservación El Triunfo	Local funding fund
GIAT	Grupo Intercomunitario de Acción Territorial de la microcuenca “La Suiza”	Community-based development organization
GRAPOS	Grupo de Asesores de Producción Orgánica y Sustentable, S.C.	Local coffee organization
INIFAP	Instituto Nacional de Investigaciones Forestales, Agrícolas y Pecuarias	Federal government entity
ISMAM	Indígenas de la Sierra Madre de Motozintla	Local coffee organization
PROCAFÉ	Programa de apoyos a pequeños productores componente Procafé e impulso productivo al café.	Federal government program
PROCAMPO	Programa de Apoyos Directos al Campo	Federal government program
PROGAN	Programa Producción pecuaria sustentable y ordenamiento ganadero y apícola	Federal government program
SAGARPA	Secretaría de Agricultura, Ganadería, Desarrollo Rural, Pesca y Alimentación	Federal government entity
UNORCAFÉ	Unión Nacional de Organizaciones Cafetaleras Ejidales	National coffee organization
PES	Payment for Environmental Services	Federal government program

Capítulo 4. Discusión general.

En el segundo capítulo se evaluó la conectividad del paisaje para tres especies de crácidos en la zona de estudio. Se encontró que la condición ecológica de la vegetación mostró que los bosques maduros presentaron la mejor calidad de hábitat, en tanto que los sistemas agroforestales de café tuvieron los mayores niveles de perturbación y la menor calidad de hábitat. Asimismo, el hábitat de las tres especies presentó un nivel de conectividad intermedio (Contag $\geq$55.9 y $\leq$68.6, IJI $\geq 57.3 \leq 72.1$%). El análisis de conectividad funcional también mostró que el hábitat está conectado para las tres especies a través de un nodo principal, debido a la alta proporción de sistemas agroforestales de café (21% a 24%) que conectan los bosques en las elevaciones medias y altas de la Sierra Madre de Chiapas.

Basándose en esos resultados, el segundo artículo (Escobar-Ocampo et al. Capítulo 3) se enfocó en la evaluación de cambios en el uso del suelo y en los factores que los causan en sistemas agroforestales de café, para con ello establecer las probabilidades de que se mantenga o no la conectividad para especies dependientes de bosques. Los resultados del segundo artículo mostraron que los cambios en el uso del suelo tienen mayor tendencia hacia la pérdida y degradación de hábitat (93%), que hacia la ganancia y mejora de hábitat (7%). Una proporción de los sistemas agroforestales de café existentes en 2005 (226 ha, 9% del área modificada), se perdieron como hábitat para convertirse en sistemas agropecuarios o asentamientos humanos (197 ha), y una proporción menor se degradó a bosques perturbados (9 hectáreas), otros mejoraron su cobertura al convertirse en bosques secundarios (19 ha), mientras que otros ganaron área hacia sistemas agroforestales de café a partir de vegetación arbustiva (30 ha). Es necesario señalar que, aunque la pérdida de la cobertura forestal detectada por los sensores remotos fue relativamente baja en comparación con la de otras regiones del estado, la degradación del hábitat fue una situación frecuente encontrada durante el trabajo de campo, por lo que es probable que los mapas obtenidos subestimaran la degradación de los sistemas agroforestales.

Estos cambios en las coberturas de uso del suelo fueron el resultado de la toma de decisiones de los productores, con base en la compleja crisis de un sector cafetalero dependiente de un fuerte apoyo estatal en toda la cadena de producción. Esta crisis se derivó de varios factores que se gestaron en décadas anteriores, entre ellos la disolución del INMECAFÉ (1989), además de la liberalización del acuerdo internacional que regulaba el precio del café (1989), lo que provocó el desplome de los precios a niveles históricamente bajos y en consecuencia, que la productividad del sector declinara, con una pérdida de ingresos agrícolas del 70% (Renard 1999; Eakin et al. 2006). Otro factor que incrementó la crisis del café fue el abandono de las prácticas de manejo de las plantaciones por falta de poder adquisitivo, lo que las hizo más vulnerables a la reaparición de la roya del cafeto (*Hemileia vastatrix*).

La degradación forestal generada en los sistemas agroforestales de café en la Sierra Madre de Chiapas puso en evidencia que la economía volátil mundial del café dificulta para muchos agricultores realizar un manejo eficaz de sus plantaciones y reveló deficiencias en la infraestructura pública institucional de la que depende el sector cafetalero (McCook and Vandermeer 2015). El cambio climático ha propiciado las condiciones para la proliferación de la enfermedad, pero el contexto socioeconómico amplificó el grado de afectación. La epidemia de roya ha coincidido con períodos de baja rentabilidad del café por descenso en el precio, a la vez que ha habido incremento en los costos de los insumos (Avelino et al. 2015). Además, las medidas posteriores para combatir el hongo “fueron aplicadas a destiempo, improvisadas y sujetas a constantes cambios y no mostraron los resultados esperados por falta de una política cafetalera sustentable" (Renard and Larroa-Torres 2017).

Por otra parte, los efectos del cambio climático se evidenciaron como una amenaza de desequilibrio ambiental, en la intensificación de lluvias, en el incremento de impactos por huracanes, en los estiajes prolongados y heladas, los cuales han afectado directa o indirectamente la productividad del café (Altieri and Nicholls 2008; Pérez-Fernández et al. 2016). Los huracanes Mitch (1998) y dentro del período de análisis, el Stan (2005) afectaron la cobertura y suelos de bosques, cafetales y cultivos. La carencia de seguros y de proyectos de mitigación de riesgos representaron pérdidas netas en los medios de subsistencia y mayor empobrecimiento de los agricultores (Saldaña-Zorrilla 2008). El cambio climático también influyó en el comportamiento agresivo del último brote de la roya, además de que propició condiciones para brotes de otras plagas del café, como la broca del café (*Hypothenemus hampei*) ((Henderson 2019). Por lo anterior, los especialistas recomiendan a los productores adaptarse a la roya, ya que no es posible su erradicación, particularmente en las zonas bajas, que sufren los mayores impactos (Avelino and Rivas 2013).

Así también, las estrategias de combate a la roya han ignorado la calidad del café y se han concentrado en aumentar el rendimiento y la resistencia a las enfermedades (Montagnon et al. 2012). Se han creado centros de investigación especializados en el cultivo de café, tales como el Centro Nacional de Investigación y Desarrollo Tecnológico del Café (CENACAFÉ, 2015) que podrían aportar elementos para mantener y potenciar la calidad del café mexicano. Sin embargo, estos conocimientos no se reflejan en la toma de decisiones del ámbito político, ya que en el campo se sigue fomentando el modelo basado en la difusión de paquetes tecnológicos con agroquímicos y variedades de mayor productividad pero de menor calidad (Pérez-

Fernández et al. 2016). En años recientes (2017), las organizaciones que exportan café orgánico han experimentado con diferentes variedades criollas resistentes a la roya, pero tolerantes a la sombra, que permitan mantener una mayor cobertura de sombra y la calidad de grano en su producción (Asesor técnico de CESMACH, com. pers., 31 de Julio, 2019). Este tipo de innovaciones si puede ser apropiada para conservar áreas de cultivo en los que las buenas prácticas de manejo contribuyan al fomento de la calidad del café y el bienestar de los ecosistemas.

Los resultados obtenidos en este estudio muestran la importancia de los sistemas agroforestales de café como corredores que facilitan la conectividad del hábitat de las tres especies de crácidos. Así también exponen la amenaza que representan las tendencias de cambio de uso de suelo hacia la pérdida y degradación del hábitat de estas especies, considerando los factores que los causan en sistemas agroforestales de café. La calidad de hábitat que pueden proporcionar los sistemas agroforestales de café para especies de interior de bosques se relaciona con el grado de intensificación del sistema de producción utilizado y la permeabilidad de movimiento que proporcionan: si tiene una cobertura forestal más alta y densa y el riesgo de depredación o de cacería es bajo, las especies pueden permanecer más tiempo, por lo que funciona como un complemento del hábitat y contribuye a la persistencia de las poblaciones (Driscoll et al. 2013; Biz et al. 2017).

Además del cambio de uso de suelo y de la fragmentación del hábitat, los riesgos de depredación y cacería son los principales factores que afectan a los individuos o grupo de individuos de crácidos al cruzar un sistema agroforestal u otros usos del suelo. Los organismos pueden maximizar los beneficios y minimizar los riesgos de depredación, o bien modifican su distribución espacial y su permanencia en las áreas menos permeables, o en el peor de los casos, mueren en el intento. En este estudio no se cuantificó el impacto de la cacería en la conectividad de las especies, pero a través del trabajo de campo y mediante las encuestas se registró la cacería frecuente de estas especies, en algunos lugares de forma furtiva y en otros se practica sin ninguna regulación por las autoridades locales, generalmente en las áreas no protegidas. La cacería furtiva es una amenaza importante que reduce la eficacia del corredor biológico para apoyar el movimiento de la vida silvestre. Cuando esta práctica se realiza de manera frecuente y sin control puede convertir a estas áreas en "sumideros" o trampas ecológicas que reducen a corto o mediano plazo la viabilidad de las poblaciones de especies que ahí transitan (Brodie et al. 2016).

Con respecto a la cobertura de bosques, también se ha estimado que el 13% de los bosques templados de México, especialmente los bosques de pino-encino, se perderán debido a efectos del cambio climático. Esto es particularmente significativo para *Oreophasis derbianus* (pavón) ya que con base en escenarios futuros se ha proyectado que su distribución se reducirá debido a la fragmentación, la pérdida de hábitat y los efectos del cambio climático (Peterson et al. 2001; Rojas-Soto et al. 2012). De ahí que la adaptación al cambio climático y la conservación de los bosques son dos asuntos muy vinculados entre sí y serán decisivos para alcanzar el éxito en las medidas de adaptación que se adopten. El CBSMS tiene la misión de mantener la conectividad de especies de flora y fauna en zonas con alto valor biológico, por medio de prácticas de fomento y conservación de territorios con usos múltiples de suelo (CONABIO 2013). Las políticas y líneas de acción para la cooperación de recursos financieros internacionales de esta área están programadas en el plan director CBM-2020 (Gestión territorial sostenible en el Corredor Biológico Mesoamericano), pero tienen un plazo de vencimiento a 2020 (CCAD 2013), por lo que aún son inciertos los planes y programas posteriores.

En toda el área forestal del CBSMS se requieren programas de sensibilización y de educación ambiental para los pobladores, autoridades, funcionarios gubernamentales y encargados de formular políticas sobre la conectividad del paisaje, fundamentalmente en las de mayor frecuencia de cacería. También se podrían implementar diferentes mecanismos interinstitucionales para disuadir la cacería, a la vez que se les capacite para favorecer el incremento de las poblaciones silvestres en vida libre, a través de actividades de agroturismo, de turismo de aves, o para el cuidado, reproducción y aprovechamiento sustentable de especies mediante Unidades de Manejo para la Conservación de la Vida Silvestre (UMA). En el área de estudio existen comunidades y organizaciones que ya han puesto en práctica estas actividades con resultados exitosos. Son ejemplo de ello el ejido Plan de Ayala, de La Frailescana, que cambiaron las prácticas de cacería furtiva por el monitoreo biológico mediante cámaras trampa y el turismo sustentable, o las comunidades cafetaleras asociadas a la Comon Yaj Noptic, de la reserva El Triunfo, que enfocan parte de su actividad productiva al agroturismo sustentable.

Para mantener y mejorar la conectividad a través de los sistemas agroforestales de café del CBSMS, se requieren políticas y programas consistentes de apoyo al sector cafetalero con una estrategia de visión integral, que permita la investigación y asistencia técnica adecuada para aumentar la resiliencia natural del café a las perturbaciones y contra futuros riesgos generados por el cambio climático, en el contexto de un mercado desregulado y de un apoyo institucional atenuado (Avelino et al. 2015). Los pequeños productores han tenido que enfrentar el mercado sin la mediación de las instituciones públicas del sector. En los ejidos estudiados, por lo menos el 62% de los productores entrevistados trabaja de forma independiente y venden sus productos a través de intermediarios, a precios inestables y generalmente bajos. En este sentido, es esencial aumentar los ingresos de los pequeños agricultores para incrementar sus capacidades de adaptación relacionadas con la producción de café. Sin embargo, la transición a una producción de calidad, incluyendo las certificaciones, requiere un acceso a información y asistencia técnica que no todos los productores tienen. Los mecanismos de difusión de las políticas y programas agrícolas de desarrollo rural y las normas que regulan el acceso al apoyo técnico, a los servicios, créditos y conocimiento, no son accesibles para todos (Castellanos et al. 2012).

Una alternativa de desarrollo la representa la asociación de productores en cooperativas de producción orgánica, lo que les permite el acceso a estímulos y asistencia técnica y agregar valor a su producto, como se observó en algunos ejidos que fueron estudio de caso (Vega del Rosario y Puerto Rico). La certificación también puede tener un impacto positivo en la prevención de la degradación forestal, lo que indica la creciente importancia de la certificación del café para la conservación de los bosques circundantes. (Haggar et al. 2017; Takahashi and Todo 2017). Además, bajo las condiciones actuales de libre mercado, las cooperativas que tienen suficiente capacidad para exportar pueden hacerlo sin esperar una autorización previa y sin competir con grandes exportadores para las cuotas (Renard 1999), lo que representa una oportunidad de posicionarse ante un nuevo mercado.

Conclusiones

Este estudio se realizó a dos escalas: el análisis de fragmentación, de conectividad funcional y de cambio de uso de suelo se realizó a escala de paisaje, en tanto que el análisis de la condición ecológica de la vegetación y de los factores causales del cambio de uso del suelo se obtuvo a escala local o de sitio. Esto permitió obtener información con mayor detalle sobre la calidad de los tipos de cobertura y de usos de suelo en los mapas a escala de paisaje, así como hacer inferencias de las causas relacionadas con el cambio de uso del suelo en sistemas agroforestales de café a partir de cuatro estudios de caso.

Las variables ambientales relacionadas con la distribución de crácidos dependientes de bosques en el CBSMS fueron: la precipitación, la elevación y la temperatura mínima. La precipitación se relacionó negativamente con la ocurrencia de *Penelope purpurascens* y de *Penelopina nigra*; la elevación se relacionó positivamente con *P. nigra* y *Oreophasis derbianus*; y la temperatura mínima estuvo asociada positivamente con *O. derbianus*.

Los bosques maduros presentaron la mejor calidad de hábitat, debido a su mayor complejidad estructural, mayor riqueza de especies arbóreas y menores niveles de perturbación. La condición ecológica de los sistemas agroforestales de café fue baja, lo que reduce la viabilidad de estos espacios como complemento de hábitat. Esto tendría efectos negativos en el hábitat de *O. derbianus*, que depende de condiciones específicas de bosque perennifolio de niebla maduro durante su etapa reproductiva y este bosque solo representa el 20% de su hábitat.

El mosaico del paisaje del CBSMS presenta un alto grado de heterogeneidad y un nivel intermedio de fragmentación, pero estuvo conectado funcionalmente para las tres especies a través de un nodo principal de gran extensión, lo que expone la importancia del CBSMS para conectar una alta proporción de hábitat de crácidos dependientes de bosques dentro y fuera de las áreas protegidas.

En el período 2005-2015 se registraron cambios en la cobertura forestal y agroforestal en una superficie de 2.631 hectáreas, que representó aproximadamente el 0.5% de la superficie de estudio. Los factores causales que influyeron predominantemente en la pérdida de hábitat fueron las inundaciones y los deslaves, en mayor medida lo fue la falta de rentabilidad del cultivo y su vulnerabilidad a la incidencia de plagas y enfermedades. Esos factores dieron lugar a una intensificación del uso del suelo, degradación y cambio de uso de los sistemas agroforestales a otros usos agrícolas. La degradación de los sistemas agroforestales del café se relacionó principalmente con la aparición de la roya del café y con el apoyo institucional, que exigió a los productores reducir la superficie de la cobertura de árboles de sombra.

El mantenimiento de la conectividad de los crácidos dependientes de bosques está condicionado a la mejora de la estructura de los sistemas agroforestales de café. Sin embargo, debido a los factores causales mencionados en el punto anterior, los sistemas agroforestales están ampliando por sí mismos la frontera de matrices hostiles a las especies dependientes de los bosques y también ejerciendo una intensa presión para cambiar el uso del suelo en las zonas adyacentes a la conectividad actual. En ese sentido, se debe promover el cultivo de café bajo sombra, pero no a expensas de los fragmentos de bosque.

La cacería furtiva e ilegal es una de las principales amenazas a la conectividad porque reduce la eficacia del corredor biológico para apoyar el movimiento de la vida silvestre. Por tal motivo, se requiere programas de sensibilización y de educación ambiental, fundamentalmente en las áreas de mayor frecuencia de cacería. Asimismo, será importante implementar mecanismos interinstitucionales para disuadir esta práctica en coordinación con los gobiernos locales, a través del fomento de actividades productivas relacionadas con el manejo y/o aprovechamiento sustentable de vida silvestre.

Con base en escenarios a futuro, se ha estimado que los efectos del cambio climático producirán la significativa pérdida de cobertura de bosques y sistemas agroforestales, así como afectarán el área de distribución de *O. derbianus*, por lo que las medidas que se planifiquen para la adaptación al cambio climático y la conservación de los bosques serán decisivas para alcanzar el éxito en estos objetivos.

Se recomienda proteger los fragmentos de bosque remanentes, que mantienen más especies de fauna asociados a bosques que los sistemas agroforestales de café, independientemente de la intensidad de manejo. Es importante también mejorar la conectividad de los fragmentos de la periferia de cada hábitat. Esta conectividad será importante en la medida en que se conectan con otras áreas más grandes y por el valor de su cobertura para la conservación de cada especie.

Por último, los mecanismos de conservación aplicados en las zonas protegidas parecen estar funcionando, ya que la mayor parte de la zona con pérdida de hábitat se localizó fuera de las zonas protegidas federales, aunque la pérdida y degradación de la vegetación en la zona de amortiguamiento de la reserva de El Triunfo fue particularmente alarmante.

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