El Colegio de la Frontera Sur

Patrones de diversidad de escarabajos copronecrófagos (Coleoptera: Scarabaeidae: Scarabaeinae) en un gradiente altitudinal del sureste de México

Tesis
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Por

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RESUMEN

Se analizaron los patrones de diversidad de escarabajos copronecrófagos (Coleoptera: Scarabaeinae) a lo largo de un gradiente altitudinal de la región central de Chiapas, México, y su relación con los factores abióticos y antrópicos. Para la recolecta de escarabajos se establecieron diez pares de trampas de caída modificadas a diferentes distancias desde el borde de la carretera, usando de forma alternada calamar y estiércol de cerdo como atrayentes. Se capturaron en total 1,233 individuos de 32 especies agrupados en 14 géneros y siete tribus. Se reportó la primera localidad de *Onthophagus atriglabrus* en México y se amplía la distribución estatal de *Onthophagus anewtoni*. La cobertura del muestreo sugiere una adecuada representación de la diversidad del gradiente. La riqueza, diversidad y el número de especies dominantes disminuye drásticamente con el aumento de la altitud. Los análisis de similitud entre la fauna de los cuatro sitios muestreados indican diferencias en su composición formando tres ensambles distintos, que corresponden a los tipos de vegetación presentes en la zona. Las variables ambientales se relacionan significativamente con la riqueza de especies, principalmente la temperatura y la altitud. El número de especies siempre fue mayor a distancias medias desde el borde de la carretera, pero con un alto porcentaje de similitud y sin mostrar diferencias estadísticas entre todas las distancias. Los grupos funcionales muestran un patrón consistente con zonas altamente modificadas y disminuyen su presencia con el aumento de la altitud. La conversión forestal cambia las condiciones microclimáticas y reduce la disponibilidad de recursos fecales, limitando los rasgos funcionales de los escarabajos y permitiendo la colonización de especies invasoras que inducen a la extirpación de especies locales, principalmente las de talla grande.

Palabras clave: Efecto de borde, Extirpación de especies, Factores abióticos, Grupos funcionales, Nuevos registros.

INTRODUCCIÓN

Patrones de diversidad

La Convención sobre la Diversidad Biológica (CBD) define Biodiversidad 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; comprende la diversidad dentro de cada especie, entre las especies y de los ecosistemas*” (UNEP 2002).

Generalmente, la diversidad biológica incluye tres niveles distintos: diversidad genética, diversidad de especies y diversidad de ecosistemas (Hooper et al. 2005). La diversidad genética se refiere a la información genética de todos los individuos de una especie o población; la diversidad de especies se basada en los patrones de distribución de las especies y sus variaciones espacio-temporales y se puede estudiar desde perspectivas taxonómicas, filogenéticas y biogeográficas, y; la diversidad de los ecosistemas se refiere a la diversidad de hábitats, comunidades y procesos ecológicos en la biosfera (De Queiroz 2007). En cada uno de estos niveles se pueden reconocer tres atributos: la identidad y variedad de los elementos (composición), la organización física o el patrón del sistema (estructura) y los procesos ecológicos y evolutivos (función) (CONABIO 2009).

Cuando los factores climáticos y geográficos son favorables, los organismos amplían activamente su distribución geográfica de acuerdo con su capacidad de dispersión, adquiriendo así su distribución ancestral. Cuando los organismos han ocupado todo el espacio disponible, su distribución puede estabilizarse, permitiendo el aislamiento de poblaciones en diferentes sectores del área y la diferenciación de nuevas especies a través de la aparición de barreras geográficas (Morrone 2009). Sin embargo, las actividades humanas constantemente modifican las áreas de distribución de las especies, creando y destruyendo hábitats, estableciendo barreras y corredores y transportando accidental o voluntariamente a las especies a nuevos lugares, facilitando la dispersión de especies invasoras (CONABIO 2009).

Los gradientes altitudinales

La descripción de patrones en la variación de la riqueza de especies a lo largo de gradientes ecológicos constituye un paso fundamental para el entendimiento de los procesos que regulan y mantienen la diversidad biológica a diferentes escalas (Grytnes y McCain 2007). En contraste a los gradientes latitudinales, los patrones de elevación ofrecen muchas características que permiten descubrir respuestas ecológicas y evolutivas de la biota hacia las variables ambientales influenciadas por las condiciones del terreno en escalas cortas, tales como la disminución de presión atmosférica y temperatura, así como, el aumento de la radiación solar. Esencialmente, estas características se pueden encontrar en cada montaña y su extensión espacial corta permite obtener los datos de campo con mayor facilidad (Körner 2007; Sanders y Rahbek 2012). Toda esta información debe considerarse en la búsqueda de probables respuestas que las especies y comunidades presentan ante el cambio climático (Hodkinson 2005).

En la relación entre la riqueza de especies y la altitud, se deben considerar dos predicciones generales: 1) la riqueza de especies disminuye uniformemente al aumentar la altitud, y 2) el incremento en la riqueza ocurre a niveles intermedios (Körner 1995). Terborgh (1971), plantea un modelo para explicar los patrones de zonación de especies animales aplicado a gradientes altitudinales en biomas tropicales. Este modelo propone tres factores principales: a) respuestas autoecológicas; b) discontinuidades de hábitat e; c) interacciones interespecíficas, principalmente competencia. No obstante, el modelo está diseñado para explicar la distribución de animales endotérmicos.

Carothers et al. (1996), amplían este modelo para incluir animales ectotérmicos, cuyos requerimientos pueden imponer restricciones a su desempeño fisiológico. Para llevarlo a cabo, una serie factores bióticos (competencia, microhábitat, depredación…) y abióticos (temperatura, humedad, características del suelo…) deben ser considerados en los análisis para obtener resultados más concluyentes, al ser determinantes en la distribución de las especies (Carothers et al. 1996; McCain y Grytnes 2010). Ambos conjuntos de factores operan a diferentes escalas, aunque generalmente se acepta que los factores abióticos actúan a escalas más amplias mientras que los factores bióticos operan a escalas menores, pero según la localización geográfica, la influencia cada uno puede variar (Lomolino 2001).

Efecto de borde

La fragmentación de los ecosistemas naturales típicamente produce la alteración de diversos factores que impulsan las respuestas de la comunidad: una disminución en el tamaño promedio de los parches, un aumento promedio en el aislamiento y complejidad de la forma de los parches, y un aumento promedio en el contraste con la matriz y la influencia del borde (Ewers y Didham 2006).

Los efectos de borde son procesos continuos que ocurren como gradientes de cambio entre los límites de un hábitat y su matriz adyacente (López-Barrera 2004). La creación de estos límites o bordes a través de la fragmentación de bosques altera inicialmente la estructura de la vegetación. Este proceso da como resultado cambios inmediatos en factores microclimáticos tales como la radiación solar, la evapotranspiración, la estocasticidad de la temperatura y la disminución de la humedad atmosférica y del suelo (Laurance et al. 2007; Laurance et al. 2011). No obstante, la extensión o distancia a la que el efecto de borde penetra en los fragmentos varía entre distintos ambientes, el tipo de matriz adyacente y el grupo sobre el que se analiza dichos efectos (López-Barrera 2004). Por lo tanto, dada la importancia relativa de los efectos de borde en paisajes fragmentados, junto con la rápida tasa de intensificación del uso del suelo, se deben tener en cuenta las características estructurales y el nivel de degradación de la matriz para comprender la magnitud de su influencia sobre los ecosistemas remanentes (Tilman et al. 2001).

Efecto de la carretera sobre la distribución de especies

Aunque la intensificación de la agricultura es un impulsor importante de la pérdida de biodiversidad (Gámez-Virués et al. 2015), la apertura del paisaje para la construcción de carreteras asume impactos ambientales más importantes a corto y largo plazo en los bosques cercanos a las áreas urbanas (Seiler 2001), pero sus efectos sobre los procesos ecosistémicos y la distribución de las especies siguen siendo poco conocidos (Delgado et al. 2013; Hosaka et al. 2014).

Fahrig y Rytwinski (2009) desarrollaron un conjunto de predicciones de las condiciones que conducen a los efectos de las carreteras sobre la abundancia de los animales. Sugieren que cuatro tipos de especies responderán negativamente a las carreteras: 1) especies que se sienten atraídas por las carreteras y no pueden evitar los automóviles; 2) especies con grandes rangos de movimiento, bajas tasas de reproducción y bajas densidades; 3) animales pequeños cuyas poblaciones no están limitadas por depredadores afectados por la carretera, evitando el hábitat cerca de las carreteras debido a la perturbación del tráfico y; 4) animales pequeños cuyas poblaciones no están limitadas por depredadores afectados por la carretera pero que no eviten las carreteras o las perturbaciones del tráfico y no puedan evitar los automóviles. Por otro lado, predicen que dos tipos de especies responderán positivamente a las carreteras: 1) especies atraídas por caminos para un recurso importante (por ejemplo, alimentos) y capaces de evitar automóviles que se aproximan y; 2) especies que no evitan la perturbación del tránsito, pero sí evitan carreteras, y cuyos principales depredadores muestran respuestas negativas a nivel de población a las carreteras. Estos efectos también dependen de características propias de la carretera como el tiempo desde la construcción (Carpio et al. 2009), tipo y dimensión de la misma (terracería, pavimentado, autopista) (Dunn y Danoff-Burg 2007).

La subfamilia Scarabaeinae como grupo de estudio

En la evaluación de los efectos naturales e inducidos sobre la biodiversidad, se han utilizado a varios grupos taxonómicos. Entre ellos, la mayoría de los insectos presentan características que les permite responder rápidamente a las alteraciones en el ecosistema, ya que su tamaño pequeño y fisiología los hace más sensibles a las variaciones o impactos ambientales (Didham et al. 1996). Las hormigas (Hymenoptera: Formicidae), mariposas diurnas (Lepidoptera: Papilionoidea) y los escarabajos de la subfamilia Scarabaeinae (Coleoptera: Scarabaeidae), han sido algunos de los principales grupos usados para evaluar estas respuestas, ya que cumplen con los criterios primordiales de un grupo indicador, principalmente, por la sencillez de su muestreo y su taxonomía relativamente resuelta (Villarreal et al. 2006).

Los Scarabaeinae son uno de los grupos mejor estudiados y más diversificados entre los Coleoptera. Se conocen alrededor de 6,200 especies en el mundo, agrupados en 267 géneros (Tarasov y Génier 2015) y 11 tribus (Bouchard et al. 2011). Esta diversidad se concentra principalmente en los trópicos, en altitudes que van desde el nivel del mar hasta los 3500 m (Morón 2003). Son conocidos por desempeñar un papel importante en el reciclaje y reincorporación de nutrientes al suelo como resultado de su actividad cavadora, generando beneficios tales como retención de nitrógeno, drenaje y aireación del suelo, facilitan el ciclo de nutrientes, sirven de control de parásitos gastrointestinales de mamíferos y dispersión secundaria de semillas, entre otros (Nichols et al 2008; Simmons y Edwards 2011). Paralelamente, responden a las alteraciones en el ecosistema, razones por las que han sido propuestos como indicadores de calidad ambiental (Spector 2006; Nichols y Gardner 2011).

Usualmente, se emplean cuatro características solas o combinadas, para identificar los grupos funcionales que componen los ensambles de escarabajos copronecrófagos, cada una con un impacto particular en las funciones del ecosistema (Barragán et al. 2011):

1. Patrones de relocalización de recursos. Los escarabajos pueden dividirse en tres grandes grupos; (a) telecópridos, especies que forman bolas de materia orgánica, y luego ruedan y entierran a una distancia variable de la fuente; (b) paracópridos, especies que crean túneles verticales o semi horizontales debajo de la fuente y colocan en ella masas de materia orgánica, y (c) endocópridos, especies que permanecen dentro de la masa de materia orgánica (Simmons y Ridsdill-Smith 2011).
2. Longitud total del cuerpo. Idealmente, el tamaño se incorporaría como una variable continua de varias longitudes corporales o como biomasa. Sin embargo, también se usa como una clasificación arbitraria para separar las especies en pequeñas y grandes (Barragán et al. 2011).
3. Horario de actividad. Considerando las horas del día que estos escarabajos están activos, se pueden clasificar en diurnos, nocturnos o crepusculares lo cual está relacionado con los horarios de producción de estiércol (Gill 1991).

4. Dieta. De acuerdo con el porcentaje de captura en los diferentes cebos utilizados para su recolecta (usualmente estiércol y carroña), las especies se pueden considerar especialistas (coprófagas o necrófagas) o generalistas (Navarrete y Halffter 2008).

El análisis de los patrones de diversidad temporal y espacial de los Scarabaeinae es un tema de estudio recurrente en diversas regiones de México. No obstante, la mayoría de estos son analizados a lo largo de gradientes de perturbación (*e.g.* Navarrete y Halffter et al. 2008; Díaz et al. 2010; Sánchez-de-Jesús et al. 2016; Alvarado et al. 2018), mientras que pocos trabajos examinan el efecto de la altitud en la distribución de los ensambles de estos escarabajos (ver Lobo y Halffter 2000; Escobar et al. 2007; Alvarado et al. 2014; Moctezuma et al. 2016). Todos estos trabajos concluyen que la riqueza de especies disminuye con el aumento de la altitud mientras que condiciones ambientales locales como la temperatura y la humedad, así como la historia biogeográfica de las especies, son determinantes en los patrones de diversidad. Por otra parte, aunque existe certidumbre sobre los efectos que conlleva el cambio de uso de suelo sobre los ensambles de Scarabaeinae (diversos monocultivos y potreros, principalmente), existe poca evidencia de las consecuencias que ejerce el establecimiento de una carretera sobre estos escarabajos (Carpio et al. 2014; Hosaka et al. 2014; Yamada et al. 2014; Edwards et al. 2017).

Bajo la premisa de que el aumento de la altitud impone requerimientos fisiológicos mínimos a los insectos, esta investigación parte de siguiente hipótesis: se espera que los patrones de diversidad de escarabajos copronecrófagos disminuyan drásticamente con el aumento de la altitud. Asimismo, el efecto de borde causado por la carretera y las condiciones abióticas locales (altitud, temperatura, humedad ambiental y cobertura de dosel) también afectará la estructura y composición de los ensambles de cada sitio del gradiente, encontrando una diversidad local y regional baja.

El objetivo principal de este trabajo fue analizar los patrones de diversidad de escarabajos de la subfamilia Scarabaeinae, considerando los efectos que ejercen la presencia de una carretera y los factores abióticos locales (altitud, temperatura, humedad ambiental y cobertura de dosel) sobre los ensambles de escarabajos a lo largo de un gradiente altitudinal de la región central de Chiapas, México.

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First report of *Onthophagus atriglabrus* Howden & Gill and new state record of *Onthophagus anewtoni* Howden & Génier (Coleoptera: Scarabaeidae: Scarabaeinae) in Mexico

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The subfamily Scarabaeinae is one of the best studied and most diversified groups of Coleoptera, with ca. 6,200 species, 227 genera (Tarasov and Génier 2015) and 11 tribes (*sensu* Bouchard et al. 2011) in the world. This diversity is mainly concentrated in the tropics, at elevations ranging from the sea level to 3500 m (Morón 2003). In Mexico, there is a record of 272 species registered (Morón 2003; Howden and Génier 2004; Kohlmann and Solís 2006 a, b; Delgado and Kohlmann 2007; Vaz-de-Mello 2008; Génier 2009; Halffter and Halffter 2009; Edmonds and Zidek 2012; Gómez 2013; González-Alvarado and Vaz-de-Mello 2014; Halffter et al. 2015; Mora-Aguilar & Delgado 2015; Arriaga-Jiménez et al. 2016; Moctezuma et al. 2016; Moctezuma et al. 2017; Moctezuma and Halffter 2017; Kohlmann et al. 2018 a, b; Kohlmann & Vaz-de-Mello 2018; Moctezuma et al. 2018), in which Chiapas, with 119 species, occupies the second place among the states with the highest diversity (Sánchez-Hernández et al. 2018). However, the greatest sampling efforts in the state of Chiapas have been focused in certain areas, particularly in the natural protected areas located in the Lacandona forest, from where the majority of the records come from. In contrast, the central and montane areas of Chiapas have been scarcely explored (Halffter and Halffter 2009), leading us to suggests that its species richness is underestimated. Through systematic samplings during 2017, using baited pitfall traps to capture copronecrophagous Scarabaeinae beetles in the central region of Chiapas, the first precise location of *Onthophagus atriglabrus* Howden & Gill, 1987 is recorded. Likewise, the geographic area of distribution in Mexico of *Onthophagus anewtoni* (Howden & Génier, 2004), which until now was only known to be found in its type localities, is extended. With the information presented in this study, the number of record for Scarabaeinae beetles from Chiapas increases to 121 species. The individuals were identified using the original descriptions of Howden and Gill (1987) and Howden and Génier (2004). The specimens were deposited in the Entomological Collection of El Colegio de La Frontera Sur, Tapachula (ECO-TAP-E) and the personal collection of Benigno Gómez (BGG).

***Onthophagus atriglabrus* Howden & Gill, 1987 (Fig. 1a, 2)**

Known distribution: This species was described from Costa Rica and Panama, and has also been reported in Colombia and Mexico, but without a specified location (Howden and Gill 1987, Escobar 2000).

Examined material: 5 specimens (2 males, 3 females). **MEXICO:** CHIAPAS: Chiapa de Corzo municipality, 12.46 km NE of Chiapa de Corzo, disturbed oak forest, 16°42'15.34" N, 92°53'19.89" W, 1085 m, 28.VII.2017, squid (2♂), pig dung (1♀), fermented fungus (2♀), G. Sánchez-Hernández, E. Rodríguez-López and J. A. Sánchez cols.

Comments: Howden and Gill (1987), reported that some subspecies occur in Mexico: "*this form has the sides of the horn of the male with parallel sides and the pronotal tumosity with only lateral lobes; also the dorsal surfaces which are finely punctate in atriglabrus are more strongly punctate in the Mexican form*". Nevertheless, until now, the presence of this subspecies in Mexico has not been confirmed. With this record we confirmed the presence of *O. atriglabrus* and provided the first precise location in Mexico, expanding considerably its distribution range nearly 1,400 km northeast of its closets known location. The extension in the distribution of this species is not uncommon, as in accordance with Halffter and Halffter (2009), some species from Central and South American origin such as *Canthon angustatus* Harold, 1867 and *Canthon lituratus* (Germar, 1813) with recent bibliographical extensions that extend their distribution towards the north until the Southern of Mexico, with Chiapas being its northern limit nowadays.

Onthophagus anewtoni **Howden & Génier, 2004 (Fig. 1b, 2)**

Known distribution: Before this record, this species was only known to be found in its type localities in the states of Guerrero, Jalisco and Oaxaca, México (Pulido-Herrera and Zunino, 2007).

Examined material: 42 specimens (24 males, 18 females). **MEXICO:** CHIAPAS: Chiapa de Corzo municipality, 8.2 km NE of Chiapa de Corzo, deciduous forest, 16°43’44.17” N, 92°55’56.91” W, 875 m, 30.VI.2017, squid (21♂ , 16♀), pig dung (1♂), G. Sánchez-Hernández, R. Dávila and A. Gómez cols., idem except 28.VII.2017, squid (2♂), pig dung (1♂), fermented fungus (1♀), G. Sánchez-Hernández, R. Dávila and C. Valdez cols.

Comments: The presence of this specie in the central region of Chiapas matches with others species of the subfamily as *Phanaeus demon* Castelnau, 1840 and *Canthidium laetum* Harold, 187, which are distributed along the Mexican pacific coast and uses the slopes of the Sierra Madre of Chiapas (La Sepultura Biosphere Reserve) to expand their distribution area towards the Central Depression of Chiapas (Kohlmann and Solís 2006a; Lizardo et al. 2017). The present record extends the distribution range approximately 300 km east to the closest known locality, in Tequesistlán, Oaxaca.

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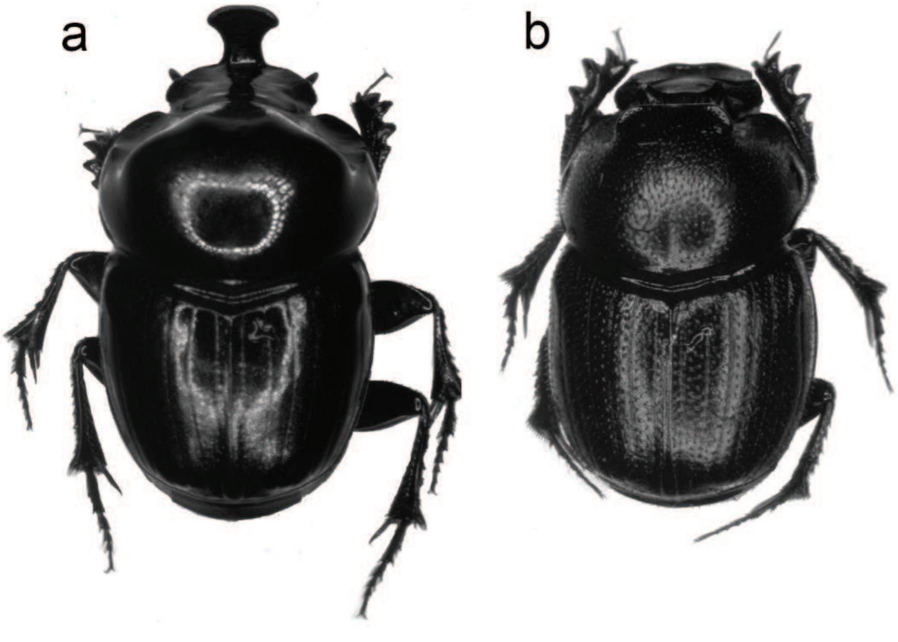

Fig. 1. Dorsal habitus of a) *Onthophagus atriglabrus* and b) *Onthophagus anewtoni*.

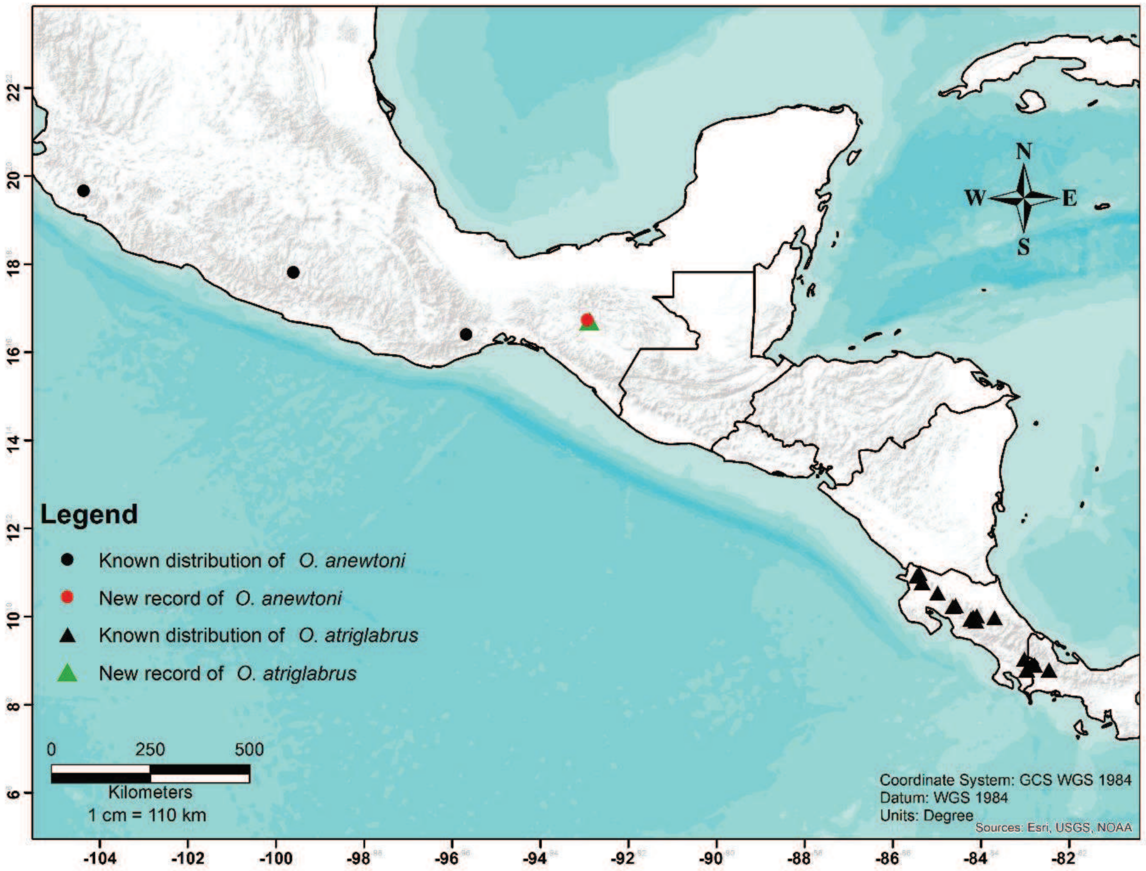

Fig. 2. Known distribution of *O. atriglabrus* and *O. anewtoni* and their new localities in the central region of Chiapas. Localities reported in Howden and Gill (1987), Howden and Génier (2004) and Kohlmann and Solís (2001).

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Diversity patterns, road edge effects and the impact of environmental variables on copronecrophagous beetle assemblages (Coleoptera: Scarabaeidae: Scarabaeinae) of an altitudinal gradient in the southeast Mexico

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Abstract

Copronecrophagous beetle (Coleoptera: Scarabaeinae) diversity patterns, and their relationship with anthropic and abiotic factors along an altitudinal gradient in the central region of Chiapas, Mexico, are analyzed. For the recollection of beetles, ten pairs of modified pitfall traps were collocated at different distances from the edge of the road. A total of 1,233 individuals of 32 species grouped in 14 genera and seven tribes were captured. The sampling coverage suggests an adequate representation of the diversity in the gradient. The richness, diversity and number of dominant species decreases drastically with an increase in altitude. Analyses of similarities between the fauna of the four sampled sites indicate differences in their composition, forming three distinct communities, corresponding to the vegetation types present in the area. The environmental variables, mainly temperature and altitude, are significantly related to the species richness. The number of species was always greater at medium distances from the edge of the road, but with a high percentage of similarity and without showing statistical differences between all distances. Functional groups show a consistent pattern with highly modified zones and decrease their presence at increased altitudes. Forest conversion changes microclimatic conditions and reduces the availability of fecal resources, limiting the functional features of beetles and allowing the colonization of invasive species that induce the extirpation of local species.

Key words: Abiotic factors, Deciduous forest, Functional groups, Human disturbance, NMDS, Species extirpation.

INTRODUCTION

Describing patterns in the variation of species richness along ecological gradients constitutes a fundamental step to be able to understand the processes that regulate and maintain biological diversity at different scales (Grytnes & McCain 2007). In contrast to the latitudinal gradients, those of elevation offer characteristics that allow to discover implicit causes in the spatial variation of the diversity, as well as ecological and evolutionary responses of the biota towards the environmental variables influenced by the terrain conditions on a small scale (*e.g.* the decrease in temperature and atmospheric pressure, as well as the increase in solar radiation) (Körner 2007; Sanders & Rahbek 2012). All this information must be considered in the search for probable responses that species and communities present to climate change (Hodkinson 2005). Additionally, the effects of geographic factors acting at a regional scale, as well as the history of taxa examined, must be taken into account in the analyses (Carothers *et al.* 1996).

Although the intensification of agriculture is a major driver in the loss of biodiversity (Gámez-Virués *et al.* 2015), the opening of the landscape for road construction results in significant environmental impacts in the forests near urban areas (Seiler 2001), however, their effects on ecosystem processes and the distribution of species remain poorly understood (Delgado *et al.* 2013; Hosaka *et al.* 2014). Given this, there is a set of predictions of the circumstances that lead to the effects of roads on the spatial distribution patterns of animals (Fahrig & Rytwinski 2009). Nonetheless, these effects also depend on road characteristics such as the time since its construction (Carpio *et al.* 2009), as well as the type and dimension of it (dirt road, paved road, highway) (Dunn & Danoff-Burg 2007).

For the evaluation of the natural and induced effects on biodiversity, several taxonomic groups have been used. Most insects have characteristics that allow them to respond quickly to alterations in the ecosystem, since their small size and physiology make them more sensitive to environmental variations or impacts (Didham *et al.* 1996). Ants (Hymenoptera: Formicidae), diurnal butterflies (Lepidoptera: Papilionoidea) and beetles of the Scarabaeinae subfamily (Coleoptera: Scarabaeidae), have been some of the main insect groups used to evaluate these responses. These meet the criteria of an indicator group, mainly because of the simplicity of their sampling and their relatively well determined taxonomy (Villarreal *et al.* 2006).

The copronecrophagous beetles (Coleoptera: Scarabaeidae: Scarabaeinae) are one of the most diverse and abundant groups among insects. They play an important role in the recycling and reincorporation of nutrients into soil as a result of their burial activity, generating benefits such as nitrogen retention, reduction in the release of greenhouse gases, drainage and soil aeration, facilitation of the nutrient cycle, control of gastrointestinal parasites of mammals and secondary dispersion of seeds among others (Nichols *et al.* 2008; Simmons & Edwards 2011). Concurrently, they respond to alterations in the ecosystem, a reason why they have been proposed in various studies as indicators of environmental quality (Spector 2006; Nichols & Gardner 2011). To do so, four characteristics are used alone or in combination to identify the functional groups that make up the beetle communities of the Scarabaeinae subfamily, each with an impact on the ecosystem functions (Barragán et al 2011): 1) type of resource relocation (paracoprids, endocoprids and telecoprids), 2) size (big and small), 3) times of activity (diurnal, nocturnal and crepuscular) and 4) diet (coprophagous, necrophagous and generalists). The objective of this work was to analyze the diversity patterns of

Scarabaeinae copronecrophagous beetles considering the influence of abiotic factors (altitude, temperature, humidity and canopy cover) and the presence of a road in its distribution site along an altitudinal gradient in the central region of Chiapas, Mexico.

MATERIALS Y METHODS

Study area

The sampling was carried out in an altitudinal gradient in the central region of the state of Chiapas, Mexico, covering an altitudinal range between 870 and 2,375 m above sea level where four sampling sites with different characteristics were established (Table 1), located adjacent to a road (Fig. 1). The area is located between two physiographic regions: 1) central depression. This is a large area with interspersed valleys, formed by sedimentary rocks and alluvial deposits. The soil is deep and of alluvial origin, and in the hill area, the soils are thin and stony. In the region, less than 2% of the vegetal cover persists, but with a high diversity of trees, predominating species of the Fabaceae family. The original vegetation is classified as low deciduous forest with remnants of semi-deciduous forest at altitudes above 800 m and oak forests above 1 500 m above sea level. (Rocha-Loredo *et al.* 2010; Villalobos-Sánchez 2013); 2) Central Depression. It features a mountainous relief, with a great amount of valleys of karstic origin. The predominant rocks are limestones and it is possible, but not common, to find rocks of volcanic origin. The soils are thin and stony and, in most cases, have steep to abrupt slopes. The vegetation is very disturbed and consists of oak and pine forests, predominating one genre over the other according to the altitude. (Villalobos-Sánchez 2013).

Sampling design

Four collections were done during the year 2017, trying to cover two seasons of sampling: dry (March and April) and rainy (June and July). Based on the design of Batilani-Filho & Hernández (2016), in each site 10 pairs of modified pitfall traps were installed (Lobo *et al.* 1988), each pair separated by a minimum distance of 30 m, totaling 80 traps per sample. The traps consisted of a plastic container with a capacity of 500 ml (10 cm in diameter and 8 cm deep) buried at ground level. The containers were filled with ~250 ml of ethylene glycol as a preservative liquid and were alternately primed with pig dung or decomposing squid (~30 g), as they are two of the most attractive baits for copronecrophagous Scarabaeinae in the Neotropical region (Chamé-Vázquez *et al.* 2012; Marsh *et al.* 2013). The traps remained active for 72 hours and plastic plates were suspended to protect the baits from precipitation and dehydration. The captured beetles were kept in plastic jars with 70% ethanol for later identification in the laboratory.

The collected specimens were reviewed with the help of a stereoscopic microscope (Carl Zeiss SteREO Discovery.V12) and the species were determined using specialized keys (Matthews 1961; Rivera-Cervantes & Halffter 1999; Kohlmann 2000; Kohlmann & Solís 2001; Cook 2002; Howden & Génier 2004; López-Guerrero 2005; Kohlmann & Solís 2006; Génier 2009; Edmonds & Zidek 2010; 2012; Génier 2012; Mora-Aguilar & Delgado 2015). The collected individuals are deposited in the Entomological Collections of El Colegio de la Frontera Sur, San Cristóbal (ECO-SC-E) and Tapachula (ECO-TAP-E).

Effects of the road

To determine the edge effect caused by the presence of a road, the traps were arranged in two transects per sampling site, located perpendicular to it. In each transect of all sampling sites, five pairs of traps were installed located at five different distances from the edge of the road: 40, 70, 100, 130 and 160 m.

Estimation of environmental variables

During each collection event some environmental variables were obtained. The values of ambient temperature (°C) and the relative air humidity were recorded using hygro-thermometers (BSIDE BTH02), which were active during the days of collection, taking measurements every hour (72 measurements) to register the fluctuations during day. The canopy coverage was determined by taking the average of four readings using a convex spherical densiometer (Forestry suppliers, Model A). Also, using a GPS (Garmin eTrex 10), the elevation in meters above sea level of three points in each sampling station was measured to eventually consider the average value of the measurements (Table 1).

Functional groups

To identify the functional groups that make up each community, the beetles were classified according to the relocation of the resource in telecoprids or rollers, paracoprids or tunnelers and endocoprids or dwellers (Simmons & Ridsdill-Smith 2011). In addition, they were classified according to the total length of the body as large (> 10 mm) and small (≤10 mm) (Barragán *et al.* 2011).

Data analysis

The sampling efficiency was obtained through the sampling coverage completeness estimator ($\hat{C}m$) (Chao & Jost 2012), and the nonparametric estimator Chao1 was used to calculate the number of potential species. The diversity of beetles was calculated with the index exponential of the Shannon entropy or diversity of the order 1 (^{1}D), where all the species are considered according to their relative frequency in the sample (Jost 2006), taking in account a more informative measure than the diversity of order ^{0}D (richness) and ^{2}D (dominance) (Moctezuma *et al.* 2016). These analyses were calculated with the iNEXT package, using 500 Bootstrap replications and 100 knots as a measure of comparison (Hsieh *et al.* 2014). Changes in the structure of the community, the richness of species and the equity of their abundances were compared using range-abundance curves, calculating the logarithm with base 10 of the relative abundances of the species in each site (Rocchini & Neteler 2012).

To graphically express the changes in the composition of the beetle community along the altitudinal gradient, the Non-metric Multidimensional Scaling Analysis (NMDS) was used. To verify this technique, a similarity analysis was applied using the ANOSIM test. These same procedures were used to verify the similarities between the different distances at which the traps were placed. All data were processed in a Bray-Curtis dissimilarity matrix with transformed and standardized data (Anderson & Willis 2003). These analyses were performed using the PAST v.3.18 software (Hammer & Harper 2017).

The response of the beetle communities to the environmental variables (temperature, humidity, canopy coverage and altitude) at each sampling site was determined through a Canonical Correspondence Analysis (CCA), a multivariate statistical method that sorts richness in a gradient by its degree of correlation with the variation in species diversity (Ter-Braak 2014). To avoid deceptive effects caused by rare species, species with an abundance <5 were excluded.

RESULTS

Diversity patterns

A total of 1,233 specimens of 32 species grouped in 14 genera and seven Scarabaeinae tribes were collected. The most abundant species were *Onthophagus anthracinus* (*n* = 261), *Phanaeus endymion* (*n* = 242), *Uroxys deavilai* (*n* = 176), and *Uroxys microcularis* (*n* = 144), representing 66.8% of the total beetle abundance. Nine species are represented by a single individual and only one species (*O. anthracinus*) is persistent in the four sampling sites, in contrast, 20 of them are solely linked to one site (DF = 11; SV = 4; PO = 4; OF = 1). The species richness decreases with increasing altitude, with the deciduous forest being the site with the highest number of recorded species (*S* = 22). In the case of abundances, it was observed that the site with secondary vegetation has the highest quantity (*N* = 657) (Table 2).

The rarefaction curves show asymptotic values only for the deciduous forest and secondary vegetation sites (Fig. 2), suggesting that they are the only ones close enough to obtain complete sampling. However, the sampling coverage in the four collection sites was over 90%, so it can be considered that an adequate characterization of the beetle communities was obtained (Table 2). Also, the non-parametric estimator Chao1 indicates that the value closest to the expected richness was obtained in the deciduous forest (23.5 ± 5), while the richness of the oak forest is well below that estimation (24 ± 7.5) (Fig.

3a). The Shannon diversity index (^{1}D) shows the deciduous forest as the most diverse site (^{1}D= 9.9 ± 0.5), while the oak forest represents the lowest diversity (^{1}D = 3 ± 0.7) (Fig. 3b). The distribution of abundances is more equitable in the deciduous forest, where a greater number of dominant species and a more homogeneous distribution in the rest of the community are observed, a similar pattern is observed in the secondary vegetation, but with a smaller number of dominant species, whereas, in the other sites, the community is dominated by a single species (Fig. 4).

Ordering all collection events shows a clear difference in the composition of the altitudinal gradient species (ANOSIM; $R = 0.6766, p = 0.0001$). After arranging the points in the NMDS analysis, the formation of three distinct groups was observed, the first formed by the deciduous forest and the secondary vegetation site (ANOSIM; $R = -0.1667, p = 0.8054$) while the oak forest and the pine-oak forest form independent groups or communities (Fig. 5), with low similarity and showing differences in their composition: DF-OF ($R = 0.8656; p = 0.0286$); DF-PO ($R = 0.8333; p = 0.0301$); SV-OF ($R = 0.7656; p = 0.0262$); SV-PO ($R = 0.8333; p = 0.0289$); OF-PO ($R = 0.9063; p = 0.0295$).

Road Edge effect

The greatest number of species was captured at the average distances to the road (70, 100 and 130 m) but never at the far ends (Fig. 6). However, all distances have a high percentage of similarity (ANOSIM) between the structure and composition of their fauna [(DF: $R = 0.01375$; $p = 0.04342$); (SV: $R = 0.02063$; $p = 0.3972$); (OF: $R = 0.016466; p = 0.3959$); (PO: $R = 0.02312; p = 0.4116$)], so it is possible that the changes in the beetle community caused by the road edge effect are distinguishable at greater distances, since all the sampling distances in each site form a single grouping in the NMDS order (Fig. 7).

Relation with abiotic factors

The two main axes of the CCA explain 83.3% of the total variation in the composition of the beetle communities (55.9% on axis 1 and 27.4% on axis 2). The evaluated environmental variables were significantly related to the variation found in the beetle assemblages (axis 1 $p= 0.003$; axis 2 $p = 0.007$) (Fig. 8). The species richness in the deciduous forest and secondary vegetation sites seems to be defined mainly by temperature, the species of the pine-oak forest by the altitude, and those of the oak forest by the canopy cover and to a lesser degree by humidity (Fig. 8).

Functionals groups

The relocation type with the greatest number of species and individuals was the one of the paracoprids ($S = 18$; $N = 1049$), followed by the telecoprids ($S = 12$; $N = 179$) while the endocoprids represent a small percentage ($S = 2$; $N = 5$). The small species have a greater richness and species abundance ($S = 20$; $N = 894$) than the large ones ($S = 12$; $N = 339$). The functional groups incidence follows the same pattern in each site. Regarding body size, the four sites follow a similar richness scheme, the number of small and large species decreases in each gradient while the abundances of both groups are higher in the secondary vegetation site (Fig. 9). The paracoprid species dominate in all four sites, but richness decreases with the increase in altitude, a situation similar to what was observed with the telecoprids, while the endocoprids only appear in the deciduous forest and oak forest. The abundances of telecoprids reduce in each gradient, being better represented in the deciduous forest, on the other hand the paracoprids display their greater abundances in the secondary vegetation site (Fig. 9).

DISCUSSION

In spite of factors such as reduced collection effort, heterogeneity of the landscape, spatial and temporal coverage of the sampling done, the number of species captured is within the range of those obtained in other nearby regions of Mexico, such as the 28 (Arellano *et al.* 2008) and 33 (Arellano *et al.* 2013) in the Central Depression of Chiapas, and the work with characteristics similar to the ones in this investigation done along altitudinal gradients in the states of Oaxaca (37) and Veracruz (31) (Alvarado *et al.* 2014).

The sampling locations are characterized by a high alteration degree of the original vegetation due to changes in land use to various monocultures, cattle ranch and the establishment of roads (Rocha-Loredo *et al.* 2010; Villalobos-Sánchez 2013). This simplification of the landscape can affect the viability of the ecosystem and diminish the capacity of the communities to respond to environmental changes and disturbances (Gámez-Virués *et al.* 2015), displaying changes in the structure and composition of the local fauna of Scarabaeinae, limiting the presence of species with a range restricted to environmental variations (Carpio *et al.* 2009; Moctezuma *et al.* 2016; Alvarado *et al.* 2018). In our case, these conditions could influence in in the way that a high percentage of the species captured have low abundances (20 spp. <10 individuals), especially those species that are abundant in conserved forests (*e.g. Ca. championi*, *Ca. euryscelis*, *Ca. morsei*, *Ca. subhyalinus*, *Ca. vazquezae*, *E. magnus*, *O. atriglabrus*) and allow the entry of others that commonly reside in edges and open areas (*e.g. Ca. humectus*, *Co. lugubris, Do. gazella*, *O. anthracinus*, *Ph. wagneri, U. deavilai*), since its distribution is associated especially with livestock dung and favored by the change in land use (Kohlmann & Solís 2001; Arellano *et al.* 2013). Therefore, according to the wealth estimation, the number of species captured is below the regional diversity.

The structure of a more equitable community allows for greater diversity (^{1}D) in the low-altitude sites (DF and SV), on the contrary, the low richness and dominance of a single species in the oak forest (*U. micros*) and pine-oak forest (*O. cyanellus*), where both represent more than 50% of the total abundances, define the low diversity of these sites. In contrast, the insignificant changes between the abundant and dominant species of the fauna captured in the deciduous forest and secondary vegetation sites allow that both form a single community (ANOSIM), even though there is a high number of species unique to each site (Moctezuma *et al.* 2016). The continuum of deciduous forest fragments between the lower-altitude sites (800 - 1500 m), which are than replaced by oak forests (≤ 1500 m) and pine or pine-oak forests (<2000 m) (Villalobos-Sánchez 2013) can also explain the low similarity and the formation of different communities, since each one presents different environmental and resource conditions.

Among the insects, the roads represent a significant barrier, especially for species which are small or do not fly (Muñoz *et al.* 2015). In the case of the Scarabaeinae, their diversity and abundance tend to decrease in the short term before the opening of roads; however, they do not show radical changes in the community structure at different distances from the edge (Carpio *et al.* 2009). In the long term, drastic negative effects can be observed in the presence of functional groups in the clearings closest to the road (Hosaka *et al.* 2014; Yamada *et al.* 2014; Edwards et al. 2017). These effects can be revealed in the reduction of the various ecological functions these beetles provide for (Hosaka *et al.* 2014). In the obtained results, it stands out that the number of species was always lower at the remotest distances (40 y 160 m), finding the highest quantities at medium distances (70 a 130 m). However, no significant statistical differences were found between the structure and composition of the fauna, while a percentage of similarity was observed between all sampling distances, probably due to the fact that the maximum distance from the edge was 160 meters, which concurs with the assertions of Edwards *et al.* (2017), who suggest that the edge effects are distinguishable even further than 170 meters inside the forest. Therefore, although it is known that edge effects can have serious impacts on species diversity and composition, the dynamics of the communities and the ecosystem services that these provide (Laurance *et al.* 2007), our results concur with the hypothesis that the edge effect caused by a road can produce more drastic changes in the copronecrophagous beetle communities (Carpio *et al.* 2009; Hosaka *et al.* 2014; Yamada *et al.* 2014; Edwards *et al.* 2017) than those caused by other land uses such as the coffee plantation (Villada-Bedoya *et al.* 2017), induced savannas (Spector & Ayzama 2003), pastures, cane crops and eucalyptus plantations (Martello *et al.* 2016), since the impacts in these environments are distinguishable at shorter distances from the edge to the interior of the forest (± 50 m), where the species with a wide tolerance to environmental conditions are replaced by species whose range of environmental tolerances is narrower.

The correlation between insect richness and altitude is a widely documented phenomenon (Rahbek 1995 and references cited). Our results indicate a decrease in the richness pattern, diversity and the presence of dominant species with the increase in altitude, even though the abundances of each gradient follow a different scheme. This phenomenon has been reported in different neotropic mountains for beetles of the Scarabaeinae subfamily (Lobo & Halffter 2000; Moctezuma *et al.* 2016; Nunes *et al.* 2016) and other insect groups (Sandoval & Fagua 2006; Carrero *et al.* 2013; Sánchez-Reyes *et al.* 2014). In the specific case of the Scarabaeinae, the abiotic environment determined by the increase in altitude linked to the decrease in primary productivity plays an important role in the composition of the assemblages and the replacement of species (Escobar *et al.* 2005). According to the CCA results, both the increase in altitude and the variation in temperature are determining factors in the distribution of the species diversity, while canopy cover and environmental humidity do not seem to show a direct association with this diversity, acting as a complement to the first two. Since a species can extend or reduce its distribution depending on changes in the environment or the availability of resources (Jiménez-Valverde & Hortal 2003), the conditions promoted by these circumstances can influence in the presence of the species represented by one or few individuals. In this way, in addition to environmental variables and a high fragmentation degree, the presence of mammals in the ecosystem (Nichols *et al.* 2009) and the introduction of livestock in the area may be limiting the Scarabaeinae distribution patterns (Escobar & Chacón de Ulloa 2000; Pulido 2009).

Also, the ecological functions of the Scarabaeinae decrease with increasing elevation, and in general, the decline is more evident than with the species richness (Nunes *et al.* 2018). In highly modified environments, Scarabaeinae assemblages are characterized by the dominance of a few species, mainly small of size, with a low representation of large species (Simmons & Ridsdill-Smith 2011). Our results show that the majority of the species captured are of small size (62.5%), of which, the generality are dominant species in each of the sites (*e.g. O. anthracinus, U. microcularis, U. micros, U. deavilai*), besides being, in general, habitual species of altered environments (Kohlmann & Solís 2001; Delgado & Kohlmann 2007), while the large species, for the most part, are represented by few individuals. Since the quantity and configuration of the trophic resource is a key factor in maintaining viable communities, large species may not find the resources to maintain a feasible population, causing local losses of species (Tonelli *et al.* 2018). Therefore, the loss of large-sized species within a community has negative consequences on the structure of the assemblage and its ecological functions can hardly be compensated by a larger number of small species (Shahabuddin *et al.* 2010; Gregory *et al.* 2015; Tonelli *et al.* 2018). In terms of nesting strategies, the high proportion of paracoprids species with respect to telecoprids and the reduced presence of endocoprids, coincides with other studies in the neotropical region (Barragán *et al.* 2011; Daniel *et al.* 2014). Paracoprid species are dominant in all sites along the gradient. This assemblage, like the telecoprids, show a negative relationship with the increase in altitude, meanwhile, the endocoprids are represented by only two species of low abundances (<5 individuals) in two of the sites. Open habitats or with a high modification degree favor the rapid drying of dung, affecting especially the species that present endocoprid and telecoprid relocation strategies, restricting both groups to extensive areas with a high plant cover percentage and microclimatic conditions that prevent the rapid desiccation of the resource, mainly to the endocoprid species that depend directly on the ephemeral character of the manure (Simmons & Ridsdill-Smith 2011). However, other aspects such as the physical characteristics (texture and humidity) and chemicals (nitrogen and magnesium levels) in the soil are also crucial for reproduction and can affect the Scarabaeinae subfamily beetle assemblages dynamics (de Farías *et al.* 2015; Nunes *et al.* 2018).

Our results show that local environmental conditions, linked to the strong changes in landscape heterogeneity induced by human activities, drastically affect the beetle structure and composition (Nichols *et al.* 2008), since forest conversion changes microclimatic conditions and reduces the availability of fecal resources of wild mammals, limiting the functional features of the beetles (Nichols *et al.* 2013). Herds of livestock (cattle in the lowlands and replaced by sheep in the highlands) allow the availability of the resource used by this beetle assemblage and is undoubtedly one of the factors that permeate Scarabaeinae distribution, all this by occupying the niche where large mammals were formerly distributed (Halffter & Edmonds 1982), also allowing the colonization of invasive species such as *D. gazella*, that restrict the populations of several species with similar behavior and inducing the extirpation of others (Filho *et al.* 2018).

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Figures

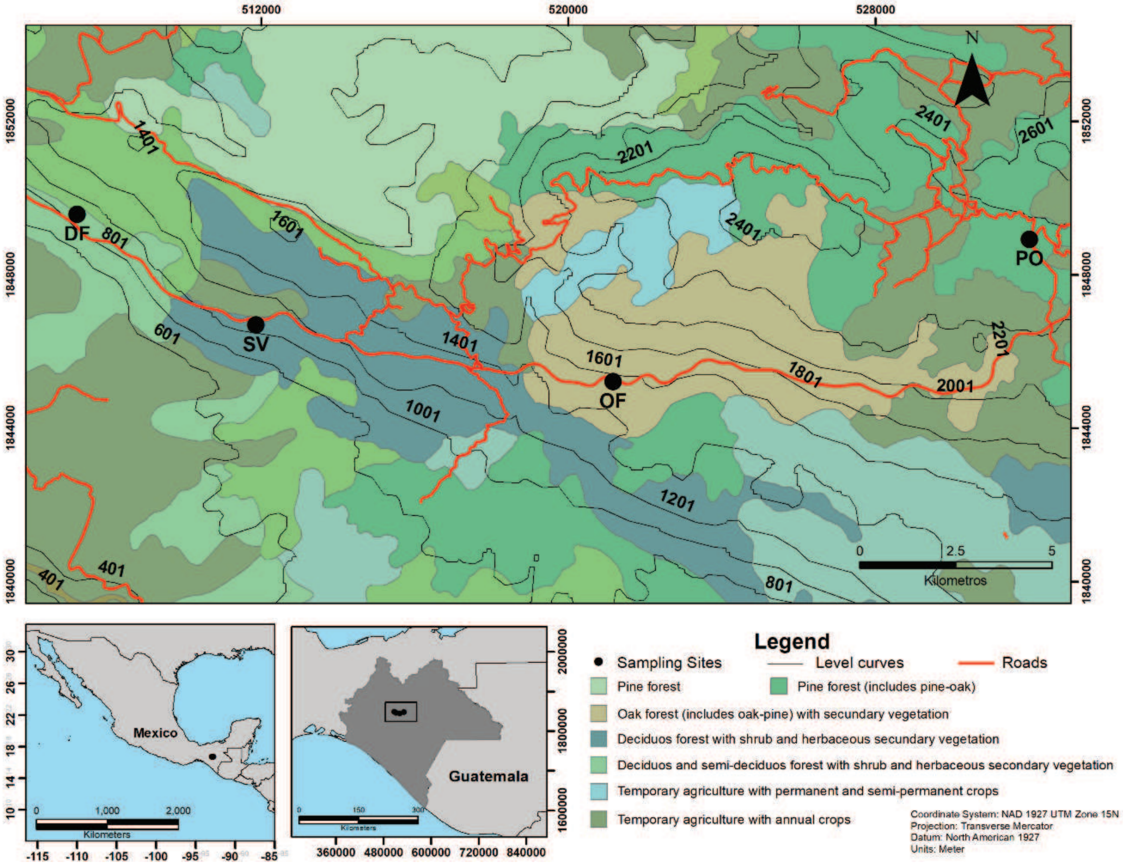

Figure 1. Location of the four sampling sites in an altitudinal gradient of the central region of Chiapas, Mexico. DF = Deciduous forest, SV = Secondary vegetation, OF = Oak forest, PO = Pine-oak forest.

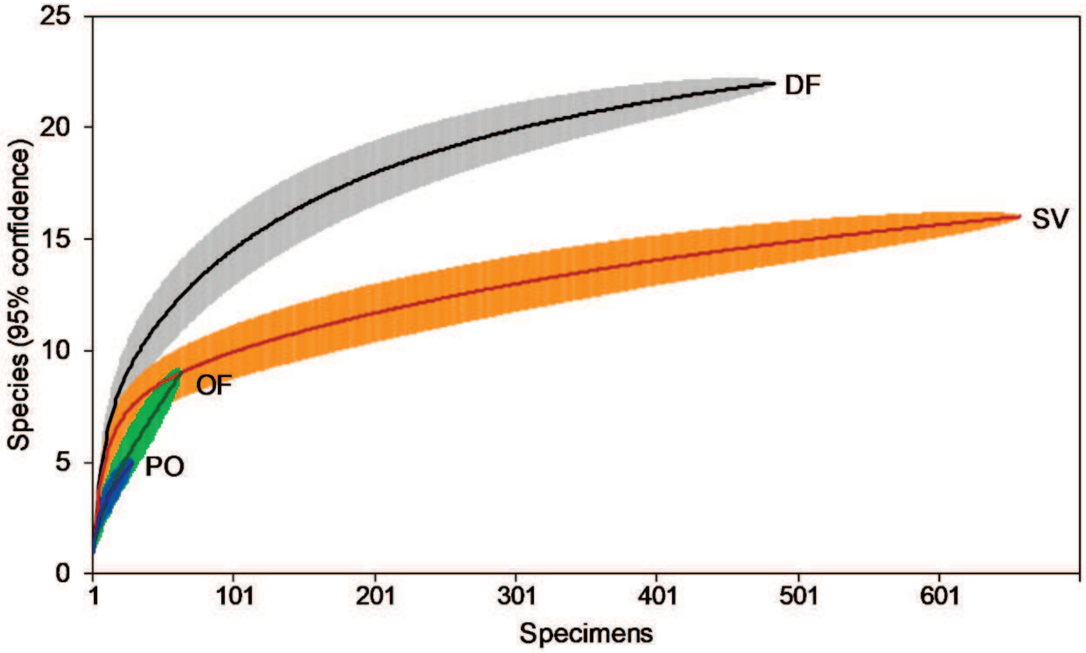

Figure 2. Rarefaction curves based on the number of individuals captured at each site of the altitudinal gradient. DF = Deciduous forest, SV = Secondary vegetation, OF = Oak forest, PO = Pine-oak forest.

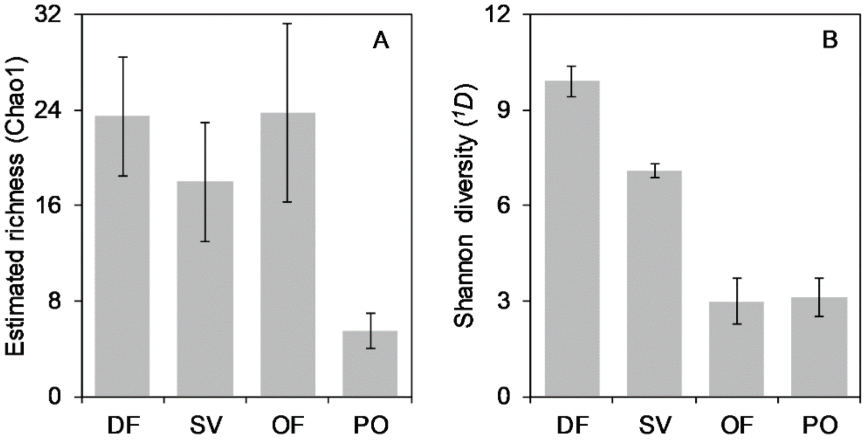

Figure 3. Estimation of species richness (a) and diversity of order ^1D (b) in the four sampling sites of the altitudinal gradient. Each line denotes the standard error (s.e.) with a

95% confidence interval calculated with 500 Bootstrap. DF = Deciduous forest, SV = Secondary vegetation, OF = Oak forest, PO = Pine-oak forest.

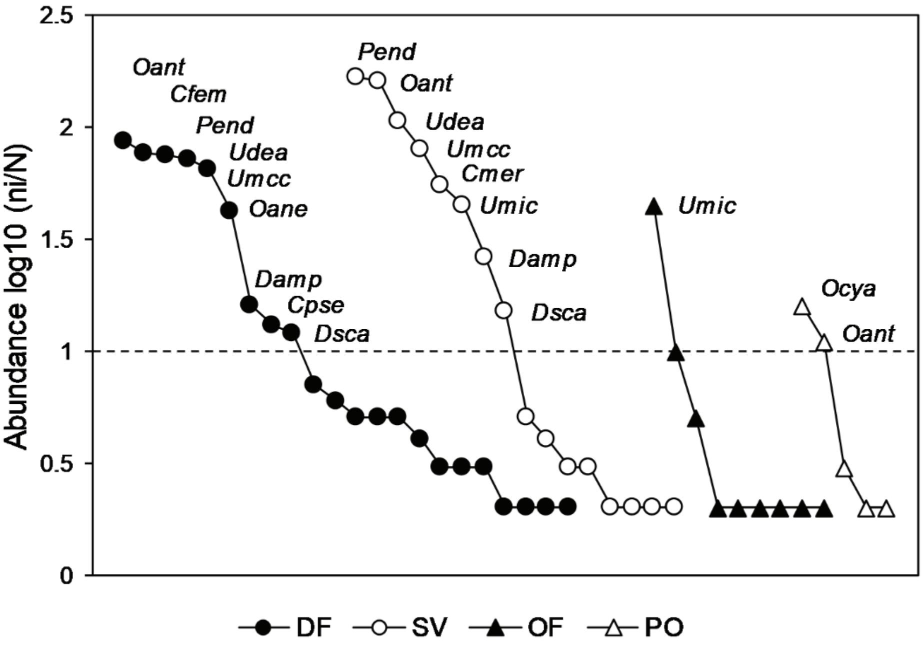

Figure 4. Rank-abundance curves based on the relative abundances of the species in each sampling site of the altitudinal gradient. The species below the dotted line are represented by less than 10 individuals. Cfem: *Canthon femoralis,* Cmer: *Canthon* aff. *meridionalis,* Dsca: *Deltochilum scabriusculum,* Damp: *Dichotomius amplicollis,* Oane: *Onthophagus anewtoni,* Oant: *Onthophagus anthracinus,* Ocya: *Onthophagus cyanellus,* Pend: *Phanaeus endymion*, Udea: *Uroxys deavilai,* Umcc: *Uroxys microcularis,* Umic: *Uroxys micros*. DF = Deciduous forest, SV = Secondary vegetation, OF = Oak forest, PO = Pine-oak forest.

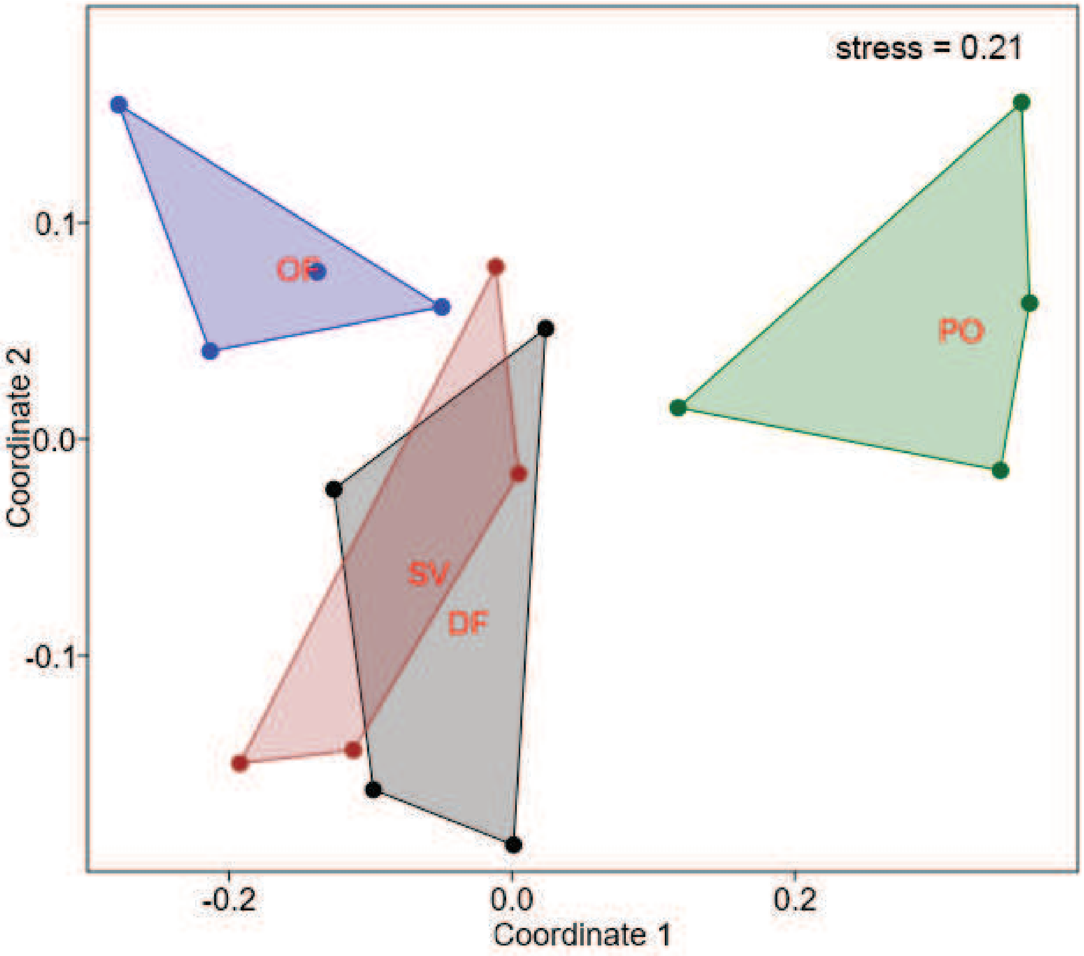

Figure 5. Non-metric Multidimensional Scaling (NMDS), constructed from the Bray-Curtis index, for the beetle communities in the four altitudinal gradient sites. DF = Deciduous forest, SV = Secondary vegetation, OF = Oak forest, PO = Pine-oak forest.

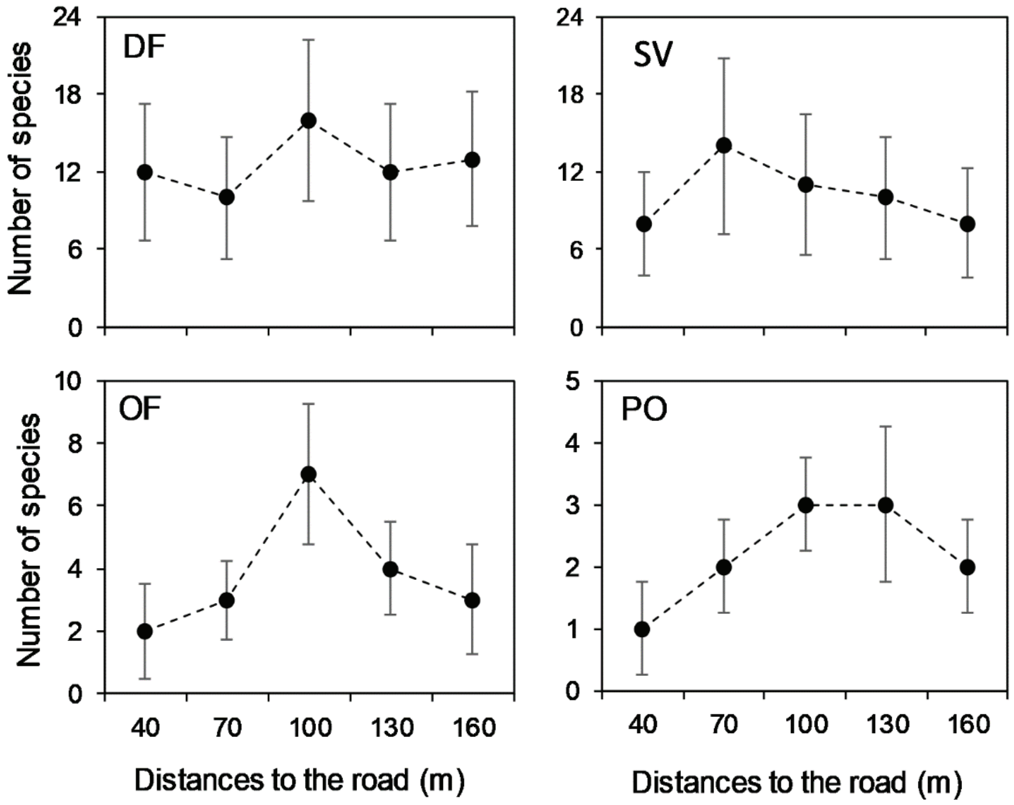

Figure 6. Number of species captured at different distances from the edge of the road (40, 70, 100, 130, 160 meters) at each sampling site of the altitudinal gradient. DF = Deciduous forest, SV = Secondary vegetation, OF = Oak forest, PO = Pine-oak forest.

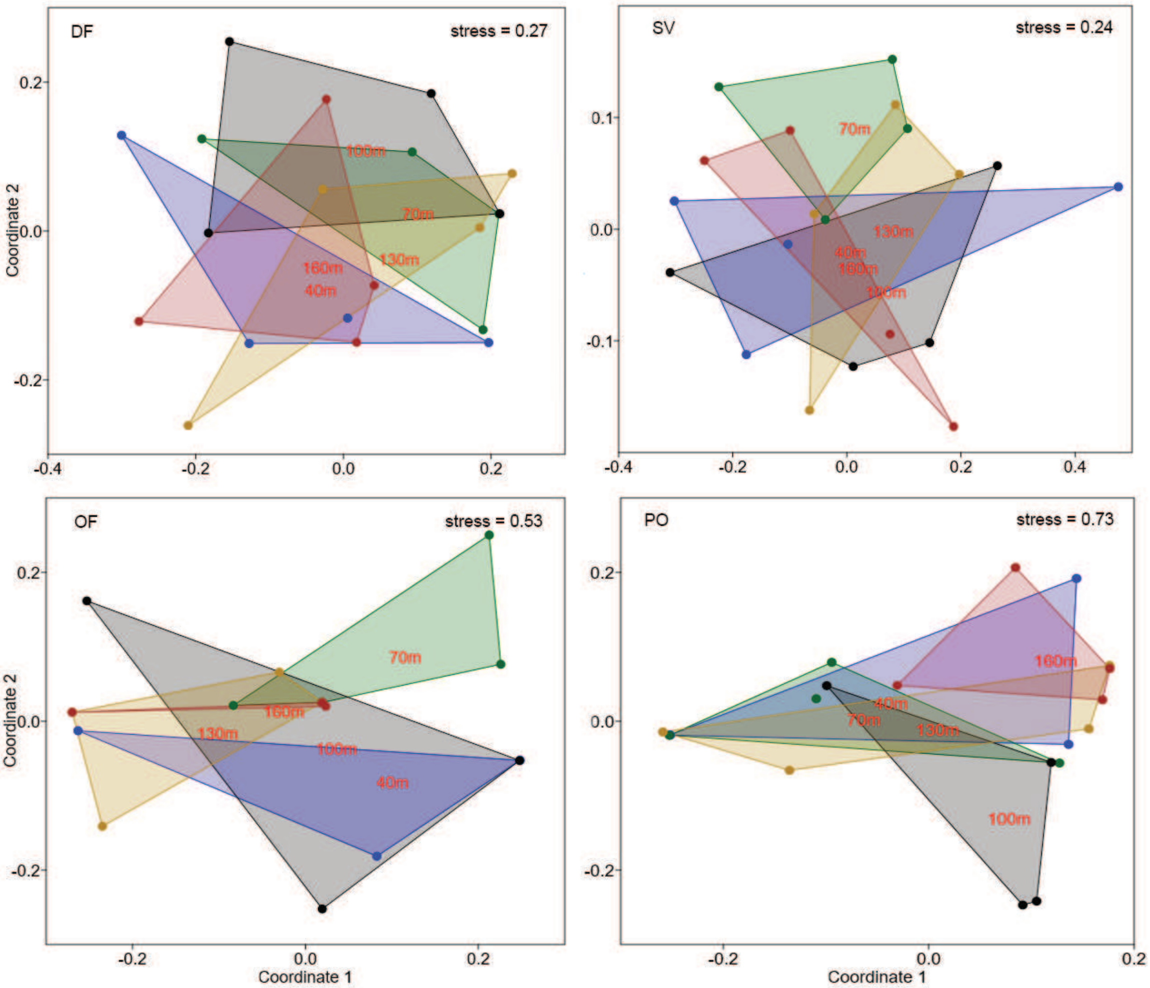

Figure 7. Non-metric Multidimensional Scaling (NMDS), constructed from the Bray-Curtis index, for beetle assemblages at five different distances from the road (40, 70, 100, 130, 160 meters) at the four gradient sites. DF = Deciduous forest, SV = Secondary vegetation, OF = Oak forest, PO = Pine-oak forest.

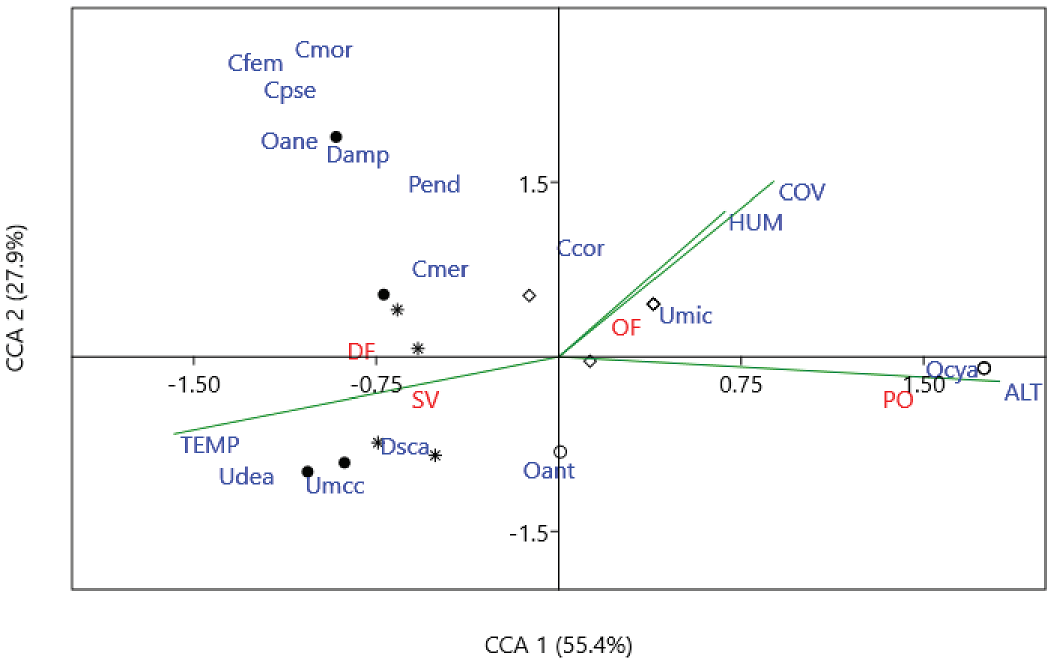

Figure 8. Canonical Correspondence Analysis (CCA) based on species with abundances ≥5 individuals and four repetitions of the environmental variables estimated during each sampling event at the collection sites. Cpse: *Canthidium pseudopuncticolle*, Cfem: *Canthon femoralis,* Cmer: *Canthon* aff. *meridionalis,* Camor: *Canthon morsei,* Ccor: *Coprophanaeus corythus,* Dsca: *Deltochilum scabriusculum,* Damp: *Dichotomius amplicollis,* Oane: *Onthophagus anewtoni,* Oant: *Onthophagus anthracinus,* Ocya: *Onthophagus cyanellus,* Pend: *Phanaeus endymion*, Udea: *Uroxys deavilai,* Umcc: *Uroxys microcularis,* Umic: *Uroxys micros*. DF (●) = Deciduous forest, SV (*) = Secondary vegetation, OF (○) = Oak forest, PO (◊) = Pine-oak forest.

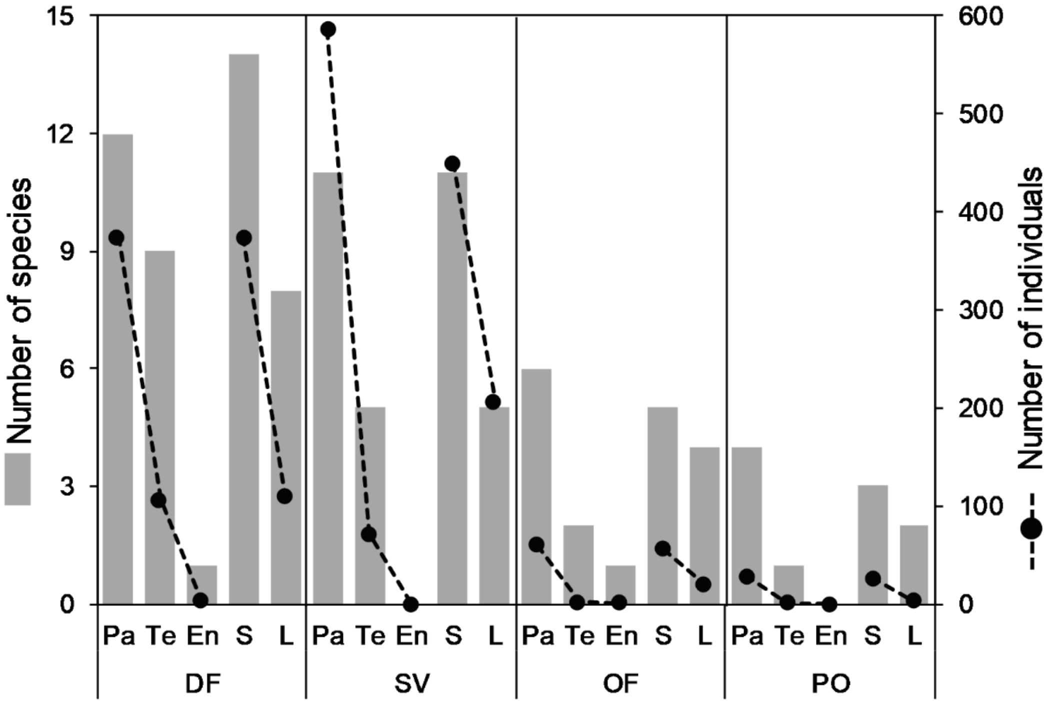

Figure 9. Contribution in the number of species and their abundances by body size and type of relocation in each sampling site of the altitudinal gradient. DF = Deciduous forest, SV = Secondary vegetation, OF = Oak forest, PO = Pine-oak forest.

Tables

Table 1. Matrix of characteristics of the sampling sites. DF: deciduous forest; SV: secondary vegetation; OF: oak forest; PO: pine-oak forest.

Sites	Matrix (soil use and vegetation)	Coordenadas geográficas	Altitud (m s.n.m.)	Humedad rel (%)	Temp. (°C)	Cobertura de dosel (%)
DF	Secondary vegetation, maize crops, cattle ranch	16°43’43.1” N 92°55’57.9” O	870±10	73.1±25.2	26.8±3.3	44.6±29.7
SV	Maize crops, deciduous forest, oak forest, cattle ranch	16°42’09.6” N 92°53’19.3” O	1100±6	72.7±24.4	24.5±3.7	52±21.5
OF	Maize and citrus crops, Secondary vegetation	16°41’22.2” N 92°48’05.1” O	1620±8	76.4±19.7	20.7±2.2	70.6±3.2
PO	Secondary vegetation, pine forest, maize and vegetable crops	16°43’22.2” N 92°42’02.1” O	2375±6	92.8±1.5	15.4±0.5	81.3±3.4

Table 2. Distribution of richness, abundance and estimated sampling coverage in the four collection sites. Rs= relocation strategy, En= endocoprid, Te= telecoprid, Pa= paracoprid; Sz= size, S= small, L= large.

Especies	**DF**	**SV**	**OF**	**PO**	**Rs**	**Sz**
ATEUCHINI						
Ateuchus rodriguezi De Borre	4				En	S
Uroxys deavilai Delgado & Kohlmann	71	105			Pa	S
Uroxys microcularis Howden & Young	64	79	1		Pa	S
Uroxys micros Bates	3	44	44		Pa	S
COPRINI						
Canthidium pseudopuncticolle Solís & Kohlmann	12	4			Pa	S
Copris chimalapensis Mora-Aguilar & Delgado				2	Pa	L
Copris costaricensis dolichocerus Matthews				1	Pa	L
Copris lugubris Boheman		1			Pa	L
Dichotomius amplicollis Harold	15	25			Pa	L
DELTOCHILINI						
Canthon championi Bates	4				Te	S

Canthon cyanellus LeConte	2				Te	S
Canthon euryscelis Bates	1				Te	S
Canthon femoralis Chevrolat	75				Te	S
Canthon humectus Say	1				Te	L
Canthon aff. *meridionalis* (Martínez, Halffter & Halffter)	6	54	1		Te	S
Canthon morsei Howden	5	1			Te	S
Canthon subhylinus Harold	1				Te	S
Canthon vazquezae (Martínez, Halffter & Halffter)		1			Te	S
Cryptocanthon cristobalensis Cook				1	Te	S
Deltochilum scabriusculum Bates	11	14	1		Te	L
ONITICELLINI						
Eurysternus magnus Castelnau			1		En	L
ONTHOPHAGINI						
Digitonthophagus gazella (Fabricius)	1				Pa	L
Onthophagus aff. *guatemalensis* Bates		2	1		Pa	S
Onthophagus anewtoni Howden & Génier	41				Pa	S
Onthophagus anthracinus Harold	85	157	9	10	Pa	S
Onthophagus atriglabrus Howden & Hill		3			Pa	S
Onthophagus cyanellus Bates				15	Pa	S
PHANAEINI						
Coprophanaeus aff. *boucardi* (Nevinson)	2				Pa	L
Coprophanaeus corythus Harold	2	2	1		Pa	L
Phanaeus endymion Harold	74	164	4		Pa	L
Phanaeus wagneri Harold	4				Pa	L
SISYPHINI						
Sisyphus mexicanus Harold		1			Te	S
Abundancia total	484	657	63	29		
Número de especies	22	16	9	5		
Cobertura del muestreo ($\hat{C}m$)	99.2	99.4	90.5	93.3		

CONCLUSIONES

- Los patrones de riqueza, diversidad y la dominancia de especies muestran una correlación negativa con el aumento de la altitud. No obstante, la cobertura de muestreo en todos los sitios sugiere una adecuada representación de la fauna de Scarabaeinae de la región.
- Con la similitud faunística se visualizan tres comunidades de escarabajos copronecrófagos, las cuales son concordantes con los tipos de vegetación en las cuales ocurren: los sitios de selva baja (DF-SV), bosque de encino y bosque de pino-encino.
- Las distancias desde la carretera en cada sitio de gradiente no muestran diferencias en la estructura y composición de los ensambles de escarabajos. Además de la presencia de un alto porcentaje de especies comunes de áreas abiertas, sugieren que el efecto de borde provocado por la carretera no se puede diferenciar a la distancia máxima de muestreo.
- Las características ambientales determinadas por el aumento de la altitud juegan un papel importante en la composición de los ensambles de escarabajos copronecrófagos. La fluctuación de las condiciones microclimáticas determinan la presencia o ausencia de especies.
- Los grupos funcionales muestran una composición de especies concordante a zonas con alto grado de perturbación. Las especies paracópridas son las que más se adecúan ante estos escenarios mientras que la presencia de telecópridos disminuye drásticamente y la de endocópridos es casi nula. A su vez, estas condiciones permiten que las especies invasoras se establezcan, induciendo la extirpación de especies menos tolerantes, principalmente las de talla grande.
- A pesar del alto grado de fragmentación y el efecto de borde causado por la carretera, los nuevos registros y la captura de algunas especies de rareza biogeográfica presentados aquí, resaltan la importancia de conservar los remanentes de bosques y selvas de la región que aún se mantienen para permitir poblaciones viables de escarabajos.

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