



El Colegio de la Frontera Sur

Patrones de diversidad de escarabajos copronecrófagos
(Coleoptera: Scarabaeidae: Scarabaeinae) en la Reserva de
Biosfera Selva El Ocote, México

Tesis
presentada como requisito parcial para optar al grado de
Maestro en Ciencias en Recursos Naturales y Desarrollo Rural
Con orientación en Ecología y Sistemática

Por

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2017



El Colegio de la Frontera Sur

_____ Miércoles _____, 31 de mayo _____ de 2017 _____.

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Patrones de diversidad de escarabajos copronecrófagos (Coleoptera:
Scarabaeidae: Scarabaeinae) en la Reserva de Biosfera Selva El Ocote,
México

para obtener el grado de **Maestro en Ciencias en Recursos Naturales y Desarrollo Rural**

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DEDICATORIA

A mi Familia... el candil de mi camino
A los que partieron, a los que siguen...
a los que permanecerán y a los que volverán
De ustedes traje de todo un poco,
Y donde vaya los llevo
¡Esta va para ustedes!
¡Gracias!

*“Aún a la vuelta de la esquina quizás todavía espere
un camino nuevo o una puerta secreta,
y aunque hoy pasemos de largo
y tomemos los senderos ocultos que corren
hacia la luna o hacia el sol
quizá mañana aquí volvamos.*

*Manzana, espino, nuez y ciruela
¡que se pierdan, se pierdan!
Arena y piedra y estanque y cañada,
¡adiós, adiós!*

*La casa atrás, delante el mundo,
y muchas sendas que recorrer
hacia el filo sombrío del horizonte
y la noche estrellada...”*

J.R.R. Tolkien, 1955

AGRADECIMIENTOS

Al M.C. Benigno Gómez. Gracias profe por el apoyo incondicional que me brindó durante todo el proceso de la tesis; desde la concepción y diseño del trabajo, hasta el último comentario de revisión. Por esas pláticas tan enriquecedoras, entretenidas y formativas para mi crecimiento personal y profesional. Por su sincera confianza en mí y en mi trabajo, y por esos “pozolas” o tacos que me convidaba después del campo. Al Dr. Mario Favila, gracias también por todas sus enseñanzas, apoyo y constancia durante la elaboración de la tesis. Por sus charlas y cuestionamientos pertinentes al “cómo, el por qué y que no hacer” en la ecología. Por su guía en el manejo y análisis de datos. Por su paciencia, enseñándome a escribir de manera académicamente correcta.

Al Dr. Darío Navarrete, por mantener su puerta siempre abierta para todas esas consultas locas que me surgían cada dos o tres días. Por su gran dedicación, compromiso, consejos y pláticas con y sin café. Por enseñarme tanto sobre las artes oscuras del SIG y de la ecología del paisaje. Por guiarme a través del intenso proceso analítico con los datos. A la Dra. Lorena Ruíz, por aceptarme en su proyecto CONACYT “Vulnerabilidad Social y Biológica ante el cambio climático en la Reserva de la Biósfera Selva El Ocote”. Por el apoyo logístico y financiero brindado para que pudiese realizar mi trabajo de campo sin contratiempos. Por sus cuestionamientos y sugerencias, obligándome siempre a poner en tela de juicio mis argumentos. En fin, gracias a todo mi comité por su profesionalismo y tiempo dedicado para un alumno tan “molestón” como yo. Gracias por forzarme a dar más, aunque ya no quisiera. Fue tremendamente grato haber sido alumno de ustedes.

Al M.C Leonardo Delgado por compartir su enorme conocimiento taxonómico. Al Dr. Alfonso Díaz y a Renato Portela Salomão por su invaluable apoyo durante mi estancia en el INECOL.

A la Dra. Paula Enríquez, al Dr. Alfonso Luna y al Dr. Guillermo Ibarra por sus valiosas sugerencias y aportes en aras de mejorar mi trabajo.

Al Colegio de la Frontera Sur, por la oportunidad de llevar a cabo mis estudios de posgrado. Al Consejo Nacional de Ciencia y Tecnología (CONACyT) y a la Fundación Heinrich Böll Stiftung por las becas otorgadas durante el posgrado.

A todas esas bonitas amistades que he forjado aquí en México. Gracias por recibir un extranjero y hacerlo sentir como en casa. Por compartir su cultura, su casa, su comida (mucho comida), sus películas pirateadas y su peculiar sentido del humor conmigo ¡Ustedes saben quiénes son malditos Marginales! (no se hagan), y otras genuinas amistades más☺.

A mis compas de laboratorio: Eddie, Gibrán, Juan y Martín, gracias por su apoyo y por mostrar un auténtico compañerismo.

A la M.C. Karla Leal y la CONANP por el apoyo durante mis jornadas de campo en Tierra Nueva y Emilio Rabasa. Al biólogo Trinidad Alejandro Guillén Díaz por movilizarme durante la etapa de campo,

A doña Jaqueline Suyapa Duarte (alias madre), a don José Francisco Rivera (alias padre). No ajusta papel para agradecerles todo lo que han hecho por mí. Gracias por el apoyo eterno. A mi hermano Alfonso y a mi cuñada Elena por recibirme siempre con las puertas abiertas en su hogar.

De manera enfática quiero agradecerles a las siguientes personas:

A Guadalupe Hernández, alias "La Lupita" y a Erick "El Chavalín" Hernández. ¡Tan Chavos!... ¡Pero como chambear! Convirtieron del campo en una experiencia inolvidable. Aguantaron avispa, abejas muerde-pelo psicópatas (va Chavalín), lluvia, piedras filosas, y mi comida rara de campo; subiendo y bajando cerros todo el día conmigo. "*¡Lupita, ya estás lista para subir corriendo el Tacaná!*". Asimismo, le quiero agradecer a las comunidades de Nuevo San Juan Chamula, San Joaquín, Emilio Rabasa, Tierra Nueva y al Rancho Monterrey por su tremenda hospitalidad y por permitirnos trabajar en sus tierras. En especial a: Don Lorenzo "Lol" Ruíz Jiménez, Don José Moisés "Moi" Gutiérrez Vásquez, Luis Fernando Gutiérrez Espinoza y su hijo Luis ("El Guicho") Gutiérrez, a Don Fernando "Fer" Hernández Pérez, Armando Sánchez Pérez, Jaime Pérez Sánchez y a Jose ("El Jose") Pérez Velasco. Gracias por su ardua labor e incontables enseñanzas.

Sin todos ustedes no lo hubiese logrado, ¡Gracias!

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INTRODUCCIÓN

Los paisajes tropicales alojan al menos dos tercios de la diversidad biológica descrita en el planeta (Brown 2014). Sin embargo, en su mayoría consisten de ecosistemas modificados bajo altas tasas de deforestación y rápidos cambios en el uso de suelo (Gardner et al. 2009). La modificación del paisaje es una de las principales causas que conlleva a la pérdida de la diversidad biológica y detrimento de los recursos naturales en el trópico (Aide et al. 2012; Haddad et al. 2015). La pérdida de la biodiversidad afecta la producción primaria, reciclado de los nutrientes, fertilidad del suelo, polinización de la vegetación, regularización del clima y el control poblacional de plagas (Cardinale et al. 2012; Naeem et al. 2016). Ante este escenario, es imperativo profundizar nuestra comprensión sobre como la alteración del paisaje afecta a las especies y así tener mejores elementos para plantear estrategias efectivas de manejo-conservación de los recursos y biodiversidad (Collinge 1996).

El presente documento se divide en tres capítulos. El primer capítulo presenta una revisión teórica y metodológica relativa al estudio del paisaje y su interacción con la biodiversidad. Se contextualiza sobre el grupo de insectos empleado en la investigación, así como el área de estudio. Asimismo, se delimitan los objetivos y preguntas de investigación. El segundo capítulo presenta el estudio acerca de los patrones de diversidad de los escarabajos copronecrófagos y el efecto del paisaje sobre sus comunidades en la Selva El Ocote, manuscrito que ha sido sometido para publicación en la revista *Insect Conservation and Diversity*. El último capítulo provee las conclusiones y recomendaciones realizadas con base en los resultados del trabajo.

Paisaje: definiendo términos

Urban et al. (1987) definen al paisaje como “*un mosaico de formas de tierra heterogéneas, tipos de vegetación y uso de tierra*”. La complejidad del paisaje está determinada por las unidades fisiográficas que lo integran, y se delimita con base en aspectos geográficos, ecológicos o administrativos en común (Halffter et al. 2001; Wu 2013). Las unidades que conforman un paisaje se denominan parches, los cuales son

áreas que difieren de su alrededor tanto en naturaleza, complejidad y apariencia (Turner y Gardner 2015). Fragmentación se define como el rompimiento de tipo de cobertura vegetal a un conjunto de parches de menor área, aislados unos de otros por una matriz (i.e. el elemento de mayor predominancia en el paisaje) (Franklin et al. 2002; Turner y Gardner 2015). Por otro lado, hábitat es el conjunto de recursos (e.g. alimento, agua, refugios) y condiciones (e.g. parámetros micro-ambientales) presentes en una área, que favorecen la ocupación, supervivencia y reproducción de los individuos o poblaciones de una especie (Hall et al. 1997).

El paisaje se describe por dos elementos particulares, su composición y configuración estructural. La composición hace referencia al número, tipos y extensión de las diferentes coberturas de suelo presentes en un paisaje. La configuración estructural del paisaje trata sobre la disposición, distribución, orientación y el arreglo de los elementos que componen al paisaje (Leitão et al. 2006; Turner y Gardner 2015). Es importante determinar la composición y arreglo espacial del paisaje, pues sus características y diferencias pueden estar correlacionadas con diversos atributos de las especies y función del ecosistema (Turner 1989; Fahrig et al. 2011).

Patrones de Diversidad

El Programa de las Naciones Unidas para el Ambiente (UNEP, por sus siglas en ingles), define la diversidad biológica como: *“la variabilidad de organismos vivos de cualquier fuente, incluidos, entre otros, los ecosistemas terrestres y marinos y otros ecosistemas acuáticos y los complejos ecológicos de los que forman parte; esto incluye la diversidad dentro de cada especie, entre las especies y de los ecosistemas”* (UNEP 1992). La diversidad biológica está compuesta de tres niveles: el genético, el poblacional y el ecológico (i.e. de comunidades) (Redford y Richter 1999). El nivel genético de la diversidad hace referencia a la variabilidad alélica que surge por mutaciones en el ADN de una especie, sub-especie o población; el nivel poblacional de la diversidad estudia la variación y estructura poblacional de las especies en una localidad o región; el nivel ecológico de la diversidad se refiere a la variedad de comunidades, ecosistemas y gremios que co-existen en una misma área y tiempo (Redford y Richter 1999; Moreno 2001). Por otro lado, Noss (1990) describe tres atributos que caracterizan cada nivel de

la diversidad biológica: la composición, la estructura y la función. La composición trata sobre la identidad y variación de los elementos constituyentes de la diversidad; la estructura describe la organización de los elementos composicionales de la diversidad, y la función detalla los procesos ecológicos y evolutivos que actúan entre los componentes de la diversidad biológica (Noss 1990; Halffter et al. 2001).

Las comunidades de especies no son entidades estáticas y aisladas dentro de un entorno neutro. Estas responden a las variaciones fisiográficas y condiciones climáticas del paisaje, lo que propicia un conjunto de comunidades diferenciadas en estructura y composición (Moreno 2001). Para facilitar la comparación entre comunidades ubicadas en diferentes localidades, Whittaker (1972) divide la diversidad biológica en tres componentes: alfa (α), beta (β) y gamma (γ). La diversidad alfa consiste en un conjunto de especies que coexisten en una localidad y tiempo particular. La diversidad beta es la tasa de remplazo o cambio de especies entre diferentes localidades. La diversidad gamma abarca tanto la diversidad alfa y la diversidad beta, por lo que se define como el conjunto total de especies en un paisaje o región (Halffter et al. 2001; Pereyra y Moreno 2013).

El estudio de los patrones de diversidad (α , β & γ) es de gran relevancia para definir las estrategias de conservación y manejo de la diversidad biológica. Sin embargo, para maximizar su utilidad, es necesario entender los mecanismos que generan y mantienen las disimilitudes entre las comunidades a lo largo de gradientes ambientales o de disturbio (Socolar et al. 2016). Por ejemplo, determinar si los procesos de diferenciación entre comunidades son producto de anidamiento o recambio de especies (Baselga 2012); o estableciendo si la disimilitud entre las comunidades es el resultado de procesos estocásticos o de límites en la dispersión de las especies debido a disturbios antropogénicos del paisaje (Chase et al. 2011).

Efecto de la destrucción del hábitat y fragmentación del paisaje sobre la biota

La fragmentación y la destrucción de los hábitats en un paisaje comúnmente generan una cascada de eventos que desestabilizan las múltiples interacciones biológicas en un ecosistema (Green et al. 2006). Sus efectos se pueden manifestar de diferentes formas según la especie, ya sea fomentando la extinción de organismos susceptibles al

disturbio o promoviendo la propagación de las especies generalistas (Fahrig 2003). La destrucción del hábitat disminuye el éxito de reproducción, forrajeo y depredación de las especies. También, favorece la extirpación de las especies nativas, el ingreso de organismos invasores, la simplificación de las redes tróficas, la pérdida de especies, y alteración de las comunidades (Collinge 1996; Fahrig 2003; Green et al. 2006; Fischer y Lindenmayer 2007; Mitchell et al. 2016; Thompson et al. 2016; Cajaiba et al. 2017; de la Mora-Estrada et al. 2017).

Los efectos de la fragmentación del paisaje pueden ser confundidos con los efectos de la destrucción del hábitat, ya que ambos disturbios se encuentran altamente correlacionados (Fahrig 2003; Smith et al. 2009). Sin embargo, existen múltiples evidencias de como la fragmentación “*per se*” puede afectar a las especies, poblaciones y comunidades (Fahrig 2003; Thornton et al. 2011). Por ejemplo, el reducir el área de los parches ocasiona descensos poblacionales, al disminuir la cantidad, calidad y disponibilidad de los recursos (Fahrig 2013). Asimismo, la fragmentación del paisaje puede incrementar el aislamiento entre los parches, afectando la movilidad, flujo genético y la persistencia de las especies en el paisaje (Fischer y Lindenmayer 2007; Prugh et al. 2008). Por otro lado, la fragmentación aumenta la densidad de los bordes en el paisaje (Turner y Gardner 2015). La presencia de bordes altera las condiciones micro-climáticas internas de los hábitats y favorece la invasión de especies exóticas (Cadenasso y Pickett 2001; Harper et al. 2005; Ewers y Didham 2008). Finalmente, tanto la destrucción del hábitat como la fragmentación del paisaje afectan los procesos de polinización, reciclado de nutrientes o control poblacional de potenciales plagas (Didham et al. 1996; Andresen 2003; Larsen et al. 2005; Wang et al. 2005; Bell y Donnelly 2006; Mitchell et al. 2013).

Modelos para el estudio del paisaje

Los estudios sobre la interacción del paisaje con la diversidad se han basado en la teoría de Biogeografía de Islas de MacArthur & Wilson (1967) o el modelo de parche-matriz-corredor de Forman (1995), en los cuales las unidades del paisaje se reconocen como elementos discretos (Lindenmayer & Fischer, 2006). Sin embargo, varios autores han argumentado que la transformación del paisaje no genera solamente parches

discretos (i.e. fragmentados), rodeados por una matriz “inhóspita” (Manning et al. 2004; Franklin y Lindenmayer 2009; Tscharrntke et al. 2012). Los cambios también pueden ser graduales y espacialmente continuos, y la matriz puede presentar distinta habitabilidad y permeabilidad para las especies (McIntyre y Barret 1992). Como alternativa a los modelos binarios de paisaje, McIntyre y Barret (1992) proponen el concepto de abigarramiento para los casos en que hubiesen gradientes de hábitat o de la cobertura vegetal en el paisaje.

McIntyre y Hobbs (1999) integran los conceptos de fragmentación y abigarramiento en un solo modelo. Estos dividen el paisaje en cuatro categorías, según el porcentaje de pérdida de la vegetación original y la intensidad de transformación del hábitat : 1) paisaje intacto (>90% de vegetación original), que consiste en sitios con poco o nada de modificación; 2) paisaje abigarrado (60-90%), el cual presenta una modificación moderada, con límites graduales o abruptos entre sus unidades; 3) paisaje fragmentado (10-60%), posee un alto grado de modificación; 4) paisaje relicto (<10%), que consiste en sitios con un grado de modificación extrema. Los límites entre las unidades del paisaje de estas últimas dos categorías son generalmente abruptos.

Con base en el modelo de alteración continua del paisaje, Halffter y Rös (2013) proponen el estudio de los patrones de diversidad mediante la ubicación geográfica de ventanas de muestreo. Las ventanas son espacios con áreas equivalentes entre sí, situadas de forma semi-aleatoria con el fin de maximizar la representatividad de la heterogeneidad vegetal y usos de suelo del paisaje (Rös et al. 2012). Las ventanas son especialmente útiles en paisajes con límites ambiguos entre sus unidades y facilitan el análisis de los patrones de diversidad entre paisajes con distinto grado de alteración humana.

Grupo de Estudio

Los escarabajos copronecrófagos de la sub-familia Scarabaeinae (Coleoptera: Scarabaeidae) son insectos cosmopolitas, con aproximadamente 6200 especies y 267 géneros descritos (Tarasov y Génier 2015). La mayoría de los Scarabaeinae se distribuyen en las regiones neotropicales y subtropicales, y su rango altitudinal va desde

el nivel del mar hasta los 3,500 m de altura (Gill 2002). La última revisión taxonómica de Scarabaeinae reporta 64 géneros y 426 especies para México (Morón 2003).

Se conocen principalmente cuatro patrones biogeográficos que explican el origen y distribución de los Scarabaeinae en México: 1) el patrón Paleoamericano: compuesto por especies originadas en Europa y Eurasia, las cuales ingresaron a México desde el norte y se distribuyen ampliamente por el país; 2) el patrón de Dispersión Neártico: Sus especies, originarias del Holoártico, se distribuyen a lo largo de los bosques coníferos de altura de México; 3) el patrón de dispersión en el Altiplano: conformado por escarabajos originados en Suramérica, los cuales se distribuyen a lo largo de las zonas altas de Oaxaca, Chiapas y Guatemala; el patrón Neotropical Típico: compuesto por las especies de origen suramericano distribuidas a lo largo de las regiones tropicales bajas de México (Halffter 1976; Favila 2012).

Los Scarabaeinae adultos consumen principalmente estiércol o carroña, que posteriormente trasladan a cámaras bajo el suelo para la alimentación de sus larvas (Halffter y Matthews 1966). Por sus preferencias alimenticias se les ha clasificado en generalistas, coprófagos o necrófagos (Cambefort y Hanski 1991); y por sus estrategias de nidificación se les ha catalogado en cavadores, rodadores, moradores y cleptoparásitos (Halffter et al. 1982). Los Scarabaeinae proveen importantes servicios al ecosistema, como el reciclado de nutrientes, bioturbación del suelo, dispersión secundaria de semillas, y control biológico de parásitos (Nichols et al. 2008). La intensidad de luz, humedad, temperatura y la disponibilidad de heces condicionan la actividad, diversidad y la abundancia de los escarabajos copronecrófagos; por lo tanto, son altamente susceptibles a cambios micro-climáticos, disturbios del hábitat, y a la extirpación de mamíferos del ecosistema (Nichols et al. 2007; Nichols et al. 2009).

Los Scarabaeinae han sido propuestos como organismos bioindicadores para evaluar la respuesta biológica y los cambios en los patrones de diversidad ante la modificación del paisaje en zonas tropicales (Favila y Halffter 1997; Spector 2006). Estudios previos han demostrado como la pérdida de hábitat y fragmentación del paisaje generan cambios drásticos en la composición y estructura de los escarabajos copronecrófagos (Klein 1989; Quintero y Roslin 2005; Navarrete y Halffter 2008; Díaz et al. 2010; Sánchez-de-Jesús et al. 2016; Cajaiba et al. 2017). Sin embargo, pocas

investigaciones con estos coleópteros han empleado el paisaje como unidad de muestreo (Numa et al. 2009; Rös et al. 2012). Ampliar el análisis hasta la escala de paisaje puede ser un método más eficaz y holístico para detectar las respuestas de las especies al disturbio antropogénico (Gardner et al. 2009); así como para determinar el efecto proporcional de cada elemento del paisaje sobre la diversidad (e.g. Ingham y Samways 1996; Lindenmayer et al. 2003; Price et al. 2009; Rös et al. 2012).

Área de Estudio

Chiapas es uno de los estados con mayor diversidad biológica de México (González-Espinosa et al. 2005). Más de la mitad de su población vive en zonas rurales, lo cual tiene implicaciones directas en el manejo y conservación de la diversidad biológica y recursos naturales (Cortés et al. 2007). Una de las principales actividades económicas y de sustento de la población rural en Chiapas es la agricultura tradicional y la ganadería a mediana y baja escala (Cayuela et al. 2006). Esto promueve paisajes dinámicos y complejos, acelerando el avance de la frontera agrícola a costa de la vegetación nativa (González et al. 2009).

La Reserva de Biosfera Selva El Ocote (REBISO), localizada en el noroeste de Chiapas, es una de las selvas más importante de México por su gran riqueza biológica y cultural (Vásquez et al. 1996; Flamenco-Sandoval et al. 2007). La mayor parte de la población de la REBISO se concentra en aproximadamente 120 localidades, las cuales históricamente se han dedicado a actividades agrícolas tradicionales (Vásquez et al. 1996). La colonización humana, las construcciones sin planeación ambiental, los frecuentes incendios forestales, aunando a la creciente deforestación para actividades ganaderas y agrícolas, han generado un complejo y difuso paisaje formado por un mosaico que incluye selvas, vegetación secundaria, pastizales y tierras de uso agrícola (Vásquez et al. 1996; Gómez y Cruz 2009). La constante alteración del paisaje y la deforestación son una potencial amenaza para la conservación de los recursos y biodiversidad en la REBISO (Flamenco-Sandoval et al. 2007). En la REBISO se han realizado estudios sobre diversidad de mamíferos (Navarrete et al. 1996), plantas (Ramírez-Marcial et al. 2017), aves (Vázquez-Pérez et al. 2009) e insectos (Gómez-Nucamendi et al. 1999). Sin embargo, la interacción entre el paisaje y la diversidad ha

recibido poca atención en la REBISO. De manera que, se desconoce el efecto de los disturbios antropogénicos del paisaje en la distribución de las especies de la región.

Objetivo de la Investigación

El objetivo del presente estudio fue evaluar los patrones de diversidad de los escarabajos copronecrófagos y el efecto del paisaje sobre sus comunidades a través de un gradiente de disturbio en la Selva El Ocote de México. La investigación la abordamos planteando las siguientes preguntas: (1) ¿Cómo se componen las comunidades de escarabajos del estiércol en paisajes con distinta intensidad de alteración? (2) ¿Qué elementos composicionales y estructurales del paisaje tienen mayor efecto sobre la diversidad, abundancia y biomasa de los escarabajos del estiércol? (3) ¿Cómo responde la diversidad beta a la alteración del paisaje, y cuál es su aporte a la diversidad gamma de la Selva El Ocote?

Con base a las preguntas de investigación, definimos los siguientes objetivos específicos:

- Describir la composición de las comunidades de escarabajos del estiércol en paisajes con distinta intensidad de alteración
- Identificar que elementos composicionales y estructurales del paisaje tienen mayor efecto sobre la diversidad, abundancia y biomasa de los escarabajos del estiércol
- Describir la respuesta de la diversidad beta a la alteración del paisaje y su aporte a la diversidad gamma de escarabajos del estiércol en la Selva El Ocote

Esperamos que nuestra investigación contribuya a mejorar la comprensión de como los atributos del paisaje afectan la distribución y diversidad de los escarabajos copronecrófagos. Esta información puede ser de utilidad para diseñar estrategias de conservación en paisajes tropicales complejos bajo distintos estados de alteración.

1 **Artículo sometido para publicación en la revista *Insect Conservation and Diversity***

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3 **Running Title:** Dung beetles response to landscape disturbance

4

5 **Response of dung beetle communities to landscape disturbance in the Selva El**
6 **Ocote, Chiapas**

7

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21 **Abstract** 1. In order to define management strategies, many studies have assessed the
22 effect of anthropogenic disturbances on tropical dung beetles. However, few have
23 transcended beyond the local approach to gain a deeper insight into the complex
24 interactions between the landscape elements and its diversity.

25 2. The diversity patterns of dung beetles and the effect of landscape attributes on their
26 communities in Mexico's Selva El Ocote was analyzed. Eight sampling windows
27 covering three states of landscape alteration were used: intact landscapes, variegated
28 landscapes and relictual landscapes.

29 3. A total of 15,457 specimens belonging to 55 species were collected. The highest
30 diversity was found in variegated landscapes (44 species), followed by relictual
31 landscapes (34) and intact landscapes (32). Landscape heterogeneity and
32 fragmentation were the factors with the greatest effect on local diversity. The area of
33 edges and the percentage of forest in the landscape were the best predictors of beetle
34 abundance and biomass, respectively. Gamma diversity resulted primarily from random
35 species turnover between sites.

36 4. The tropical forest in addition to landscape heterogeneity contributes to an increased
37 local diversity and the presence of large beetles of functional importance, as well as to
38 the stochastic turnover of species between sites. Landscapes under different regimes of
39 disturbance, coupled with the physiographic variability in the study region, led to an
40 increment of beta diversity, which in turn resulted in a very high gamma diversity.

41 Promoting variegated landscapes could be an excellent strategy for the restoration of
42 degraded tropical sites.

43

44 **Keywords:** Diversity patterns, true diversity, conservation, variegated landscapes,
45 fragmentation, Scarabaeinae, Selva El Ocote Reserve, landscape management.

46

47 **Introduction**

48 The anthropogenic changes of the landscape have a profound impact on Earth's
49 biodiversity (Newbold *et al.*, 2015). Its effects range from the loss of native species,
50 homogenization of communities, changes in diversity patterns, and deterioration of
51 ecosystem services (de Castro Solar *et al.*, 2015; Haddad *et al.*, 2015). Given this
52 scenario, it is imperative to understand how the disturbance of the landscape affect the
53 components and distribution of diversity to define effective conservation strategies
54 (Gardner *et al.*, 2009; Socolar *et al.*, 2016). This is particularly relevant in complex
55 tropical landscapes such as Selva El Ocote, one of the most diverse, heterogeneous
56 and altered remnants of tropical forest in Mexico (Flamenco-Sandoval *et al.*, 2007). In
57 Selva El Ocote, the interaction between landscape and diversity has received little
58 attention. Consequently, the effect of anthropogenic disturbances of the landscape on
59 the species communities is unknown.

60 Dung beetles (Scarabidae: Scarabaeinae), are ideal bioindicators to assess the
61 effects of the alteration of landscape on diversity (Favila & Halffter, 1997). Previous
62 studies have shown how habitat loss and landscape fragmentation led to drastic
63 changes in the diversity, abundance and biomass of dung beetles (Klein, 1989; Quintero
64 & Roslin, 2005; Nichols *et al.*, 2007; Navarrete & Halffter, 2008; Díaz *et al.*, 2010;
65 Sánchez-de-Jesús *et al.*, 2016). However, little research on these beetles have used the
66 landscape as a sampling unit (*e.g.* Numa *et al.*, 2009; Rös *et al.*, 2012). Broadening the
67 analysis to the landscape scale could be a more holistic approach to detect the

68 responses of species to anthropogenic disturbance (Gardner *et al.*, 2009), since the
69 overall impact of land uses, vegetation and landscape configuration on diversity is
70 assessed (Halffter & Rös, 2013). In addition, the relative effect of each landscape
71 element on diversity is determined more effectively using a landscape-scale approach
72 (e.g. Cushman & McGarigal, 2003; Lindenmayer *et al.*, 2003; Price *et al.*, 2009; Rös
73 *et al.*, 2012).

74 The studies about the effects of landscape disturbance on diversity have been
75 traditionally based on the theory of island biogeography (MacArthur & Wilson, 1967) or
76 the patch-corridor-matrix model (Forman, 1995), in which landscape units are
77 considered as discrete elements (Fischer & Lindenmayer 2007). However, several
78 authors have pointed out that the fragmentation of the landscape does not only result in
79 isolated patches within an “inhospitable” matrix (Manning *et al.*, 2004; Franklin &
80 Lindenmayer, 2009; Tschardtke *et al.*, 2012). Changes may also be gradual and
81 spatially continuous, and the matrix may display a differential suitability and permeability
82 for species (Fischer & Lindenmayer 2007). Habitat variegation was proposed as an
83 alternative model for landscapes with gradients of vegetation cover or habitat quality
84 (McIntyre & Barret, 1992)

85 A conceptual scheme that integrate both the variegation and fragmentation model
86 to study the effects of anthropogenic activities on the landscape was developed by
87 McIntyre & Hobbs. These authors divide the landscape into four categories, according to
88 the percent loss of the original vegetation and the intensity of habitat transformation: 1)
89 intact landscape (>90% of the original vegetation), which consists of sites with little or no
90 modification; 2) variegated landscape (60-90%), which has been subjected to moderate
91 alterations, with gradual or abrupt limits between its units; 3) fragmented landscape (10-

92 60%), which displays a high degree of alteration; 4) relictual landscape (<10%),
93 consisting of sites with an extreme degree of modification. Based on this landscape
94 scheme, Halffter & Rös (2013) propose the study of biodiversity through the geographic
95 location of windows as sampling units. Windows are sites with an identical surface area,
96 located in a semi-random pattern in order to maximize the representativeness of the
97 plant heterogeneity and land uses of the landscape.

98 The aim of this study was to evaluate the diversity patterns of dung beetles, and
99 the effect of landscape attributes on their communities, through a landscape-scale
100 disturbance gradient in Selva El Ocote, Mexico. The research addressed the following
101 questions: (1) What is the composition of dung beetle communities in landscapes with
102 different intensity of alteration? (2) What compositional and structural landscape
103 attributes have a greater effect on dung beetle diversity, abundance and biomass? (3)
104 How does beta diversity respond to landscape disturbance, and what is its contribution
105 to the gamma diversity of dung beetles in Selva El Ocote? Our research work aims to
106 contribute to a better understanding of how disturbances affect the distribution, diversity
107 and composition of dung beetles at a landscape-scale. This information may be useful in
108 the design of conservation strategies in complex tropical landscapes under different
109 states of alteration.

110

111 **Materials and Methods**

112 **Area of Study**

113 The study was carried out in Selva El Ocote Biosphere Reserve (REBISO), located in
114 the northwestern region of the state of Chiapas, between the municipalities of
115 Ocozocoautla de Espinosa and Cintalapa (16°45'42" - 17° 09' 00" North and 93° 54' 19"

116 - 93° 21' 20" West, Fig. 1). Geologically, the area comprises mostly dolomites and
117 limestone rocks, with dominance of water-soluble sedimentary rocks. The flow and
118 acidification of water have resulted in folded and highly fractured karst soils (Domenici,
119 2016). The predominant climate types are hot and humid (Am type) and warm-subhumid
120 (Am(f) type), with heavy rainfall throughout the year and a mean annual temperature of
121 22 °C (SEMARNAT/CONANP, 2001). The REBISO currently displays a high plant
122 heterogeneity, product of its complex geological and climatic structure (Flamenco-
123 Sandoval *et al.*, 2007). The predominant vegetation is evergreen tropical forest, with the
124 partial presence of deciduous forest (Ramírez-Marcial *et al.*, In press). The majority of
125 human populations that inhabit REBISO are concentrated in approximately 120
126 localities, which historically have been dedicated to traditional agriculture (Vásquez
127 *et al.*, 1996). The frequent forest fires, added to the growing deforestation for livestock
128 and agricultural activities, have all led to a complex and diffuse landscape that
129 comprises a mosaic including tropical forests, secondary vegetation (known locally as
130 “acahuales”), pasture land and agricultural crops (Vásquez *et al.*, 1996;
131 SEMARNAT/CONANP, 2001; Flamenco-Sandoval *et al.*, 2007).

132

133 **Sampling Design**

134 The REBISO cartography was generated by the supervised classification method with
135 QGIS v2.12.3 (QGIS Development Team, 2016), using a SPOT6 2014 multispectral
136 image that included the study area. The classification categories used were evergreen
137 tropical forest, secondary vegetation, areas dedicated to agriculture and cattle raising,
138 water bodies, clouds and human settlements. Based on the classification scheme of
139 McIntyre & Hobbs (1999), eight sampling windows were identified and classified into

140 three landscape alteration scenarios: intact landscapes, two windows; variegated
141 landscapes, three windows; relictual landscapes, three windows (Fig. 1, Table 1). As
142 sampling units, windows are especially useful in landscapes with ambiguous boundaries
143 between different vegetation (Halffter & Rös, 2013).

144 Each window comprised 1 km² (80 ha), assuming that this area is suitable for
145 sampling by incorporating a large part of landscape variability (Sánchez-de-Jesús *et al.*,
146 2016). Also, the average flight distance travelled by various tropical dung beetle
147 specimens can be of 400 m in less than 15 days (da Silva & Hernández, 2015).
148 Accordingly, sampling windows were separated 2 km apart, hence ensuring the capture
149 of species that live in the area covered by the window, and reducing the spatial
150 correlation between sampling units.

151 To characterize the landscape attributes in each window, the proportion of
152 evergreen tropical forest, secondary vegetation and agricultural land (i.e. crops and
153 pasture) was estimated (Table 2). Also, the compositional diversity of the landscape,
154 which indicates the heterogeneity and proportional evenness between vegetation types
155 in each window, was also calculated. The spatial configuration of the landscape
156 elements was evaluated by calculating: a) the contrast-weighted edge density, which
157 weighs edges based on contrast and length in the landscape; b) the area-weighted
158 mean shape index, which estimates the geometric complexity of patches by weighting
159 the relative size of each in the landscape (Leitão *et al.*, 2006); c) the splitting index,
160 which quantifies the number of patches present in the landscape, hence being a
161 measure of fragmentation (Sánchez-de-Jesús *et al.*, 2016). The metrics of landscape
162 composition and spatial configuration were obtained with the program FRAGSTAT
163 v4.2.1 (McGarigal *et al.* 2012). For further details on indexes and equations, refer to

164 Leitão *et al.*, (2006) and McGarigal *et al.*, (2012).

165 The sampling was conducted in two periods in 2016, the first during the dry
166 season (March to May) and the second during the rainy season (July - August).
167 Proportional sampling is more sensitive to variations in the landscape and changes in
168 beta diversity (Schoereder *et al.*, 2004). Therefore, seven subsets of six pitfall traps
169 were placed in each window (42 traps/window), covering proportionally the vegetation
170 composition within individual windows. One subset of traps was placed in the center of
171 the window, and two on the top and bottom of the window; the latter were separated by
172 360 m from the center. The last four subsets of traps were distributed in the periphery of
173 the center, separated by 250 m from the center (Fig. 1). The traps of each subset were
174 placed following a rectangular layout. The separation between traps was 50 m to ensure
175 the maximum independence between them (Larsen & Forsyth, 2005). Fisher's exact test
176 was used, with a 95% confidence, to confirm that the distribution of the 42 traps would
177 not deviate significantly from the theoretical expected proportion, i.e., under the
178 assumption that the distribution of the 42 traps was proportionally accurate relative to
179 the plant composition in each window (Table 3).

180 Each pitfall trap consisted of a 1 L plastic container buried at ground level.
181 Containers were filled with 300 ml of ethylene glycol as a preservative liquid. Two types
182 of bait were used: the first consisted of 70 g of pig feces combined with human feces in
183 a 80:20 ratio; the second consisted of 70 g of squid. Three traps per type of bait were
184 placed for each subset of traps. Plastic dishes were used to protect baits from
185 precipitation and desiccation due to sun radiation. The traps remained active for 48
186 hours, after which the beetles captured were preserved in 80% alcohol for identification
187 in the laboratory.

188 Certain modifications were made over the course of the sampling period. In the
189 case of intact landscape windows, mobility within these was very limited due to the
190 steep slopes. Therefore, it was decided to carry out the sampling along 2.1 km transects
191 (Fig. 1). In Armando Zebadua (RW3, Table 2), due to the unsafe environment generated
192 by conflicts between farmers, the sampling design was adjusted to include only sites
193 where permission was granted (Fig 1). Finally, the rectangular design of some subsets
194 of traps was modified due to the impossibility of access to some regions. In all cases,
195 however, the proportional sampling and the analysis of landscape to 80 ha were
196 maintained (Table 3).

197 Ten randomly selected specimens of each species were oven-dried at 70 °C for
198 72 hours. Subsequently, each specimen was weighed with an analytical balance
199 (Explorer Pro 0.1 mg readability) to obtain the average dry biomass by species; from
200 these values, the biomass of each species per window was obtained by multiplying
201 average biomass by species abundance for each window. The specimens collected
202 were deposited in the entomological collection at *Colegio de La Frontera Sur, San*
203 *Cristóbal de las Casas*, and at *Instituto de Ecología, A.C.*, Xalapa.

204

205 **Estimate of local vegetation variables**

206 At each sampling point, the canopy coverage was recorded using a convex
207 densiometer. Tree density and average basal area were estimated for each window
208 using the nearest neighbor method (Krebs, 1999) (Table 2). From each trap as a
209 random point, the distance to the nearest tree and its diameter at breast height (dbh>10
210 cm) were measured with a diameter tape; the process was repeated with the next
211 nearest tree. The basal area was calculated based on tree diameter.

212

213 **Data Analysis**

214 The completeness of sampling in each window was determined using the coverage
215 estimator by Chao & Jost (2012). This richness estimator is more robust, as it is based
216 on proportions rather than gross abundance values. It also maintains the mathematical
217 principle of replicability, which is essential for making comparisons of diversity between
218 multiple sites (Chao & Jost, 2012). Alpha diversity was determined based on Hill's 0D , 1D
219 and 2D numbers, which give the effective number of species (Jost, 2006). 0D is
220 equivalent to species richness, which is insensitive to abundance (Jost, 2006); 1D is the
221 exponent of the Shannon index and gives the abundant species in a community (Jost,
222 2006); 2D corresponds to the inverse of the Simpson index and gives the dominant
223 species in a community (Jost, 2006).

224 Interpolation and extrapolation curves for Hill's numbers were obtained for each
225 window. Both the coverage estimator and the interpolation-extrapolation curves were
226 calculated with the package iNEXT v2.0.11 (Hsieh *et al.*, 2016). Besides, rank
227 abundance curves were constructed to explore the proportional contribution and
228 homogeneity among the species per window. The abundance of beetles was
229 transformed to base 10 logarithm.

230 Generalized linear models were used to assess the effect of landscape metrics
231 (Table 2, Table S1) and local vegetation structure on dung beetle diversity (0D , 1D y 2D),
232 abundance and biomass (Table 4). Diversity was standardized to the lowest coverage
233 value among samples (Chao *et al.*, 2014). The distribution of the error was selected
234 based on the type of response variable, namely Poisson for count or frequency data, or
235 Gaussian for continuous data, after data normality was confirmed with the Shapiro-Wilk

236 test. Data were log-transformed as needed, and collinearity between independent
237 variables was evaluated. In each case, the minimum model was obtained with the
238 method of progressive elimination method, using deviance tests and the Akaike
239 Information Criterion (AIC) (Crawley, 2013). In order to avoid biases, only abundance
240 and biomass data for the rainy season, when the Scarabaeinae are most active
241 (Halffter, 1991), were used.

242 Beta diversity was analyzed under three different approaches. 1) True beta
243 diversity, or the effective number of communities in the landscape, which was
244 determined by the multiplicative partitioning method (Jost, 2007). Only the 0D and 1D
245 true beta diversity were calculated, since the partitioning of beta diversity above 1D
246 requires that communities have equitable weights (Jost, 2007). 2) Jaccard's dissimilarity
247 index was used with the package Betapart v1.3 (Baselga & Orme, 2012), to determine if
248 the ecological differentiation between communities resulted from species turnover or
249 nesting. 3) Null models were used to determine if beta diversity patterns resulted from
250 random changes in alpha and gamma diversity or from underlying deterministic
251 mechanisms in communities or the landscape (Chase *et al.*, 2011). Null models were
252 obtained using the algorithm by Chase *et al.*, (2011) for the beta Raup-Crick index (β_{R-C}
253 $_C$), based on 9999 randomizations. Chase's β_{R-C} compares the beta diversity observed
254 versus the null expectation of beta diversity, standardizing the results to a range from -1
255 to 1. Two communities can be significantly more different than expected by chance (0.95
256 $< \beta_{R-C} < 1$), more similar than expected by chance ($-0.95 > \beta_{R-C} > -1$), or be random
257 species assemblages ($-0.95 < \beta_{R-C} < 0.95$). The statistical analysis and the models were
258 performed in R v.3.3.1 (R Development Core Team, 2015).

259

260 **Results**

261 A total of 15,457 specimens belonging to 55 species were collected (Table S2). The
262 sampling coverage was 99% for all windows (Table 4). The most abundant species
263 throughout the sampling was *Deltochilum mexicanum* Burmeister (15%), followed by
264 *Onthophagus corrosus* Bates (13%), *Eurysternus maya* Génier (12%), *Canthon*
265 *vazquezae* (Martinez, Halffter & Halffter) (11%), *Onthophagus batesi* Howden &
266 Cartwright (8%) and *Ontherus mexicanus* Harold (7%). Sites in variegated landscapes
267 (VL) attained the highest richness of dung beetles, with 42 species in total, as well as
268 28, 37 and 35 species collected in VW1, VW2 and VW3, respectively (Table 4). *C.*
269 *vazquezae* was the dominant species in variegated landscapes, followed by *E. maya*,
270 *Eurysternus angustulus* Harold, *Eurysternus caribaeus* (Herbst), *Onthophagus incensus*
271 Say, *D. mexicanum* and *O. corrosus* (Fig. 2).

272 In intact landscape (IL), a total of 32 species were collected, with 22 species in
273 IW1 and 24 species in IW2 (Table 4). The dominant beetle species were *D. mexicanum*,
274 *C. vazquezae*, *E. maya*, *O. mexicanus* and *Deltochilum pseudoparilae* Paulian (Fig. 2).
275 On the other hand, a total of 35 species were recorded in relictual landscapes (RL). The
276 main species were *O. batesi*, *O. corrosus* and *Copris lugubris* Boheman in RW1 and
277 RW2, with 23 and 24 species collected, respectively. Of the 26 species collected in
278 RW3, *O. corrosus* and *Onthophagus landolti* were the dominant beetle species.

279 The species richness dropped significantly in IL and RL sites relative to VL sites
280 ($F_{2,5} = 8,403$, $p = 0.02$). However, no differences between the richness in IV and RV
281 sites were found ($P = 0.8$). The average biomass in IL was significantly higher than the
282 biomass in VL and RL ($H = 93.2$; $P < 0.0005$). Average abundance did not differ
283 significantly between any sampling sites ($H = 13.42$; $P = 0.056$).

284 The three accumulation curves for 0D in VL reached their asymptote through the
285 extrapolation method. In contrast, IL and RL curves had a steeper slope (Fig. 3a). All the
286 accumulation curves reached the species asymptote for the diversity estimators 1D and
287 2D . The windows with the highest diversity were VW2 and VW3 (Fig. 3b, c).

288 Our models indicated that 0D diversity was positively correlated with the Shannon
289 index of landscape composition, while the splitting index was positively correlated with
290 1D and 2D . Beetle abundance was negatively associated with the contrast and density
291 between edges, and biomass increased along with the percentage of forest in each
292 window (Table 5). No significant effects were detected from any combination of factors.
293 Similarly, no effect of the local vegetation (*i.e.* tree density and basal area) on the
294 response variables was detected.

295 The value of $\beta {}^0D$ was 2.01 (γ 55, α 27.37), and $\beta {}^1D$ was 2.23 (γ 15.84, α 7.09),
296 indicating the presence of two different communities in REBISO. The dissimilarity
297 dendrogram is consistent with the presence of the two effective communities, one
298 including the three RL sites and the other including IL and VL sites (Fig. 4a). The
299 species turnover was 0.71 (Table S3), which accounted for 91.6% of the overall
300 dissimilarity (0.78). Less than 7% (0.06) of the dissimilarity between communities
301 derived from nesting processes (Fig. 4b). The values of β_{R-C} between IW1 and the three
302 RL sites indicated that the differences observed exceeded the beta diversity null
303 expectation (Table 6). The rest of paired comparisons suggest that the differences or
304 similarities of β_{R-C} between windows are mainly the result of random processes (Table
305 6).

306

307 **Discussion**

308 **α diversity patterns**

309 The species richness of dung beetles in variegated landscapes was higher versus intact
310 and relictual landscapes. Similar results have been found in mountain cloud forests of
311 Sierra Norte de Puebla (Rös *et al.*, 2012). Heterogeneous landscapes have a greater
312 variety of micro-habitats, hence increasing the number and diversity of available niches,
313 which can sustain a high number of species (Ritchie & Olf, 1999; Tscharrntke *et al.*,
314 2012). This explains why beetle richness was significantly higher in the variegated
315 landscapes of our study. Being more heterogeneous in terms of vegetation composition
316 and land use, the variegated landscapes possibly favoured the conditions needed for
317 the establishment of species with different habitat requirements. For example, native
318 species of forest habitats such as *C. vazquezae*, *E. caribaeus*, *Onthophagus incensus*
319 Say, and *D. mexicanum*, as well as species typically inhabiting edges and open areas
320 such as *E. amplicollis angustulus*, *Dichotomius* Harold, *Canthon cyanellus* LeConte and
321 *Dichotomius annae* Kohlmann & Solis.

322 The total species richness in intact landscapes was similar to the richness
323 observed in other non-fragmented tropical forests of Mexico and Guatemala (Avendaño-
324 Mendoza *et al.*, 2005; Barragán *et al.*, 2011; Sánchez-de-Jesús *et al.*, 2016). However,
325 relictual sites showed a higher number of species relative to intact sites. This difference
326 is likely due to the extra inflow of species from forest remnants still present in relictual
327 landscapes. In these remnants, some beetles typical of tropical forest habitats were
328 collected, including *Canthon femoralis* Chevrolat, *C. vasquezae* and *Dichotomius Satan*
329 (Harold).

330 Of the specimens collected in relictual sites 1 and 2, 85% corresponded to *O.*

331 *batesi*, *O. corrosus*, *Digitonthophagus gazella* (Fabricius, 1787), *O. landolti*, *C. lugubris*
332 and *Canthon indigaceus* LeConte. On the other hand, more than 50% of individuals
333 collected in relictual site 3 were species of *O. corrosus*. Landscapes dominated by
334 pastureland and extensive monocultures, such as the relictual landscapes of our study,
335 foster the loss of species susceptible to disturbance (Filgueiras *et al.*, 2016). Hence, our
336 data suggest that beetle communities in relictual landscapes are currently undergoing a
337 biotic homogenization process. Homogenization increases the vulnerability of
338 communities to disturbance, facilitates the entry of invasive species and jeopardizes the
339 functioning and stability of the ecosystem (Olden *et al.*, 2004).

340 Landscape fragmentation showed a positive correlation with the number of
341 abundant species (¹D) and dominant species (²D). Given that variegated landscapes
342 obtained the highest fragmentation values, these displayed the greatest number of
343 dominant and abundant species. Fragmentation may promote coexistence mechanisms
344 between the species by increasing the complementation and/or supplementation of
345 resources in heterogeneous landscapes (Fahrig *et al.*, 2011; Tschardtke *et al.*, 2012).
346 Since variegated landscapes in our study are more heterogeneous and fragmented,
347 these are likely to have high levels of resource complementation and/or
348 supplementation. Both features reduce the probability of a single species monopolizing
349 the resources, since these are scattered (*i.e.* fragmented) across multiple locations. As a
350 result, the diversity and evenness among species increases (Hillebrand *et al.*, 2008). In
351 this study, twice the number of abundant and dominant species were collected in the
352 variegated landscapes relative to the other landscapes. Also, the evenness between
353 species was higher in variegated landscapes, as indicated by the slopes of rank-
354 abundance curves. Similar to our results, Kadiri *et al.*, (1997) showed that diversity and

355 evenness among dung beetle species increase in sites with greater heterogeneity of
356 resources.

357

358 **Dung beetles abundance and biomass**

359 In this study, dung beetles showed a lower abundance of individuals in landscapes with
360 higher edge density. This density was favored by the land-cover heterogeneity and the
361 greater fragmentation in variegated landscapes. Thus, the relative abundance of beetles
362 was lower in variegated landscapes. The increase of edges in the landscape affects the
363 internal microclimatic conditions of habitats (Chen *et al.*, 1999). Most dung beetles are
364 highly susceptible to changes in the microclimate of the habitat (Halffter *et al.*, 1992).
365 Also, dung beetles have been shown to experience population declines under sub-
366 optimal climatic conditions (Roslin *et al.*, 2009). For example, in the variegated
367 landscapes studied here, the abundance of tropical forest species such as *C.*
368 *vazquezae* decreased by 39% from forest to secondary vegetation; *E. maya*, 22%; and
369 *D. mexicanum*, 7.1%; whereas the abundance of these species increased considerably
370 in the non-fragmented forests corresponding to intact landscapes. Our results suggest
371 that the increase of edges in variegated landscapes inhibits the population growth of
372 some dung beetle species. Further studies are required to assess in detail the effect of
373 edges on species in variegated landscapes.

374 Biomass is the most relevant functional feature in dung beetles, as it is related to
375 the dung removal and burial efficiency (Nervo *et al.*, 2014). The results of this study
376 indicate that the biomass of beetle communities from intact landscapes was significantly
377 higher. The loss of large species affects the efficiency of feces processing, soil
378 bioturbation, as well as forest regeneration through secondary seed dispersal (Nichols

379 *et al.*, 2008; Braga *et al.*, 2013). Consequently, intact landscapes are likely the sites with
380 the highest functional productivity of our study, a finding that underlines the importance
381 of protecting them.

382 In agreement with Sánchez *et al.*, (2016), in this study the increase in the
383 biomass of beetle communities is positively related to the percentage of forest in the
384 landscape. This is likely due to the fact that forests represent high-quality habitats for
385 tropical dung beetles (Halffter, 1991). For example, faeces keep the moisture,
386 attractiveness and nutritional quality for a longer period of time in tropical forests
387 (Horgan, 2005). In addition, the percentage of forest in the landscape is linked to the
388 presence and richness of large and medium-sized mammals — the main suppliers of
389 resources for large dung beetles (Nichols *et al.*, 2009; Garmendia *et al.*, 2013). In this
390 way, forests are an evident protection target in the region, and its increase in the
391 landscape may promote the presence of large and functionally important dung beetles.

392

393 **β diversity patterns**

394 The partition of diversity reveals two effective communities for both the typical species
395 (0D) and the abundant species (1D) in the region. One community was formed by the
396 subset of sites located in relictual landscapes and the other by tropical forest landscapes
397 (*i.e.* variegated and intact landscapes). The partition of diversity indicates that the
398 severe disturbance that characterizes relictual landscapes has resulted in a community
399 differing in composition from those of tropical forest landscapes. On the other hand, the
400 findings that beetles in variegated and intact landscapes are a single effective
401 community suggests that landscape variegation does not have a significantly negative
402 effect on the diversity of Scarabaeinae.

403 The species turnover was the main component of beta diversity across our study
404 area. There were 3 to 27 species not shared between localities, with each site
405 contributing 2 to 3 unique species to gamma diversity. Consequently, our results
406 suggest that diversity in the Selva El Ocote is not distributed homogeneously. The high
407 complementarity among communities possibly reflects the variety of landscapes under
408 the different regimes of disturbance, structural vegetation complexity and landforms in
409 the region. These features increase the divergence between communities and beta
410 diversity (de Castro Solar *et al.*, 2015). Variegated landscapes were particularly
411 important for beta and gamma diversity maintenance in Selva El Ocote. Their high local
412 diversity increased the species turnover rate in the region, compensating for the low
413 richness of intact sites and mitigating the impact of relictual landscapes on regional
414 diversity. It should be noted that this is the tropical landscape with the highest gamma
415 diversity of Scarabaeinae (55 species) recorded in Mexico. In similar ecosystems, 49
416 species have been reported for the Lacandona tropical forest (Navarrete & Halffter,
417 2008) and 44 species in Los Tuxtlas (Favila, 2005).

418 Null models showed that the similarity between communities in landscapes within
419 the same alteration category was higher than expected by chance. That is, the
420 composition of these communities reflected the extent of alteration of the landscapes
421 regardless of their locality. On the other hand, the intense alteration of the landscape in
422 relictual sites likely caused a non-stochastic divergence relative to the forest
423 communities of intact site 1. An area devoid of tree cover, as in relictual landscapes,
424 represents a barrier to the mobility and survival of forest dung beetles (Spector &
425 Ayzama, 2003). In addition, in relictual landscapes the availability of resources is
426 represented mainly by bovine cattle feces that have undergone heavy insolation and

427 desiccation. So only generalist beetles survive in these conditions (Horgan, 2007).

428 In general, the species turnover between variegated landscapes with the relictual
429 and intact landscapes was not significantly different from the expected outcome of
430 stochastic assemblage processes. The randomness in beta diversity may increase as a
431 result of the constant flow of species between landscapes with high porosity (Gravel
432 *et al.*, 2006; Chase, 2010). Therefore, it is feasible that the landscape at REBISO keeps
433 a sufficient plant cover and diversity of resources to maintain the flow of dung beetles
434 between sites. This is evidenced by the high abundance of *D. mexicanum* in intact and
435 variegated landscapes, considering that this species is highly susceptible to the loss of
436 vegetation cover (Rös *et al.*, 2012). On the other hand, variegated landscapes with
437 secondary vegetation have shown to facilitate the mobility of species among localities,
438 besides acting as reservoirs of dung beetles that are susceptible to disturbance
439 (Quintero & Roslin, 2005; Navarrete & Halffter, 2008; Costa *et al.*, 2017). In this sense,
440 our results highlight the importance of variegated landscapes to maintain the flow of
441 species across the region. Therefore, coinciding with Rös *et al.* (2012), the conversion of
442 highly altered landscapes to a variegated state should be a goal in the management of
443 tropical reserves, since it leads to an increased connectivity and regional diversity of the
444 landscape.

445 The turnover of species between intact site 2 and the relictual sites was no
446 different from the null expectation of beta diversity. This suggests that a flow of species
447 between both communities may still occur. For example, species typical of agricultural
448 ecosystems such as *C. lugubris* and *O. batesi* were recorded 800 m away from the edge
449 of intact site 2. Unlike the intact site 1 in Sierra Monterrey, the intact site 2 in Sierra
450 Veinte Casas lacks a buffer zone between the nearest agricultural land and the reserve.

451 Edges lacking any sort of buffer zone cause negative effects to the interior of tropical
452 forests, by reducing the barrier of mature vegetation for invasive species (Didham *et al.*,
453 1998; Cadenasso & Pickett, 2001). The negative effects of edges may be more evident
454 in subsequent years. Therefore, the impact of edges on the beetle communities in intact
455 site 2 should be monitored.

456 In summary, our study evidences the importance of the forest, landscape
457 heterogeneity and permeable matrices for buffering the anthropogenic disturbance of
458 the landscape. These elements favor the presence of large beetles that play a key
459 functional role, the dynamic flow of species between localities, and prevent the reduction
460 of diversity that results from the homogenization of communities. In this respect, caution
461 should be exercised regarding the increase of open areas and the loss of vegetation
462 cover. This research supports the significant biological value of Selva El Ocote and
463 highlights the need to maximize its protection based on the complementarity between
464 localities. Promoting the variegation of landscapes could be an excellent strategy for the
465 recovery of degraded sites, as well as for the conservation of regional diversity. Future
466 studies should focus on assessing the ecological functionality and dispersal
467 mechanisms of species across the different categories of landscape alteration.

468

469 **Acknowledgments**

470 To Emilio Rabasa, Nuevo San Juan Chamula, San Joaquin and Tierra Nueva land owners for
471 allowing us to carry out our work in their communities; to REBISO/CONANP for the logistical
472 support provided. To Maria Guadalupe Hernandez Lopez and Erick Hernandez Baltazar for their
473 support during data collection. Thanks also to CONACYT and the Heinrich Böll Stiftung
474 Foundation for the grants awarded to José Daniel Rivera to pursue the master's degree at

475 Colegio de la Frontera Sur, San Cristóbal de las Casas, Chiapas, Mexico. To Paula Enríquez,
476 Alfonso González y Guillermo Ibarra for their valuable comments and suggestions. This
477 research was funded by the CONACYT Project "Biological and social vulnerability to climate
478 change in Selva El Ocote Biosphere Reserve" (PDCPN2013-01-214654). María Elena Sánchez-
479 Salazar translated the manuscript into English.

480

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711

712 **Tables**713 **Table 1.** Landscape alteration category description in our study area

Intact Landscapes (IL):	The vegetation characterized by a dense canopy, belongs to a mature successional state. The most common tree species in the area are <i>Pseudolmedia spuria</i> , <i>Louteridium donnell-smithii</i> , <i>Manilkara sapota</i> , <i>Swietenia macrophylla</i> and <i>Quararibea funebris</i> (SEMARNAT/CONANP, 2001; Ramírez-Marcial <i>et al.</i> , In press).
Variegated Landscapes (VL)	The landscape is characterized by a heterogeneous mosaic of tropical forest, secondary vegetation, seasonal crops, and pastures. The largest proportion of tree species present in the variegated sites belong to an intermediate successional stage, dominated by <i>Heliocarpus appendiculatus</i> and <i>Eugenia acapulcensis</i> (SEMARNAT/CONANP, 2001; Ramírez-Marcial <i>et al.</i> , in press).
Relictual Landscapes (RL)	Most of the landscape is devoid of trees. The matrix is composed mainly of pasture and agricultural fields, along with small remnants of tropical forest and secondary vegetation distributed across the landscape.

714

715 **Table 2.** Landscape cover type composition and vegetation parameters for each
 716 sampled window.

Landscape window code/locality ^a	Landscape cover type composition (%) ^b			mBA (± SE) ^c	VD ^d	mCC% (± SE) ^e
	F	SV	P & A			
IW1/SMR	90.38	9.61	0	853.86 (101.66)	53267.66	91.46 (0.46)
IW2/SVC	90.38	9.61	0	1235.33 (329.76)	50343.50	89.22 (1.05)
VW1/NSJC	37.23	52.6	10.08	800.37 (203.45)	13653.67	62.64 (5.33)
VW2/NSJC	43.06	48.19	8.73	495.44 (74.51)	25056.80	54.91 (4.85)
VW3/SJ	35.27	59.24	5.48	282.08 (26.25)	83234.29	57.67 (5.53)
RW1/TN	5.77	10.71	83.50	670.96 (97.07)	7736.70	14.50 (3.78)
RW2/TN	0	10.54	89.45	965.71 (149.53)	5093.48	11.07 (3.38)
RW3/AZ	1.91	45.31	52.76	1204.26 (184.67)	4532.35	13.05 (1.04)

717 ^aLandscape window code/locality: IW: Intact Window; VW: Variegated Window; RW: Relict Window; SMR:
 718 Sierra Monterrey; SVC: Sierra Veinte Casas; NSJC: Nuevo San Juan Chamula; SJ: San Joaquín; TN:
 719 Tierra Nueva; AZ: Armando Zebadua

720 ^bLandscape cover type composition (%): F: Forest; SV: Secondary vegetation; P&A: Pasture and
 721 agriculture

722 ^cmBA: Mean Basal Area (m²)

723 ^dVD: Vegetation Density (tres/ha)

724 ^emCC: mean canopy cover (%)

725 **Table 3.** Exact Fisher test comparing between the theoretical numbers of traps (left/),
 726 under the supposition that the sampling was proportionally exact to the landscape
 727 composition in each window, and the actual number of traps placed (/right).

Landscape composition	Windows							
	IW1	IW2	VW1	VW2	VW3	VRW1	RW2	RW3
Forest	38/37	38/36	16/19	18/17	15/16	2/1		1/1
Secondary Vegetation	4/5	4/6	22/19	20/18	25/18	5/7	4/3	19/16
Pasture & Agriculture			4/4	4/7	2/8	35/34	38/39	22/25
P. Value-	0.67	0.53	0.89	0.68	0.09	0.81	0.99	0.82

728

729 **Table 4.** Dung beetles sample coverage, diversity, abundance and biomass per
 730 sampling window

Window	SC	⁰ D	¹ D	² D	Mean	Mean
					abundance/trap (± SE)	biomass/trap (± SE)
IW1	0.998	22	5.36	4.48	27.6 (4.68)	7.73 (0.98)
IW2	0.997	24	4.97	3.91	25.2 (4.75)	6.79 (0.92)
VW1	0.996	28	8.69	5.79	12.42 (2.51)	1.45 (0.27)
VW2	0.995	37	16.4	10.7	9.28 (2.51)	1.64 (0.24)
VW3	0.999	35	17.5	12.3	17.91 (1.74)	3.39 (0.39)
RW1	0.996	23	6.56	4.35	8.34 (3.23)	0.82 (0.13)
RW2	0.998	24	7.61	5.47	25.96 (6.18)	1.72 (0.24)
RW3	0.996	26	5.49	3.01	17.08 (7.01)	2.06 (0.37)

731 ^a SC: Sample Coverage

732

733 **Table 5.** Minimum general lineal models results

Explanatory Variables		Estimate (±SE)	DF	P	d ² /r ^{2,e}	AIC	ΔAIC ^f
⁰ D	LDI ^a	1.08 (0.29)	6	0.0001	0.82	46.4	7.55
¹ D	SI ^b	0.23 (0.05)	6	<0.0001	0.87	37.1	8.75
² D	SI	0.23 (0.06)	6	0.001	0.84	34.1	7.02
Abundance	ECWD ^c	-0.02 (0.002)	6	0.001	0.84	2.4	2.25
Biomass	FC (%) ^d	0.02 (0.004)	6	0.009	0.68	14.1	2.29

734 ^a Landscape Diversity Index

735 ^b Splitting Index

736 ^c Edge Contrast Weighted Density

737 ^d Forest Cover

738 ^e d²: amount of deviance accounted for Poisson regressions; r²: amount of variance accounted for linear
739 regressions.

740 ^f AIC difference between the complete and minimum model

741 **Table 6.** β Raup Crick pairwise comparisons

β Raup Crick	IW1	IW2	VW1	VW2	VW3	RW1	RW2
IW2	-0.8						
VW1	-0.95[†]	-0.93					
VW2	0.17	-0.08	-0.95[†]				
VW3	0.25	-0.44	-0.99[†]	-1[†]			
RW1	1[°]	0.92	0.76	0.79	-0.32		
RW2	0.99[°]	0.64	-0.52	0.37	-0.76	-0.99[†]	
RW3	0.99[°]	0.86	-0.46	-0.29	-0.97[†]	-0.96[†]	-1[†]

742 † Significantly more similar than expected by chance

743 ° Significantly more different than expected by chance

744 **Figures**

745 **Figure Legends**

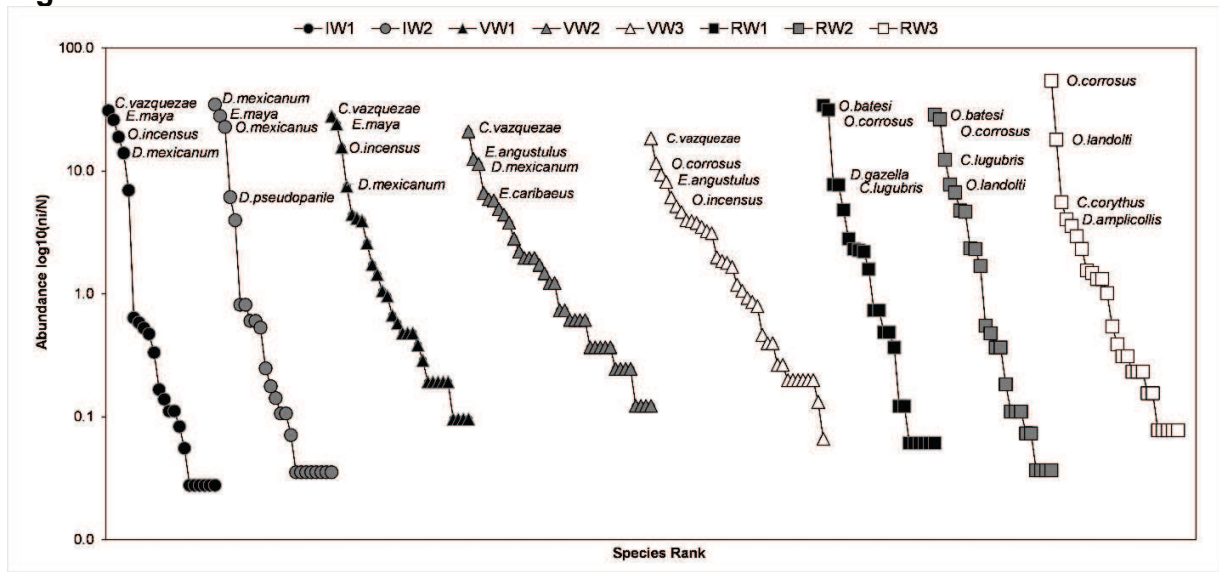
746 **Fig. 1.** Study area and location of the sampling windows. The colors inside the bars
747 indicate the proportion of area covered by forest, secondary vegetation and agricultural
748 land in each sampling window.

749 **Fig. 2.** Rank abundance curves (converted to \log_{10}) per sampled window

750 **Fig. 3.** Interpolation – extrapolation curves based on Hill Numbers; solid lines:
751 interpolation, dashed lines: extrapolation; species richness (a); Shannon diversity (b);
752 Simpson diversity (c)

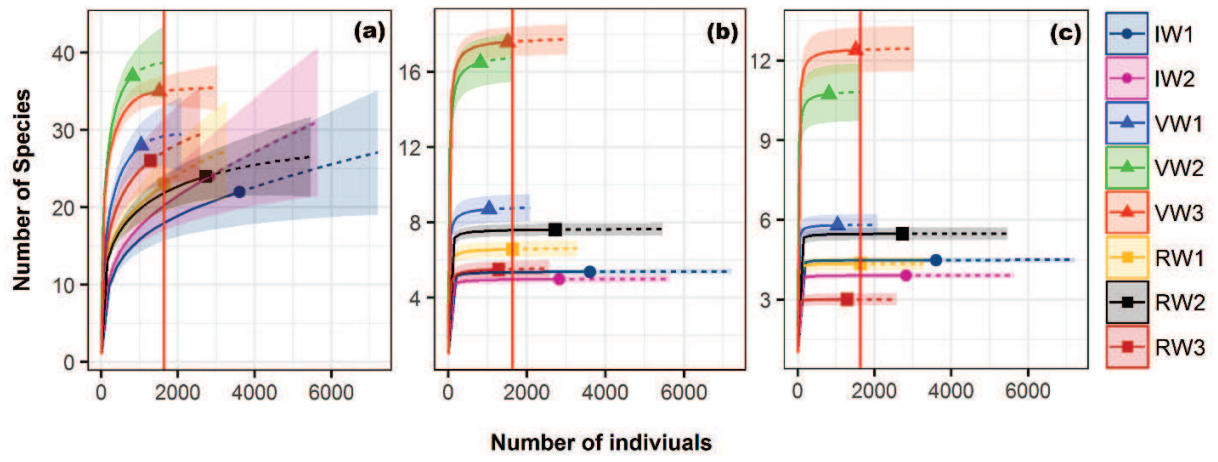
753 **Fig. 4.** Jaccard dissimilarity density graph (a); Jaccard cluster dendrogram (b). β Jacc:
754 Beta Jaccard, β JNess: Beta Jaccard Nestedness; β Jturn: Beta Jaccard Turnover

757 Fig 2.



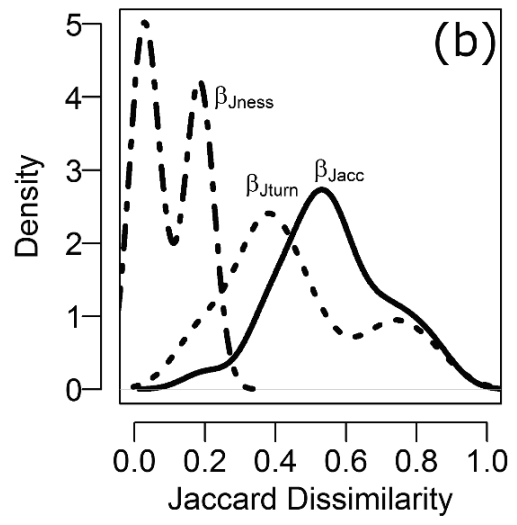
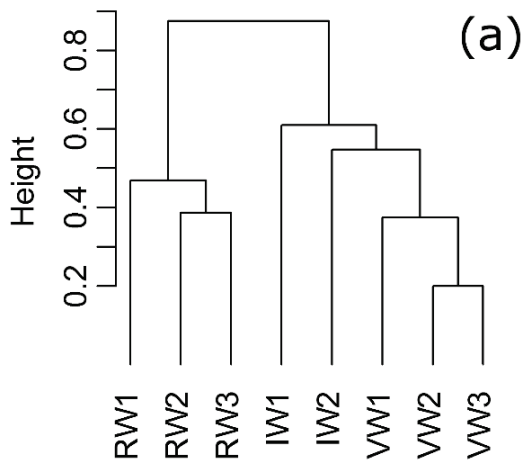
758

759 **Fig. 3**



760

761 **Fig. 4.**



762

Supplementary Material

Supplementary Table 1. Landscape variables per sampling Windows

	S^a	Sh-DI^b	CWED^c	Shape AW^d
IW1	1.2216	0.3166	22.4986	3.0171
IW2	2.4492	0.3215	19.6386	1.9866
VW1	3.4525	0.9369	94.2346	3.7185
VW2	6.1462	0.9276	88.5485	2.8047
VW3	6.2579	0.837	92.4422	2.9973
RW1	1.4558	0.5545	75.1083	2.9672
RW2	1.2477	0.3368	39.0901	2.5751
RW3	2.6487	0.7717	69.6293	3.2744

^a S-I: Splitting Index

^b Sh-DI: Landscape Shannon Diversity

^c CWED: Contrast-Weighted Edge Density

^d Shape AW: Shape Area-Weighted

Supplementary Table 2a. Species abundance

	IW1		IW2		VW1		VW2		VW3		RW1		RW2		RW3		N
	F	SV	F	SV	F	SV	F	SV	F	SV	F	SV	F	SV	F	SV	
Tribe Ateuchini Perty, 1830																	
<i>Ateuchus candezei</i> (Harold, 1868)	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
<i>Ateuchus perezvelai</i> Kohlmann, 2000	1	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	3
<i>Ateuchus rodriguezii</i> Preudhomme de Borre, 1886	4	0	0	0	6	12	31	0	0	3	9	0	0	0	0	0	65
<i>Bdelyopsis newtoni</i> Howden, 1971	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	2
<i>Scatimus ovatus</i> Harold, 1862	0	0	0	0	0	0	0	3	2	5	40	2	1	0	0	26	99
<i>Uroxys boneti</i> Pereira & Halffter, 1961	3	0	3	0	1	0	1	0	0	0	2	0	0	0	0	0	11
<i>Uroxys deavilae</i> Delgado & Kohlmann, 2007	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
<i>Uroxys microcularis</i> Howden & Young, 1981	0	0	0	0	0	0	0	18	0	0	0	0	0	0	0	0	18
<i>Uroxys micros</i> Bates, 1887	1	0	3	1	0	15	4	4	2	2	1	0	0	0	0	0	34
<i>Uroxys platypygga</i> Howden & Young, 1981	0	0	0	0	0	0	5	1	0	0	0	0	0	0	0	0	6
Tribe Coprini Leach, 1815																	
<i>Canthidium centrale</i> (Boucomont, 1928)	0	0	0	0	0	0	4	10	2	0	3	0	0	0	0	2	21
<i>Canthidium moroni</i> Kohlmann & Solis, 2006	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	3
<i>Canthidium pseudoperceptibile</i> Kohlmann & Solis, 2006	1	0	0	0	0	0	2	0	0	0	2	1	0	0	0	0	7
<i>Canthidium pseudopuncticolle</i> Solis & Kohlmann, 2004	0	0	0	0	0	0	0	0	0	0	0	6	0	13	0	2	49
<i>Copris laeviceps</i> Harold, 1869	0	0	1	0	0	0	1	1	0	3	21	1	0	5	0	5	49
<i>Copris lugubris</i> Boheman, 1858	0	0	1	0	0	0	0	2	1	1	21	8	1	15	110	34	537
<i>Copris sallei</i> Harold, 1869	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1
<i>Ontherus mexicanus</i> Harold, 1868	404	99	535	108	8	3	0	0	0	0	0	0	0	0	0	0	1157
Tribe Dichotomiini Tarasov & Dimitrov, 2016																	
<i>Dichotomius amplicollis</i> Harold, 1869	0	0	0	0	2	3	17	17	13	9	14	5	6	17	23	0	193
<i>Dichotomius annae</i> Kohlmann & Solis, 1997	0	0	0	0	2	0	1	3	8	1	13	4	0	0	0	0	66
<i>Dichotomius satanas</i> (Harold, 1867)	0	0	16	1	1	0	1	0	0	9	7	0	0	0	0	0	38
Tribe Deltochilini Lacordaire, 1856																	
<i>Canthon cyanellus</i> LeConte, 1859	0	0	0	0	0	0	0	2	0	1	6	42	0	6	32	0	284
<i>Canthon eurycelis</i> Bates, 1887	0	0	1	0	0	0	2	0	1	2	2	0	0	0	0	0	8
<i>Canthon femoralis</i> Chevrolat, 1834	0	0	0	0	0	0	0	0	0	0	0	0	0	0	12	0	79
<i>Canthon indigeus</i> LeConte, 1866	0	0	0	0	0	9	1	2	13	0	0	27	0	0	8	1	127
<i>Canthon leechi</i> (Martinez, Halffter & Halffter, 1969)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
<i>Canthon morsei</i> Howden, 1966	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
<i>Canthon subhyalinus</i> Harold, 1867	5	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	7
<i>Canthon vazquezae</i> (Martinez, Halffter & Halffter, 1964)	909	28	106	6	167	124	69	93	9	212	64	3	0	1	0	0	1794
<i>Cryptocanthon aff. brevisetosus</i>	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	2
<i>Deltochilum mexicanum</i> Burmeister, 1848	1016	97	791	188	54	24	60	33	0	46	14	0	0	0	0	0	2323
<i>Deltochilum pseudoparile</i> Paulian, 1938	232	19	153	20	26	15	25	9	2	33	45	0	0	0	0	0	580
<i>Deltochilum sublaeve</i> Bates 1887	6	0	7	0	1	1	2	1	0	25	27	1	0	0	0	0	76
<i>Pseudocanthon perplexus</i> LeConte, 184	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	11

Supplementary Table 2b. Species Biomass

	Mean Biomass (g) (\pm S.E)	
Tribe Ateuchini Perty, 1830		
<i>Ateuchus candezei</i> (Harold, 1868)	0.01210	
<i>Ateuchus perezvelai</i> Kohlmann, 2000	N/A	
<i>Ateuchus rodriguezi</i> Preudhomme de Borre, 1886	0.02116	0.0009
<i>Bdelyropsis newtoni</i> Howden, 1971	0.00515	0.0004
<i>Scatimus ovatus</i> Harold, 1862	0.00576	0.0057
<i>Uroxys boneti</i> Pereira & Halffter, 1961	0.00190	0.0001
<i>Uroxys deavilai</i> Delgado & Kohlmann, 2007	N/A	
<i>Uroxys microcularis</i> Howden & Young, 1981	0.00196	0.0002
<i>Uroxys micros</i> Bates, 1887	0.00374	0.0006
<i>Uroxys platypyga</i> Howden & Young, 1981	0.00383	>0.001
Tribe Coprini Leach, 1815		
<i>Canthidium centrale</i> (Boucomont, 1928)	0.05200	0.0245
<i>Canthidium moroni</i> Kohlmann & Solis, 2006	0.00365	0.0005
<i>Canthidium pseudoperceptibile</i> Kohlmann & Solis, 2006	0.00467	0.0008
<i>Canthidium pseudopuncticolle</i> Solis & Kohlmann, 2004	0.00484	0.0005
<i>Copris laeviceps</i> Harold, 1869	0.03107	0.0048
<i>Copris lugubris</i> Boheman, 1858	0.09668	0.0112
<i>Copris sallei</i> Harold, 1869	0.05600	
<i>Ontherus mexicanus</i> Harold, 1868	0.05402	0.0053
Tribe Dichotomiini Tarasov & Dimitrov, 2016		
<i>Dichotomius amplicolis</i> Harold, 1869	0.24788	0.0187
<i>Dichotomius anae</i> Kohlmann & Solis, 1997	0.41015	0.0642
<i>Dichotomius satanas</i> Harold, 1867	0.34456	0.0322
Tribe Deltochilini Lacordaire, 1856		
<i>Canthon cyanellus</i> LeConte, 1859	0.01807	0.0029
<i>Canthon eurycelis</i> Bates, 1887	0.00580	0.0009
<i>Canthon femoralis</i> Chevrolat, 1834	0.01305	0.0026
<i>Canthon indigaceus</i> LeConte, 1866	0.04236	0.0026
<i>Canthon leechi</i> (Martínez, Halffter & Halffter, 1969)	0.00662	0.0006
<i>Canthon morsei</i> Howden, 1966	0.01500	
<i>Canthon subhyalinus</i> Harold, 1867	0.00240	
<i>Canthon vazquezae</i> (Martínez, Halffter & Halffter, 1964)	0.01723	0.0008
<i>Cryptocanthon</i> aff. <i>brevisetosus</i>	0.00180	
<i>Deltochilum mexicanum</i> Burmeister, 1848	0.34822	0.0302
<i>Deltochilum pseudoparile</i> Paulian, 1938	0.06758	0.0033
<i>Deltochilum sublaeve</i> Bates 1887	0.45730	0.0541
<i>Pseudocanthon perplexus</i> LeConte, 184	0.00357	0.0002
Tribe Oniticellini Kolbe, 1905		
<i>Euoniticellus intermedius</i> Reiche, 1849	N/A	
<i>Eurysternus angustulus</i> Harold, 1869	0.01732	0.0008
<i>Eurysternus caribaeus</i> (Herbst, 1789)	0.06959	0.0080
<i>Eurysternus foedus</i> Guérin, 1844	0.08363	0.0220
<i>Eurysternus magnus</i> Castelnau, 1840	0.05454	0.0081
<i>Eurysternus maya</i> Génier, 2009	0.07834	0.0045
<i>Eurysternus mexicanus</i> Harold, 1869	0.03970	0.0034
Tribe Onthophagini Burmeister, 1846		
<i>Digitonthophagus gazella</i> (Fabricius, 1787)	0.02342	0.0029
<i>Onthophagus batesi</i> Howden & Cartwright, 1963	0.01467	0.0016
<i>Onthophagus corrosus</i> Bates, 1887	0.00381	0.0002
<i>Onthophagus crinitus</i> Harold, 1869	0.02530	0.0021
<i>Onthophagus cyanellus</i> Bates, 1887	0.01849	0.0015
<i>Onthophagus incensus</i> Say, 1835	0.01869	0.0018

<i>Onthophagus landolti</i> Harold, 1880	0.00372	0.0004
<i>Onthophagus maya</i> Zunino, 1981	0.01190	
<i>Onthophagus veracruzensis</i> Delgado & Pensado, 1998	0.00625	0.0019
<i>Onthophagus yucatanus</i> Delgado, Peraza & DeLoya, 2006	0.00360	
Tribe Phanaeini Hope, 1838		
<i>Coprophanaeus corythus</i> (Harold, 1863)	0.66386	0.0525
<i>Phanaeus endymion</i> Harold, 1863	0.13686	0.0104
<i>Phanaeus sallei</i> Harold, 1863	0.17534	0.0180
<i>Sulcophanaeus chryseicollis</i> Harold, 1863	0.20057	0.0149

Supplementary Table 3. Jaccard beta pairwise dissimilarity between Windows

$\beta D^+ / \beta D^\ddagger$	IW1	IW2	VW1	VW2	VW3	RW1	RW2	RW3
IW1		0.02	0.11	0.22	0.18	0.00	0.00	0.02
IW2	0.53		0.07	0.20	0.18	0.00	0.00	0.01
VW1	0.37	0.4		0.18	0.15	0.04	0.05	0.03
VW2	0.37	0.34	0.19		0.04	0.16	0.18	0.17
VW3	0.42	0.34	0.19	0.15		0.19	0.20	0.18
RW1	0.87	0.75	0.64	0.46	0.35		0.02	0.05
RW2	0.81	0.70	0.5	0.4	0.28	0.41		0.04
RW3	0.77	0.70	0.51	0.32	0.21	0.41	0.34	

[†] β Jaccard turnover, lower triangular matrix

[‡] β Jaccard nesstedness, upper triangular matrix

Supplementary Table 4. Pairwise comparison: Shared Species and Non Shared Species

SS ^a	IW1	IW2	VW1	VW2	VW3	RW1	RW2	RW3	IW1	IW2	VW1	VW2	VW3	RW1	RW2	RW3	NSS ^b
IW1	22	14	17	17	16	5	7	8	0	10	11	20	19	18	17	18	IW1
IW2	14	24	18	19	19	9	11	11	8	0	10	18	16	14	13	15	IW2
VW1	17	18	28	25	25	12	16	17	5	6	0	12	10	11	8	9	VW1
VW2	17	19	25	37	32	16	18	21	5	5	3	0	3	7	6	5	VW2
VW3	16	19	25	32	35	18	20	23	6	5	3	5	0	5	4	3	VW3
RW1	5	9	12	16	18	23	17	17	17	15	16	21	17	0	7	9	RW1
RW2	7	11	16	18	20	17	24	19	15	13	12	19	15	6	0	7	RW2
RW3	8	11	17	21	23	17	19	26	14	13	11	16	12	6	5	0	RW3

^a SS: Shared Species

^b NSN: Non Shared Species

CONCLUSIONES

Con base en los resultados del presente estudio, referente a las comunidades de Scarabaeinae de la región de la Selva El Ocote, se concluye lo siguiente:

- Ponemos de relieve el efecto conjunto de dos elementos particulares del paisaje para el incremento de la diversidad local de los Scarabaeinae en la región de la Selva El Ocote: La heterogeneidad composicional del paisaje y su grado de fragmentación
- Las comunidades de escarabajos copronecrófagos en los paisajes relictuales se encuentran bajo un proceso de homogenización biótica
- Nuestro estudio sugiere que el incremento del área y contraste entre los bordes del paisaje reprime el aumento poblacional de los escarabajos copronecrófagos. El efecto negativo de los bordes sobre las comunidades de los escarabajos copronecrófagos fue más evidente en los paisajes abigarrados
- Entre todos los sitios muestreados, los paisajes intactos albergaron la mayor biomasa de Scarabaeinae. Por lo tanto, estos deben de ser uno de los sitios más productivos y funcionalmente importantes de la REBISO, lo que realza la importancia de su conservación
- El porcentaje de selva en el paisaje es importante para la presencia y proliferación de los Scarabaeinae de mayor biomasa, los cuales son funcionalmente más productivos que las especies pequeñas. De manera que, las selvas son un elemento inequívoco de protección en la región, y su aumento en el paisaje puede propiciar la permanencia de especies grandes y funcionalmente importantes
- El intenso disturbio en los paisajes relictuales ha generado una comunidad composicionalmente distinta a la de los paisajes selváticos
- La diversidad en la reserva no se distribuye homogéneamente, es decir que, cada localidad contribuye al mantenimiento de la diversidad regional. La alta complementariedad entre las comunidades posiblemente sea reflejo de la variedad de paisajes bajo distintos regímenes de disturbio, así como de la compleja estructura vegetal y geoformas de la región

- El abigarramiento del paisaje pueden ser importante para el aumento de la diversidad gamma en la Selva El Ocote por los siguientes motivos: 1) Incrementan significativamente la diversidad local del paisaje; 2), Estos paisajes pueden compensar la baja diversidad alfa en otras localidades o la pérdida de especies por disturbios fuertes, por medio del recambio de especies y la divergencia entre las comunidades
- Nuestro estudio presentó la mayor diversidad gamma de Scarabaeinae registrado para México, y el muestreo más representativo de estos coleópteros para la REBISO
- Atribuimos a la selva tropical y a las matrices porosas de los paisajes abigarrados la predominancia de procesos aleatorios en el ensamblaje de las comunidades de los escarabajos copronecrófagos. Esto implica que las comunidades pueden estar en continua divergencia producto del flujo constante de las especies entre sitios, previniendo la pérdida local de escarabajos por aislamiento o competencia

Recomendaciones

El modelo de paisaje y método de muestreo empleado en esta investigación demostraron ser herramientas eficaces para estudiar cómo los atributos del paisaje pueden afectar a las comunidades de Scarabaeinae. El muestreo por ventanas supera las limitantes de estudios basados en modelos de paisajes binarios y reduccionistas, al no considerar los elementos del paisaje como unidades cerradas. Además, las ventanas priorizan más en la heterogeneidad del paisaje, integrando el impacto conjunto de los usos de suelo y tipos de vegetación sobre la diversidad. Mediante las ventanas los investigadores y manejadores de áreas naturales protegidas pueden tener un panorama más general y práctico del efecto del paisaje sobre la diversidad. Por lo tanto, sugerimos enfáticamente su implementación para el monitoreo de la biodiversidad en la REBISO y otras áreas protegidas con paisajes complejos.

Es crucial mantener la conectividad entre las diferentes localidades de la reserva para conservar la diversidad de los Scarabaeinae. En este sentido, mantener y promover el abigarramiento del paisaje puede ser una importante estrategia de manejo.

Los paisajes abigarrados heterogéneos que incluyen selvas, vegetación secundaria, así como sistemas agroforestales u otros usos de suelo de bajo impacto pueden: 1) incrementar la diversidad local y regional; 2) amortiguar los impactos de disturbios fuertes sobre la diversidad regional; 3) funcionar como refugios temporales para especies susceptibles al disturbio; y 4) facilitar el flujo de especies entre localidad.

Independiente del tipo de paisaje, la selva es un elemento inequívoco de protección. Estas representan hábitats de alta calidad para los escarabajos copronecrófagos y otros grupos de animales relacionados (e.g. mamíferos, reptiles, anfibios). Asimismo, las selvas están relacionadas íntimamente a los atributos funcionales de los Scarabaeinae. Por lo tanto, para que el ecosistema se beneficie de las importantes funciones ecológicas de estos coleópteros, se debe de conservar y e incrementar las selvas en el paisaje.

Nuestros resultados de diversidad beta proveen diversas directrices que los manejadores de la REBISO pudiesen considerar para el manejo y conservación de los recursos y diversidad en la reserva. Por ejemplo, el alto recambio de especies entre las localidades muestreadas sugiere que los manejadores deben de esforzarse en proteger la variación y heterogeneidad ambiental de los paisajes selváticos. En su defecto, se pueden homogenizar las comunidades selváticas con las comunidades de sitios los abiertos, disminuyendo así la diversidad alfa y beta por pérdida de especies susceptibles al disturbio. Por otra parte, el alto componente de aleatoriedad en la diversidad beta sugiere que se debe maximizar el área a proteger, e incluso incluir los bosques circundantes a la reserva. Esto se debe a que cada localidad es importante para el mantenimiento de la alta diversidad gamma de la región. En este sentido, coincidiendo con Socolar et al. (2016), sugerimos la creación de redes de protección dentro de la reserva con la finalidad de abarcar en la medida de lo posible todo el compendio de comunidades en ella. Asimismo, es recomendable integrar la reserva a una red de protección que conecte a la REBISO con otros remanentes de selvas importantes del sureste de México.

Finalmente, instamos que se realicen estudios futuros que profundicen sobre la funcionalidad ecológica y la dispersión de las especies considerando los diferentes elementos del paisaje.

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