UNIVERSIDAD AUTONOMA DE CIENCIAS Y ARTES DE CHIAPAS

INSTITUTO DE CIENCIAS BIOLOGÍCAS

ELABORACIÓN DE TEXTOS

Ensambles de escarabajos peloteros en fragmentos de bosque y matriz adyacente: ¿son importantes las cercas vivas para preservar la diversidad en un paisaje fragmentado?

QUE PARA OBTENER EL TÍTULO DE

Licenciado en Biología

PRESENTA

MARTIN ALBERTO HERNÁNDEZ MOLINA

TUXTLA GUTIÉRREZ. CHIAPAS MARZO 2026

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RESUMEN

La fragmentación del bosque tropical caducifolio es uno de los principales procesos de transformación del paisaje en el sureste de México, donde la expansión de la agricultura y la ganadería ha generado un mosaico de fragmentos de vegetación natural inmersos en una matriz productiva. En este contexto, las cercas vivas elementos lineales formados por vegetación arbórea nativa que delimitan áreas ganaderas podrían desempeñar un papel relevante en la conservación de la biodiversidad al facilitar la conectividad entre fragmentos de bosque. El presente estudio evaluó los cambios en la diversidad, composición y estructura de los ensamblajes de escarabajos coprófagos (Coleoptera: Scarabaeidae: Scarabaeinae) en un paisaje fragmentado de la Depresión Central de Chiapas. El estudio se desarrolló en el Centro Universitario de Transferencia de Tecnología (CUTT) San Ramón ubicado en el municipio de Villaflores, Chiapas, donde se seleccionaron tres tipos de hábitat representativos del paisaje: fragmentos de bosque tropical caducifolio, cercas vivas y pastizales ganaderos. El muestreo se realizó durante la temporada de lluvias de 2019, utilizando trampas de caída cebadas con estiércol de cerdo. Se obtuvo un total de 2,025 individuos pertenecientes a 23 especies y 14 géneros. Los estimadores de cobertura indicaron una eficiencia de muestreo superior al 99 % en los tres hábitats. Los fragmentos de bosque presentaron la mayor riqueza y diversidad de especies, así como especies exclusivas, lo que resalta su importancia para la conservación de la fauna coprófaga. Las cercas vivas mostraron valores intermedios de riqueza y diversidad, mientras que los pastizales registraron la menor riqueza, aunque con altas abundancias dominadas por pocas especies. En términos de composición, los análisis de ordenación y similitud revelaron una alta afinidad entre los ensamblajes del bosque y las cercas vivas, sin diferencias estadísticamente significativas entre ambos, mientras que los pastizales presentaron una composición claramente diferenciada. Estos resultados sugieren la existencia de dos ensamblajes, uno asociado a hábitats con cobertura arbórea y otro característico de áreas abiertas. Funcionalmente, los ensamblajes estuvieron dominados principalmente por escarabajos paracópridos grandes en los tres tipos de hábitat, lo que indica una mayor tolerancia de este grupo a la perturbación. En contraste, los telecópridos presentaron bajas abundancias y una mayor sensibilidad a los cambios en el uso del suelo. En conclusión, los resultados demuestran que, aunque las cercas vivas no sustituyen a los fragmentos de bosque como hábitat primario, desempeñan un papel clave en la conectividad del paisaje, facilitando el movimiento de especies forestales a través de la matriz ganadera. Por ello, se destaca la importancia de promover y conservar cercas vivas como una estrategia complementaria para la conservación de la biodiversidad y el mantenimiento de funciones ecosistémicas en paisajes tropicales fragmentados.

ABSTRACT

The fragmentation of tropical deciduous forests is one of the main processes transforming the landscape in southeastern Mexico, where the expansion of agriculture and livestock farming has created a mosaic of natural vegetation fragments immersed in a productive matrix. In this context, living fences—linear elements formed by native tree vegetation that delimit livestock areas—could play an important role in biodiversity conservation by facilitating connectivity between forest fragments. The present study evaluates changes in the diversity, composition, and structure of dung beetle assemblages (Coleoptera: Scarabaeidae: Scarabaeinae) in a fragmented landscape of the Central Depression of Chiapas. The study was conducted at the Centro Universitario de Transferencia de Tecnología (CUTT) San Ramón, where three habitat types representative of the landscape was selected: fragments of tropical deciduous forest, live fences, and livestock pastures. Sampling was carried out during the 2019 rainy season, using pitfall traps baited with pig dung. A total of 2,025 individuals belonging to 23 species and 14 genera were obtained. Sampling coverage estimators indicated a sampling efficiency of over 99% in all three habitats. The forest fragments presented the greatest species richness and diversity, as well as exclusive species, highlighting their importance for the conservation of dung beetle fauna. The live fences showed intermediate values of diversity, while the pasture recorded the lowest richness, although with high abundances dominated by a few species. In terms of composition, ordination and similarity analyses revealed a high affinity between forest and living fence assemblages, with no statistically significant differences between them, while pasture showed a clearly differentiated composition. These results suggest the existence of two assemblages, one associated with tree-covered habitats and the other characteristic of open areas. Functionally, the assemblages were dominated mainly by large paracoprid beetles in all three habitat types, indicating a greater tolerance of this group to disturbance. In contrast, telecoprid beetles were less abundant and more sensitive to changes in land use. In conclusion, the results show that, although living fences do not replace forest fragments as primary habitat, they play a key role in landscape connectivity, facilitating the movement of forest species through the livestock matrix. Therefore, the importance of promoting and conserving living fences as a strategy is highlighted.

I. INTRODUCCIÓN

La fragmentación es un proceso mediante el cual una extensión de bosque continuo se transforma en una serie de fragmentos pequeños, aislados entre sí y rodeados por una matriz distinta al hábitat original, generalmente agrícola o ganadera (Fahrig, 2003). Como consecuencia de la fragmentación y la destrucción del hábitat, se producen cambios progresivos en la configuración del paisaje, reflejados en la pérdida regional de cobertura vegetal, la reducción del tamaño de los fragmentos y el incremento de la distancia entre ellos (Santos y Tellería, 2006). Los bosques tropicales son los ecosistemas con mayor diversidad biológica del planeta, al albergar cerca del 70 % de la flora y fauna mundial. Por ello, su fragmentación y deforestación representan uno de los principales problemas para la conservación y el manejo de la biodiversidad, ya que provocan la disminución de las poblaciones de numerosas especies y pueden conducir a extinciones locales o regionales (Wilson et al., 2016).

El estado de Chiapas, ubicado en el sureste de México, es una región de gran relevancia ecológica. Su posición geográfica y compleja fisiografía han favorecido el desarrollo de una amplia diversidad de ecosistemas. Dentro de esta compleja orografía, la región fisiográfica de la Depresión Central se distingue por ser una extensa zona semi plana que cubre aproximadamente el 12 % (8,712 km^2) del territorio estatal. La vegetación predominante en esta región es el bosque tropical caducifolio, el cual es particularmente importante por albergar elementos endémicos de diversos grupos de plantas, principalmente de las familias Asteraceae y Fabaceae (Pérez-Farrera y Espinoza, 2010; Pérez-Farrera y Sánchez, 2010). Sin embargo, debido a su historia de uso del suelo y a las características de este tipo de vegetación, la Depresión Central ha sido una de las regiones más transformadas del estado. Actualmente, la cobertura de bosque primario no supera el 2 % del territorio, mientras que el resto está dominado por diversos usos del suelo y áreas de vegetación secundaria en diferentes etapas sucesionales (Rocha-Loredo et al., 2010). Entre las principales amenazas a la vegetación de la región se encuentran la ganadería extensiva y la agricultura, particularmente los monocultivos como el maíz, cuyas prácticas de manejo, como la agricultura de roza, tumba y quema, han generado impactos negativos significativos (Pérez-Farrera y Espinoza, 2010; Pérez-Farrera y Sánchez, 2010).

Con frecuencia, para delimitar áreas destinadas a la agricultura y la ganadería, los productores locales implementan elementos lineales arbolados conocidos como cercas vivas (Harvey et al., 2005). Dependiendo del número de especies y de la altura del dosel, las cercas vivas pueden clasificarse como simples o multiestrato. Las cercas simples están conformadas por una o dos especies dominantes y suelen ser podadas periódicamente, presentando una alta capacidad de rebrote. En contraste, las cercas multiestrato incluyen más de dos especies con diferentes alturas y usos (maderables, frutales, forrajeros, medicinales u ornamentales), generalmente sin podas frecuentes, lo que permite una mayor cobertura vegetal a lo largo del año (Villanueva et al., 2005). Las cercas vivas contribuyen a la conservación de especies arbóreas nativas, ayudan a mantener condiciones de humedad, reducen la temperatura ambiental y disminuyen la erosión del suelo (Harvey et al., 2003; Martínez-Camilo et al., 2007; Zamora Pedraza et al., 2022). Asimismo, tienen un alto potencial para proporcionar hábitat y recursos a diversos grupos taxonómicos, incrementando la conectividad entre parches de vegetación aislados dentro de paisajes dominados por matrices agrícolas (Estrada y Coates-Estrada, 2001; Lang et al., 2003; Garbach et al., 2010; Tobar y Ibrahim, 2010; Ramírez-Albores, 2010).

Entre los diferentes taxones utilizados para evaluar los efectos de la fragmentación sobre la biodiversidad, numerosos grupos de invertebrados principalmente insectos responden de manera diversa a distintas escalas espaciales (Gerlach et al., 2013). En regiones tropicales, los escarabajos coprófagos de la subfamilia Scarabaeinae (Coleoptera: Scarabaeidae) han sido identificados como un grupo ideal para estudiar el impacto de las actividades humanas sobre la biodiversidad, debido a su alta sensibilidad a los cambios en el uso del suelo, su diversidad de rasgos funcionales y su fuerte dependencia de la estructura de la vegetación (McGeoch et al., 2002; Spector, 2006; Nichols et al., 2008; Otavo et al., 2013; Noriega et al., 2021a). Además, por la forma en que manipulan el recurso alimenticio, las especies de Scarabaeinae desempeñan funciones ecosistémicas clave, como la descomposición del estiércol, el reciclaje de nutrientes, la bioturbación del suelo, la dispersión secundaria de semillas y el control de gases de efecto invernadero (Nichols et al., 2008; Ridsdill-Smith y Edwards, 2011; Slade et al., 2016). A ello se suma que su biología y taxonomía son relativamente bien conocidas y que son fáciles y económicas de muestrear y monitorear (Favila y Halffter, 1997; Spector, 2006).

II. OBJETIVOS

2.1 Objetivo general

Evaluar los ensamblajes de los escarabajos del estiércol (Coleoptera: Scarabaeidae: Scarabaeinae) en un paisaje fragmentado en la región fisiográfica Depresión Central de Chiapas, México.

2.2 Objetivos específicos

- Determinar la diversidad de escarabajos del estiércol en tres hábitats contrastantes (bosque, cercas vivas, pastizal) en un paisaje fragmentado de la depresión central de Chiapas
- Comparar la estructura y composición de especies entre los tres hábitats de estudio
- Identificar las especies de importancia ecológica para cada uno de los hábitats analizados

III. MÉTODO

3.1 Área de estudio

El área de estudio se localizó en el Centro Universitario de Transferencia de Tecnología (CUTT) San Ramón (16°15’20” N, 93°15’19” O; 560 m s. n. m.), ubicado en el municipio de Villaflores, en la región fisiográfica de la Depresión Central de Chiapas, México. El CUTT San Ramón es un centro de investigación agrícola de la Universidad Autónoma de Chiapas (UNACH) con una extensión de 117 ha, cuya vegetación original corresponde a selva baja caducifolia. Actualmente, el área se utiliza principalmente para la ganadería extensiva, con zonas de pastizal abierto delimitadas por cercas vivas compuestas por vegetación nativa remanente (multiestrato). Entre estas cercas persisten pequeños fragmentos de selva baja caducifolia y áreas de vegetación secundaria (Fig. 1).

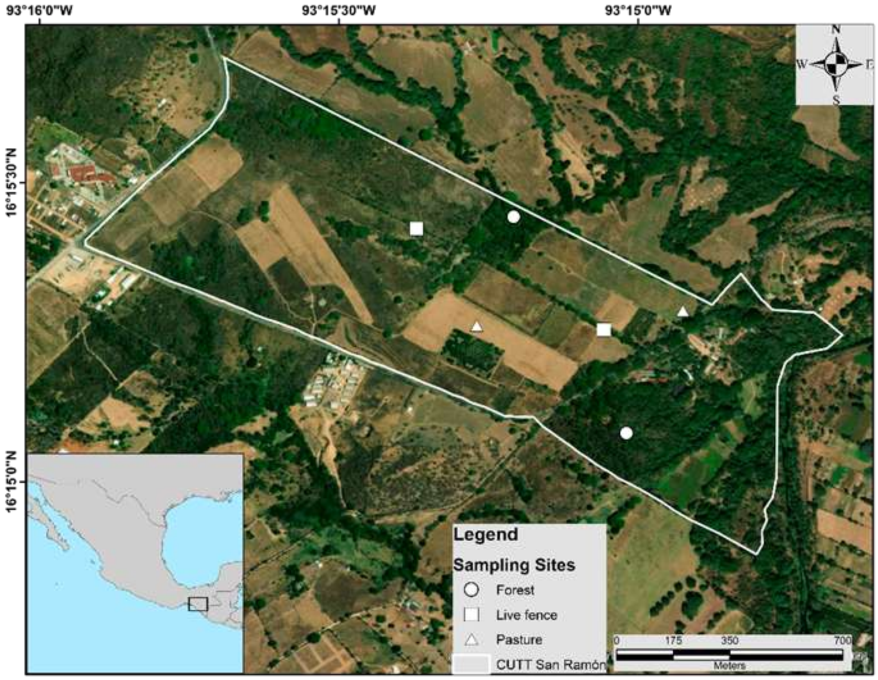

Figura 1. Ubicación de transectos de muestreo en tres hábitats del CUTT San Ramón, Villaflores, Chiapas, México.

De acuerdo con la clasificación climática de Köppen (García 2004), la región presenta un clima cálido subhúmedo con marcada estacionalidad en la precipitación, caracterizada por una temporada de lluvias entre mayo y octubre (≈90 % de la precipitación anual) y una temporada seca entre noviembre y abril.

3.2 Muestreo de escarabajos

Estudios previos han reportado una mayor abundancia y riqueza de escarabajos coprófagos durante la temporada de lluvias en la Depresión Central de Chiapas (Rodríguez-López et al. 2019; Sánchez-Hernández et al. 2021). Por ello, el muestreo se realizó cada tres semanas entre julio y octubre de 2019 (seis muestreos en total), considerando los meses con mayor precipitación y maximizando el éxito de captura.

El muestreo se llevó a cabo en tres tipos de hábitat predominantes en la región (Fig. 1): fragmentos de selva baja caducifolia, pastizales ganaderos adyacentes y cercas vivas multiestrato, formadas por vegetación nativa remanente que delimita los potreros. En cada hábitat se establecieron dos transectos con seis trampas de caída (12 trampas por hábitat). Las trampas dentro de cada transecto se separaron por una distancia mínima de 50 m para evitar interferencias entre ellas y permanecieron activas durante un periodo efectivo de 48 h, considerado el tiempo mínimo para un muestreo eficiente (Mora-Aguilar et al. 2023).

Las trampas consistieron en recipientes de 10 cm de diámetro y 8 cm de profundidad (500 ml), enterrados a nivel del suelo. Cada trampa se cebó con aproximadamente 30 g de estiércol de cerdo doméstico Sus scrofa (L. 1758), ya que es uno de los cebos más recomendados y el que atrae el mayor número de especies en la región (Sánchez-Hernández et al. 2018; Mora-Aguilar et al. 2023). En el interior de cada trampa se vertieron 250 ml de una solución de agua con detergente a baja concentración para romper la tensión superficial y evitar que los individuos escaparan. El cebo se colocó en una gasa sostenida con alambres a nivel de la superficie del recipiente.

3.3 Determinación taxonómica

Los escarabajos capturados se preservaron en etanol al 70 % y se identificaron hasta nivel de especie mediante el uso de diversas claves taxonómicas y descripciones originales (Rivera-Cervantes y Halffter 1999; Kohlmann y Solís 2001; Génier y Kohlmann 2003; Peraza y Deloya 2006; Delgado y Kohlmann 2007; Edmonds y Zídek 2012; Kohlmann y Vaz-de-Mello 2018; Moctezuma et al. 2019; Chamé-Vázquez et al. 2020; Moctezuma et al. 2021). Asimismo, las identificaciones se corroboraron mediante comparación con ejemplares de referencia depositados en la Colección Entomológica de El Colegio de la Frontera Sur (ECOSUR), Tapachula, Chiapas, México (ECO-TAP-E).

3.4 Análisis de datos

La cobertura de muestreo se estimó para evaluar la completitud del muestreo (Chao y Jost 2012). La diversidad se estimó en términos del número efectivo de especies o diversidad de orden. El exponente q determina la influencia de la abundancia de las especies en los valores de diversidad y varía de 0 a infinito (Jost 2006). En este estudio se utilizaron: 0D, que mide la riqueza de especies y es insensible a la abundancia; 1D, obtenido a partir del exponencial del índice de Shannon y sensible a las especies abundantes; y 2D, obtenido mediante el inverso del índice de Simpson y sensible a las especies dominantes de la comunidad (Jost 2006).

Los análisis se realizaron con 500 réplicas bootstrap y con intervalos de confianza del 95 % como criterio estadístico de comparación, utilizando el paquete iNEXT (Hsieh et al. 2016) en el software R v.3.6.2 (R Core Team 2021). Se elaboraron curvas de rango-abundancia para examinar la estructura de los ensamblajes y determinar cambios en la identidad de las especies más frecuentes o dominantes entre los tres hábitats. Los cambios en la distribución de abundancias indican diferencias en la equidad de especies entre ensamblajes (Magurran 2004). Estas curvas se graficaron con el paquete ggplot2 en R (Wickham 2016).

Se utilizó un escalamiento multidimensional no métrico (NMDS) para visualizar los patrones de agrupamiento en la composición de especies de escarabajos coprófagos entre los hábitats analizados. Asimismo, se aplicó un análisis de similitud (ANOSIM) para evaluar diferencias en la composición de especies entre hábitats. Ambos análisis se realizaron en el software PAST v.4.1 (Hammer et al. 2001), utilizando el coeficiente de similitud de Morisita-Horn, considerado uno de los índices más confiables e informativos (Jost 2007).

El valor indicador (IndVal) propuesto por Dufrêne y Legendre (1997) se utilizó para evaluar la asociación de las especies con alguno de los tres hábitats de estudio. Este método considera la frecuencia (presencia/ausencia) y la abundancia relativa promedio de cada especie en una muestra. El IndVal expresa la especificidad y fidelidad de una especie a un hábitat, alcanzando su valor máximo cuando todos los individuos de una especie se encuentran exclusivamente en un solo sitio y están presentes en todas las muestras de dicho sitio. Este análisis se realizó en el software PAST v.4.1 (Hammer et al. 2001).

Las especies muestreadas se clasificaron en grupos funcionales con base en sus estrategias primarias de relocalización del recurso alimenticio (gremios): endocópridos, paracópridos y telecópridos (Tonelli 2021). Las especies endocópridas viven dentro del excremento y no realizan asignación del recurso; las paracópridas construyen túneles debajo o adyacentes a la fuente de alimento y transportan el estiércol al fondo; mientras que las telecópridas remueven porciones de estiércol, las hacen rodar y posteriormente las entierran. Cada especie también se asignó a una de tres categorías de tamaño corporal, según Noriega et al. (2021b): grande (>18 mm), mediano (10–18 mm) o pequeño (<10 mm). La combinación de gremio y tamaño corporal permitió definir los grupos funcionales.

Los ensamblajes por abundancia de grupos funcionales en cada sitio se compararon mediante un modelo lineal generalizado con distribución de Poisson. Cuando se observaron diferencias significativas, se aplicó un método de contrastes directamente sobre el modelo, utilizando el paquete gmodels de R (Warnes et al. 2022). Para evitar sesgos (ausencia de varianza), los grupos funcionales representados por dos o menos individuos en cada hábitat no se incluyeron en el análisis.

IV. ARTÍCULO CIENTÍFICO

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ORIGINAL RESEARCH ARTICLE

Dung beetle assemblages in forest fragments and adjacent matrix: are live fences important for preserving diversity in a fragmented landscape?

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Abstract

The fragmentation of tropical deciduous forests in the Mexican state of Chiapas has resulted in small remnants immersed in an agricultural matrix. Often, these forest fragments are delimited by live fences, which may be ecologically important in terms of the potential habitat connectivity. In this work, we compared the structure, diversity, and species composition of dung beetle assemblages in three representative habitats (forest, live fences, and cattle pastures) in the region. Six samplings were conducted during the 2019 rainy season, using pitfall traps baited with pig dung. A total 2,025 individuals of 23 species and 14 genera, were captured. Diversity was higher in the forest, but species composition reveals a high similarity of this habitat with the live fence, while the cattle pasture composition shows a clear segregation, indicating the existence of two different assemblages between the three habitats. The high similarity with forest in species composition and the presence of an indicator species suggest that live fences function as conspicuous elements that allow high connectivity between forest patches, facilitating the movement of some species that avoid open areas in the agricultural landscape.

Keywords Agricultural matrix · Cattle pastures · Corridors · Indicator species · Neotropics · Scarabaeinae

Introduction

Fragmentation is a process in which an extension of a continuous forest is transformed into a series of small fragments, isolated from each other, where a matrix different from the original one predominates (e.g., usually an agricultural or grazing area such as a pasture; Fahrig 2003). With the fragmentation and subsequent destruction of habitats, there is a progressive change in the configuration of the landscape, which is reflected in variables such as regional loss in terms of the decrease in coverage of a given habitat, a reduction in the size of the resulting fragments and an increase in the distance between them (Santos and Telleria 2006). Tropical forests are the most biologically diverse ecosystems because they are home to nearly 70% of the planet's flora and fauna. Therefore, their fragmentation and consequent deforestation represent one of the main problems in the conservation and management of biodiversity, since it implies a decrease in the populations of many species and can lead to local or regional extinction (Wilson et al. 2016).

The state of Chiapas, located in southeastern Mexico, comprises an area of great ecological relevance. Factors such as geographic position and physiography of the state have allowed the development of a great diversity of ecosystems. In its complex orography, the Central Depression

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is a physiographic region distinguished for being an extensive semi-flat area that covers about 12% (8,712 km^2) of the state's territory. The predominant vegetation of this region is tropical deciduous forest and is characterized by being important for endemic elements of different plant groups, mainly of the Asteraceae and Fabaceae families (Pérez-Farrera and Espinoza 2010; Pérez-Farrera and Sánchez 2010). However, due to the vegetation type and land use history, this area has been one of the most transformed in the state. Its forest cover is quite degraded and currently, the total area of forest with primary vegetation covers no more than 2% of the region, while the rest of the territory is dominated by diverse land uses and areas of secondary vegetation in different stages of succession (Rocha-Loredo et al. 2010). Among the most significant threats to the vegetation in the area are extensive cattle ranching and agriculture, mainly monocultures such as maize, where cultivation techniques (slash-and-burn agriculture) have had very negative effects (Pérez-Farrera and Espinoza 2010; Pérez-Farrera and Sánchez 2010).

Frequently, for the delimitation of areas dedicated to agriculture and livestock, local farmers and ranchers implement linear wooded elements, known as live fences (Harvey et al. 2005). Depending on the number of species and the height of the canopy, live fences can be called simple or multi-strata. Simple fences are those with one or two dominant species. These fences are usually pruned every few years and have a high regrowth capacity. Multi-strata have more than two species of different heights and uses (timber, fruit, forage, medicinal, ornamental). Usually, species in the multi-strata fence are not pruned and generate a greater cover throughout the year (Villanueva et al. 2005). Live fences can contribute to the conservation of various native tree species, help maintain humidity conditions, keep temperatures low, and reduce soil erosion (Harvey et al. 2003; Martínez-Camilo et al. 2007; Zamora Pedraza et al. 2022). Additionally, they have an important potential to provide habitats and resources for different taxonomic groups, increasing connectivity between isolated patches of vegetation amid a predominantly agricultural landscape (Estrada and Coates-Estrada 2001; Lang et al. 2003; Garbach et al. 2010; Tobar and Ibrahim 2010; Ramírez-Albores 2010).

Among the different taxa used to assess the effect of fragmentation on biodiversity, numerous invertebrate groups, mainly insects, respond in diverse ways at diverse scales (Gerlach et al. 2013). In tropical regions, dung beetles of the subfamily Scarabaeinae (Coleoptera: Scarabaeidae) have been identified as an ideal group to study the impact of human activities on biodiversity due to their responses to land-use change, as well as their diversity of functional traits and high dependence on vegetation structure (McGeoch et al. 2002; Spector 2006; Nichols et al. 2008; Otavo et al. 2013; Noriega et al. 2021a). Because of the way they manipulate their resources, Scarabaeinae species perform many ecosystem functions, including manure decomposition, nutrient recycling, bioturbation, secondary seed dispersal, and greenhouse gas control (Nichols et al. 2008; Ridsdill-Smith and Edwards 2011; Slade et al. 2016). In addition, their biology and taxonomy are relatively well known, and they are easy and inexpensive to sample and monitor (Favila and Halffter 1997; Spector 2006).

This study aims to evaluate changes in the diversity, composition, and structure of dung beetle assemblages in three habitats in a fragmented landscape of the Central Depression of Chiapas, Mexico. We also evaluated the potential habitat preference of the species found and whether live fences represent a suitable habitat for the fauna. Are live fences important for maintaining the connectivity of dung beetle assemblages in fragmented landscapes? Our working hypothesis was that species diversity would be higher in forest fragments, as they offer suitable conditions for a variety of species with different habitat preferences; in turn, live fences are expected to have a high percentage of similarity to forest fragments, as they may come to act as corridors that facilitate species movement between habitats at the landscape scale.

Materials and methods

Study area

The study area was located at the Centro Universitario de Transferencia de Tecnología (CUTT) San Ramón (16°15'20" N, 93°15'19" W, 560 m a.s.l.), located in the municipality of Villaflores, in the physiographic region Central Depression of Chiapas, Mexico. CUTT San Ramón is a center for agricultural research of the Universidad Autónoma de Chiapas (UNACH) covering 117 ha, whose original vegetation is tropical deciduous forest. Currently, this area is mainly used for cattle ranching with open pasture areas, limited by live fences made up of remnant native vegetation (multi-strata), among which, small fragments of tropical deciduous forest and areas of secondary vegetation persist (Fig. 1). According to Köppen's climate classification (García 2004), the region where this area is located is characterized by a warm sub-humid climate and a marked seasonality of precipitation, defined by a rainy season between May and October

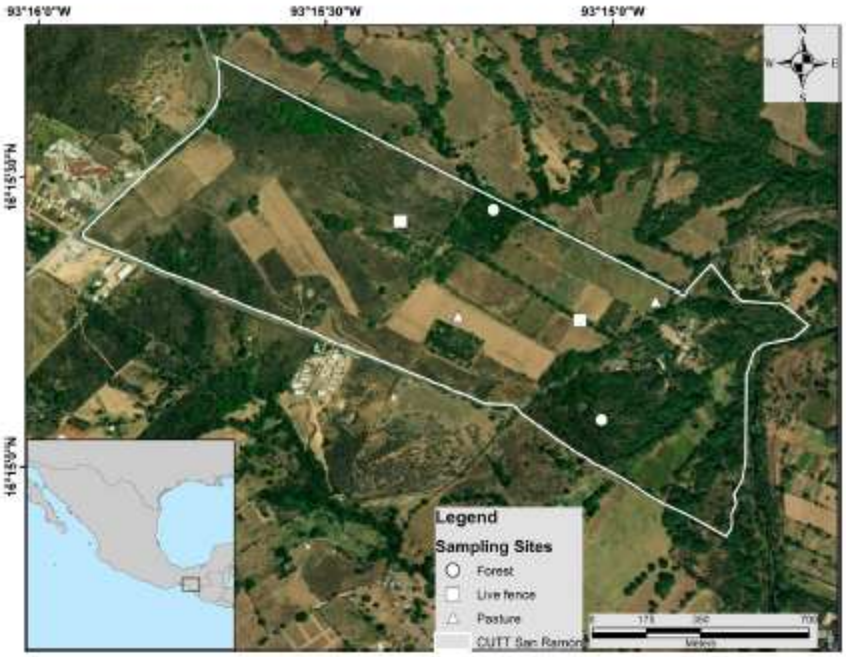

Fig. 1 Location of sampling transects in cattle pasture (triangles), live fences (squares) and forest fragments (dots) in the CUTT San Ramón, Central Depression of Chiapas, southern Mexico

(~90% of total rainfall) and a dry season between November and April.

Dung beetle sampling

Previous studies observed a higher abundance and richness of dung beetles during the rainy season of the Central Depression of Chiapas (Rodríguez-López et al. 2019; Sánchez-Hernández et al. 2021), therefore sampling was conducted every three weeks between July and October 2019 (six samplings in total), considering the months of higher rainfall and maximizing the success in captures. Sampling was conducted in three types of habitats predominant in the region (Fig. 1): patches of tropical deciduous forest (DF, 3.5 and 8 ha), adjacent cattle pastures (CP, 6.7 and 7 ha), and multi-strata live fences (LF, 350 and 450 m in length), made up of remnant native vegetation that delimits pasturelands. At each habitat, two transects with six pitfall traps (12 per habitat) were established. The traps of each transect were separated by a minimum distance of 50 m to prevent inter-trap interference and they were active for an effective period of 48 h, considered the minimum time for efficient sampling (Mora-Aguilar et al. 2023). The traps consisted of containers of 10 cm diameter and 8 cm deep (500 ml), buried at ground level. Each trap was baited with approximately 30 g of *Sus scrofa* (L. 1758) domestic pig manure, as it is one of the most recommended baits and the one that attracts the highest number of species in the region (Sánchez-Hernández et al. 2018; Mora-Aguilar et al. 2023). Inside each trap, 250 ml of water and detergent solution at low concentration was poured to break the surface tension and prevent individuals from escaping. The bait was placed in a gauze held with wires at the surface level of the container.

Taxonomic determination

Captured beetles were preserved in 70% ethanol and identified to species level using various taxonomic keys and original descriptions (Rivera-Cervantes and Halffter 1999; Kohlmann and Solís 2001; Génier and Kohlmann 2003; Peraza and Deloya 2006; Delgado and Kohlmann 2007; Edmonds and Zídek 2012; Kohlmann and Vaz-de-Mello 2018; Moctezuma et al. 2019; Chamé-Vázquez et al. 2020; Moctezuma et al. 2021); they were also compared with reference specimens deposited in the Insect Collection of El Colegio de la Frontera Sur (ECOSUR), Tapachula, Chiapas, Mexico (ECO-TAP-E).

Data analysis

Sample coverage ($\hat{C}m$) was estimated to measure the sampling completeness (Chao and Jost 2012). Diversity was estimated in terms of the effective number of species or diversity orders qD. The exponent q determines the influence of species abundance on diversity values and ranges from 0 to infinity (Jost 2006). In this study we used: ^{0}D, which measures species richness and is insensitive to species abundance; ^{1}D, obtained using the entropy of Shannon's exponential and is sensitive to abundant species; and ^{2}D, which was obtained using the inverse of Simpson's index and is sensitive to dominant species in the community (Jost 2006). Analyses were conducted with 500 Bootstrap replicates and 95% confidence intervals as the statistical criteria for comparison using the iNEXT package (Hsieh et al. 2016) in R software v.3.6.2 (R Core Team 2021). Rank/abundance curves were performed to examine assemblage structure and determine changes in the identity of the most frequent or dominant species among the three habitats. Information related to changes in the distribution of abundances indicates differences in species evenness among assemblages (Maguran 2004). These curves were plotted with the ggplot2 package in R (Wickham 2016).

We used a non-metric multidimensional scaling (NMDS) to visualize the grouping patterns in dung beetle species composition for the different habitats analyzed. We also used an analysis of similarity (ANOSIM) to test for differences in dung beetle composition between habitats. These analyses were performed in PAST v.4.1 software (Hammer et al. 2001), using the Morisita-Horn similarity coefficient, as this index is considered one of the most reliable and informative (Jost 2007).

The indicator value (IndVal) proposed by Dufrêne and Legendre (1997) was used to evaluate the associations of beetle species to one of the three study habitats. This method considers the frequency (presence/absence) and average relative abundance of each species in a sample. The IndVal expresses the specificity and fidelity of a species to a habitat, i.e., it reaches a maximum value when all individuals of a given species are found exclusively at a single site and are present in all samples at that site. This analysis was performed in PAST v.4.1 software (Hammer et al. 2001).

We classified the sampled species into functional groups based on their primary food relocation strategies (i.e., guilds): endocoprids, paracoprids or telecoprids (Tonelli 2021). Endocoprid species live within a dung pat and do not exhibit resource allocation; paracoprid species construct tunnels below or adjacent to the food source and transport dung to the bottom; and telecoprid species remove portions of dung, which are rolled and then buried. Each species was also assigned to one of three size categories, as proposed by Noriega et al. (2021b): large (> 18 mm), medium (10–18 mm), or small (< 10 mm). We combined guilds and average body size to define functional groups (Table 1). Assemblages by abundances of functional groups within each site were compared with a generalized linear model (GLM) with Poisson distribution. Where significant differences were observed, a contrast method was used directly over the model using the R package *gmodels* (Warnes et al. 2022). To avoid bias (no variance) in the results, when functional groups were represented by two or fewer individuals in each habitat they were not included in the analysis.

Results

A total of 2,025 individuals belonging to 23 species and 14 genera of the subfamily Scarabaeinae were captured (Table 1). *Onthophagus* Latreille, 1802 was the genus with the highest species richness (s = 4 spp), while *Dichotomius* Hope, 1838 had the highest abundance (*n* = 808, 39.9%). *Dichotomius amplicollis* (Harold, 1869) (*n* = 741), *Canthidium laetum* Harold, 1867 (*n* = 404), *Phanaeus balthasari* Arnaud, 2001 (*n* = 230), *Canthidium pseudoperceptibile* Kohlmann & Solís, 2006 (*n* = 205) and *Phanaeus demon* Castelnau, 1840 (*n* = 174) were the most abundant species and account 86.6% of the individuals collected. In contrast, *Canthon humectus* (Say, 1832), *Deltochilum sublaeve* (Bates, 1887), *Euoniticellus intermedius* (Reiche, 1849), *Onthophagus corrosus* Bates, 1887 and *Onthophagus hoepfneri* Harold, 1869 were represented by only one individual.

The sample coverage estimator revealed a high sampling efficiency, with completeness values above 99% in the three habitats (Table 1), indicating an adequate methodological design to capture the local diversity of Scarabaeinae. The forest presented the highest richness with 18 species (*n* = 711, 35.11%), finding four exclusive species (*D. sublaeve*, *O. corrosus*, *O. guatemalensis* Bates, 1887 and *O. hoepfneri*). In the live fence, 15 species were recorded (*n* = 563, 27.80%), with no exclusive species. In the cattle pasture, 13 species were obtained (*n* = 751, 37.09%) with three exclusive species (*C. humectus*, *Digitonthophagus gazella* (Fabricius, 1787), and *E. intermedius*).

Species diversity of order ^{0}D between habitats showed that the richness achieved in the forest was higher than in the cattle pasture, while the live fence did not differ significantly from the other two habitats (Fig. 2A). Shannon's exponential and inverse of Simpson's index showed that the number of abundant (^{1}D = 6.2) and dominant (^{2}D = 4.9) species were higher in the forest. Diversity ^{1}D indicated a similar number of effective species between the live fence and the cattle pasture (Fig. 2B), as diversity ^{2}D shows an intermediate value of dominant species in the cattle pasture and the lowest diversity in the live fence (Fig. 2C).

The structure of the assemblage shows a similar distribution in the three habitats, where few species were dominant and a high proportion of them was rare, with changes in hierarchical order according to their abundances (Fig. 3). The most abundant species in each habitat were: *C. pseudoperceptibile*, *C. laetum*, and *D. amplicollis* in the forest; *D. amplicollis* and *C. laetum* in the live fence and; *D. amplicollis*, *P. balthasari*,

Table 1 Dung beetle assemblage composition, abundances, and sample coverage in three habitats of a fragmented landscape in the central depression of Chiapas, Southern Mexico. DF=forest; LF=live fence; CP=cattle pasture. FG=functional group; SP=small paracoprids; MP=medium paracoprid; LP=large paracoprid; MT=medium telecoprid; ST=small telecoprid; LT=large telecoprid

Species	Code	FG	Habitats			*N*
			DF	LF	CP	
Agamopus lampros Bates, 1887	Alam	ST	30	10	-	**40**
Ateuchus rodriguezi De Borre, 1886	Arod	SP	2	-	1	**3**
Canthidium laetum Harold, 1868	Clae	SP	183	221	-	**404**
Canthidium pseudoperceptibile Kohlmann & Solís 2006	Cpse	SP	203	2	-	**205**
Canthon cyanellus LeConte, 1859	Ccya	ST	-	4	11	**15**
Canthon femoralis (Chevrolat, 1834)	Cfem	ST	2	3	-	**5**
Canthon humectus (Say, 1832)	Chum	MT	-	-	1	**1**
Copris lugubris Boheman, 1858	Clug	LP	1	1	6	**8**
Coprophanaeus corythus (Harold, 1863)	Ccor	LP	-	2	3	**5**
Deltochilum sublaeve (Bates, 1887)	Dsub	LT	1	-	-	**1**
Dichotomius amplicollis (Harold, 1869)	Damp	LP	153	263	325	**741**
Dichotomius colonicus Say, 1835	Dcol	LP	25	18	24	**67**
Digitonthophagus gazella (Fabricius, 1787)	Dgaz	MP	-	-	12	**12**
Euoniticellus intermedius (Reiche, 1848)	Eint	SP	-	-	1	**1**
Onthophagus batesi Howden & Cartwright, 1963	Obat	SP	8	5	5	**18**
Onthophagus corrosus (Bates, 1887)	Ocor	SP	1	-	-	**1**
Onthophagus guatemalensis Bates, 1887	Ogua	MP	2	-	-	**2**
Onthophagus hoepfneri Harold, 1869	Ohoe	SP	1	-	-	**1**
Phanaeus balthasari Arnaud, 2001	Pbal	LP	26	14	190	**230**
Phanaeus demon Castelnau, 1840	Pdem	LP	4	8	162	**174**
Scatimus ovatus Harold, 1862	Sova	SP	26	2	10	**38**
Uroxys deavilai Delgado and Kohlmann 2007	Udea	SP	12	3	-	**15**
Uroxys microcularis Howden & Young, 1981	Umic	SP	31	7	-	**38**
Total number of individuals			**711**	**563**	**751**	**2025**
Total number of species			**18**	**15**	**13**	**23**
Sample coverage (%)			**99.4**	**99.8**	**99.6**	

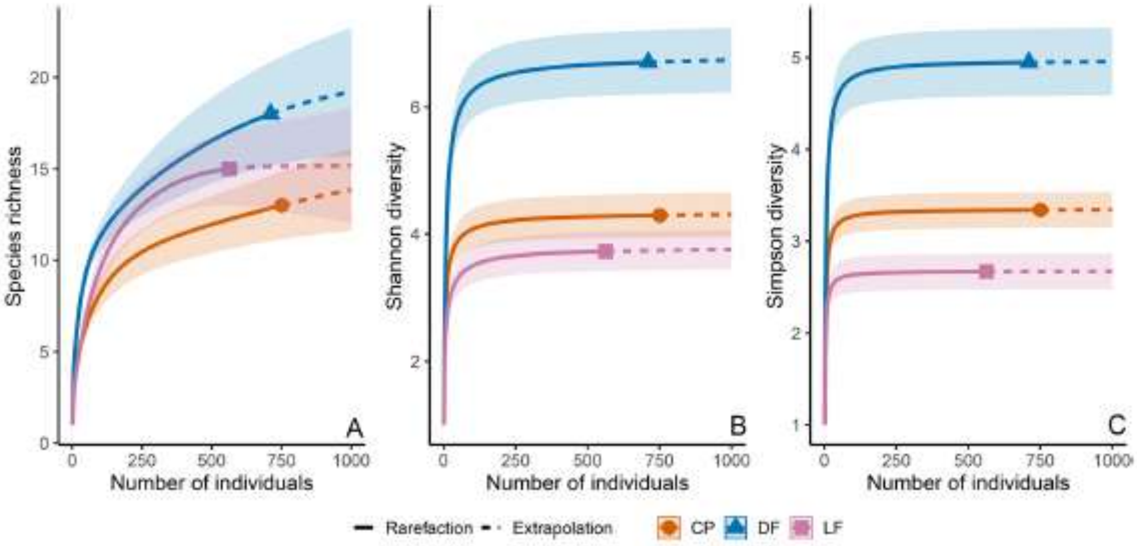

Fig. 2 qD-order diversity values of dung beetle assemblages with 95% confidence intervals (shaded area): Species richness (^{0}D), exponential of Shannon (^{1}D), and inverse of Simpson diversity (^{2}D). DF=forest; LF=live fence; CP=cattle pasture

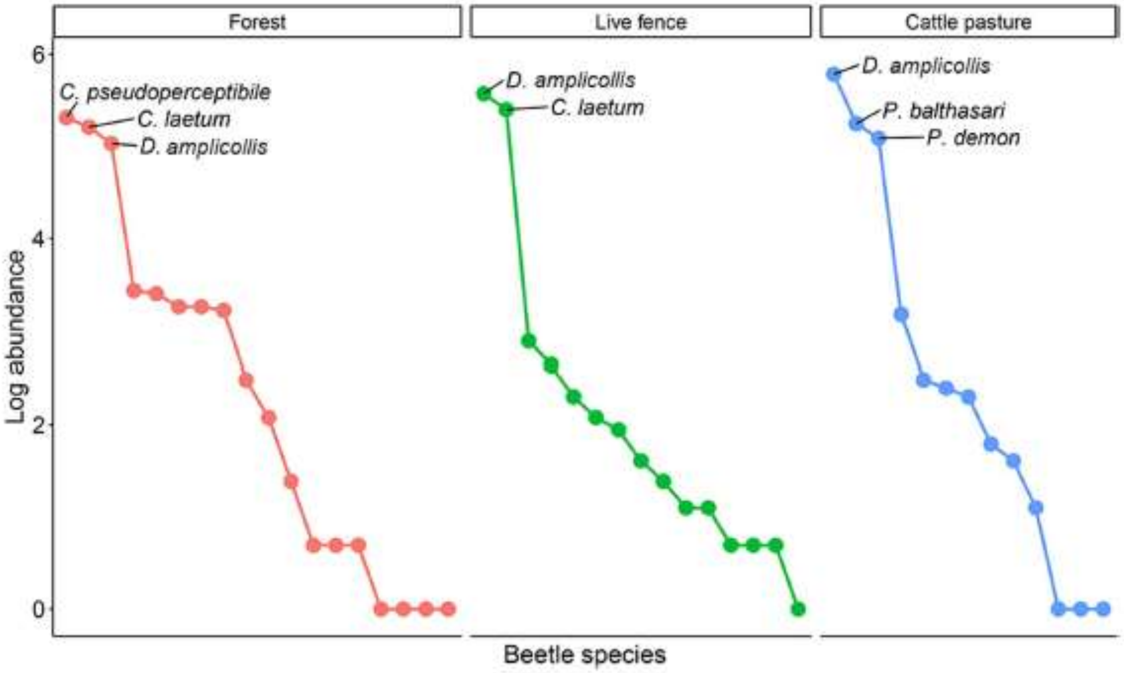

Fig. 3 Rank-abundance curves of the dung beetle assemblages' structure, showing the most abundant species in each habitat

and *P. demon* in the cattle pasture. In the live fence 66.7% of the species (s = 10), presented less than ten individuals, while, in the forest and cattle pasture, these species represent 50% (s = 9) and 46.1% (s = 6), respectively.

ANOSIM results revealed significant differences in overall species composition (Global: $R = 0.41$, $p = 0.0002$). The habitats that presented significant differences were cattle pasture-live fence ($R = 0.67$, $p = 0.007$) and cattle pasture-forest ($R = 0.49$, $p = 0.008$), while forest-live fence had no statistical differences in species composition, but a high percentage of similarity ($R = 0.078$, $p = 0.46$). This similarity is corroborated by the NMDS result, where the species composition of these two habitats overlaps almost completely, while the composition of the cattle pasture shows clear segregation, indicating the existence of two distinct assemblages in the study area (Fig. 4).

According to the IndVal analysis, only nine species showed significant association probabilities with any of the three habitats (indicator species). Four species were associated with the forest, four with the cattle pasture, and only one with the live fence (Fig. 5). The remaining 14 species showed no or very low probabilities of being considered as habitat characteristics, either because of their generalist habits or because of their low abundances (Table 1).

Species were grouped into a total of seven functional groups (Table 1), showing clear differences in group structure between habitats (Fig. 6). In the cattle pasture, six functional groups were represented but with a significantly higher abundance of large paracoprids ($X^2 = 4.77$, $p < 0.0001$). In the forest, five functional groups were present, where small paracoprids were statistically more abundant than the rest of the groups ($X^2 = 3.73$, $p < 0.0001$); while only three groups were captured in the live fence, where large paracoprids were significantly higher abundant ($X^2 = 4.11$, $p < 0.0001$).

Discussion

The species richness obtained in this study (23 spp.) represents 18.5% of the estimated Scarabaeinae diversity in the state of Chiapas (Sánchez-Hernández and Gómez 2018; Sánchez-Hernández et al. 2019). Although Scarabaeinae assemblages may exhibit well-defined seasonal patterns (Arellano et al. 2008; Rodríguez-López et al. 2019), our results indicate that a high sampling efficiency was obtained, and the richness recorded is comparable to that reported in other works related to this region. This is true even when in them both seasonal periods (dry and rainy) were included or different types of attractants were used for surveys (Arellano et al. 2008; Rodríguez-López et al. 2019, 2021; Sánchez-Hernández et al. 2021; Gómez-Méndez et al. 2023).

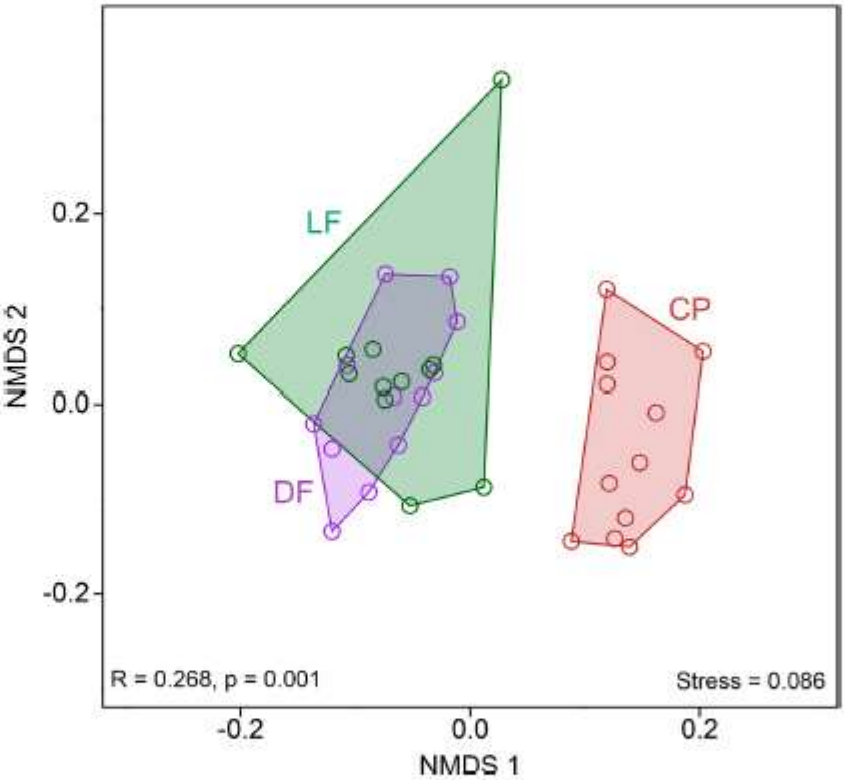

Fig. 4 Non-Metric Multidimensional Scaling (NMDS) ordination diagram of Scarabaeinae assemblages based on the Morisita-Horn dissimilarity index. DF = forest; LF = live fence; CP = cattle pasture

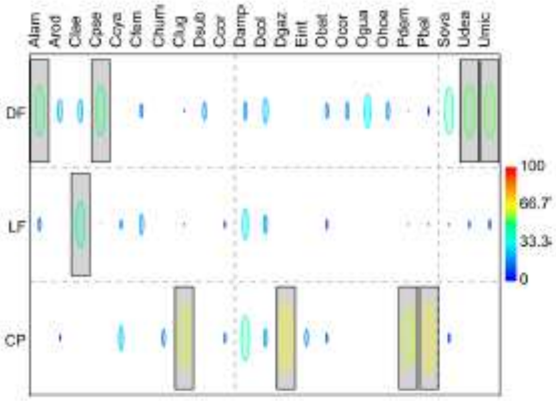

Fig. 5 Indicator value (IndVal) of Scarabaeinae species significantly associated with one of the three study habitats. The range of values indicates the indicator value (0–100) and the ovals within a rectangle indicate the species significantly associated with one of the habitats ($P < 0.05$). Species are indicated by the codes in Table 1. DF = forest; LF = live fence; CP = cattle pasture

The study landscape is characterized by a fragmented structure caused by the action of land use change, formed by mosaics of agricultural and livestock use, secondary vegetation, and small remnants of primary deciduous forest vegetation (Pérez-Farrera and Espinoza 2010; Rocha-Loredo et al. 2010). This heterogeneous landscape is characterized by generalist dung beetle assemblages and, in turn, allows some species that maintain abundant populations in other habitat types to establish (Rodríguez-López et al. 2019; Sánchez-Hernández et al. 2021). The broad dominance of a few species (five species accounted for > 86% of total abundance) is typical of fragmented landscapes where the structural diversity of forest cover is poor compared to much denser forested areas (Navarrete and Halffter 2008; Sánchez-Hernández et al. 2018, 2022; Gómez-Méndez et al. 2023).

Our results show that the diversity and composition of dung beetle assemblages changed as a function of the characteristics of each habitat. As expected, in contrast with the live fence and grassland, high values of species diversity (qD) were found in forest fragments. Despite their limited extent and isolation, these forest remnants can maintain populations of species that are widely distributed in the Central Depression of Chiapas. These fragments also possess exclusive species of Scarabaeinae, so habitat loss due to forest conversion may cause the disappearance of some species and alter the structure and composition of dung beetle assemblages in the landscape (Nichols et al. 2007;

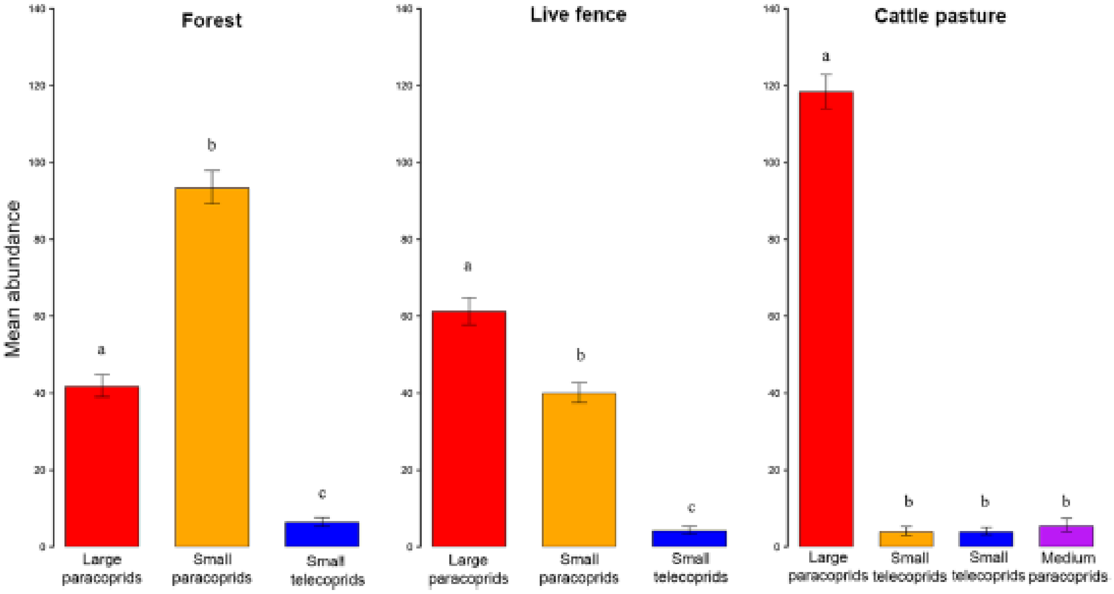

Fig. 6 Mean abundances of functional groups for each study habitat. Only functional groups with more than two individuals are represented

Rodríguez-García et al. 2021; Correa-Cuadros et al. 2022; López-Bedoya et al. 2022; Gómez-Méndez et al. 2023). This highlights the importance of forest remnants in maintaining regional species populations and ensuring local diversity of dung beetle assemblages.

However, the ordination diagram and analyses of similarity showed the formation of two dung beetle assemblages, one of them formed by the species associated with the live fence and the forest, with similar dominant species and low species turnover rate, very different from what was observed in the cattle pasture. Despite their limited extent, live fences promote spatial heterogeneity within agricultural landscapes, thus representing an important component of forest cover by reducing the effects of isolation between forest patches (Harvey et al. 2003). Several studies have shown that live fences stand out as habitats of a high diversity of different taxa in fragmented landscapes dominated by an agricultural matrix, such as birds (Lang et al. 2003; Ramírez-Albores 2010), bats (Estrada and Coates-Estrada 2001), diurnal butterflies (Tobar and Ibrahim 2010), and plants (Zamora Pedraza et al. 2022).

Live fences are generally limited in extent and often lack physical connection to vegetation patches, so they cannot support species diversity like these fragments do. However, the obtained data aligns with other studies that suggest this type of habitat can be vital, functioning as biological corridors for several taxa, including Scarabaeinae species, allowing them to move between forest remnants and, thus, reducing competition for resource availability mainly for those species that avoid open areas (Estrada et al. 1998; Díaz et al. 2010; Rangel-Acosta and Martínez-Hernández 2017). This does not suggest that live fences can replace primary habitats, but it does show that multi-strata live fences can be of great importance in the provision of resources (Garbach et al. 2010). In this sense, live fences can help species with restricted movement capacity and little dispersal to successfully occupy other habitat types, such as areas of secondary vegetation (Sánchez-Hernández et al. 2018), patches of remnant vegetation (Rodríguez-López et al. 2019) and areas of primary vegetation (Sánchez-de-Jesús et al. 2016). This was observed with the species identified as forest (*A. lampros*, *C. pseudoperceptibile*, *U. deavilai*, and *U. microcularis*) and live fence (*C. laetum*) indicators which, despite being generalist, rarely invade open areas such as pastures or livestock paddocks. Therefore, the absence or low frequency of some species in live fences commonly observed in forest patches is associated with the isolation produced by large areas of pastures.

Species composition in the cattle pasture, for its part, indicates a clear difference in the dung beetle assemblages that prefer these habitats versus those that avoid open areas, i.e., forest species. Although the pasture areas presented the lowest species richness, they had high values of abundance, due to the predominance of two heliophilous species (i.e., *P. balthasari*, and *P. demon*), which together accounted for 46.9% of the total abundance in this habitat and whose occurrence showed a high degree of fidelity to this habitat. These types of species are favored by the continuity of large extensions of open or highly disturbed areas, with the presence of cattle that provide greater volumes of manure, which allows them to maintain much larger populations (Arellano et al. 2008, 2013; Edmonds and Zídek 2012). *Phanaeus demon* and *P. balthasari* are two large borrowing species that provide a valuable service in the removal of large masses of fecal matter in the grasslands. These large paracoprids beetle can remove a greater volume of dung, as well as contribute more effectively to the biological control of flies and helminths of veterinary importance (Bang et al. 2005; Shahabuddin et al. 2008; Gregory et al. 2015). For its part, *Digitonthophagus gazella* was exclusive to cattle pasture and despite its low abundance, it stands out as an indicator species of this habitat. This is because *D. gazella* is a specialist coprophagous species, favored by anthropogenic activities, mainly cattle ranching. This allowed it to rapidly establish itself in grasslands of tropical and subtropical regions of Mexico and Central America, but without penetrating forest areas (Montes de Oca and Halffter 1998; Noriega et al. 2020).

Digitonthophagus gazella and *Euoniticellus intermedius* are two exotic species that present high dispersal power, adaptability, and colonization potential due to a high reproductive rate (Noriega et al. 2011; Pablo-Cea et al. 2017), so they would be expected to be dominant in cattle pastures. However, in this study and numerous dung beetle surveys conducted in several areas of Chiapas (Morales et al. 2004; Arellano et al. 2008, 2013; Rivera et al. 2020), the number of individuals found of both species is very low compared to the dominant native species, which could indicate that these species are still in the establishment phase, without yet becoming locally invasive (Noriega et al. 2011). In addition, macrocyclic lactones (ML) are commonly used to treat livestock against parasites, and fecal residues have negative effects on dung beetle assemblages and their ecological functions (Basto-Estrella et al. 2014). Although it cannot be confirmed that the low representativeness of these species is a negative response to the presence of ML residues in excreta, it is known that the immature stages of *D. gazella* and *E. intermedius* are particularly susceptible to them, even more so than native species (Pérez-Cogollo et al. 2018; Rodríguez-Vivas et al. 2021).

Conversely, some species succeed in maintaining abundant populations because of their generalist capacity, enabling them to invade different habitat types in the landscape, regardless of the level of disturbance, highlighting their broad ecological tolerance (Estrada et al. 1998). *Dichotomius amplicollis* was the most abundant and dominant species in the three habitats. This species is restricted to Mexico but is widely distributed in tropical forests, mainly in the deciduous forests along the Mexican Pacific slope (Chamé-Vázquez et al. 2020; Moguel-López et al. 2024). In this region of Chiapas, *D. amplicollis* has been found as a dominant species, both in areas of primary vegetation and in open or highly disturbed areas (Arellano et al. 2008, 2013; Navarrete and Halffter 2008; Sánchez-de-Jesús et al. 2016; Sánchez-Hernández et al. 2018, 2022; Gómez-Méndez et al. 2023). In general terms, *Dichotomius* species are considered fast burrowers, an important characteristic in fragmented areas (Davis 1996), since it allows the manure to be recycled quickly and not be exposed to the environment for prolonged periods, thus slowing the proliferation of pests, as well as allowing the soil to be oxygenated to a greater extent due to the body size of this species group (Gregory et al. 2015).

We found that the functional groups responded similarly in each habitat type. When present, telecoprids, where the most sensitive, while paracoprids were particularly dominant in all three habitats. Most telecoprid species were found at low abundances. Conversely, paracoprids, especially large-sized species, did not change and even increased in abundance along the disturbance gradient, suggesting that these species may be more tolerant to environmental stressors related to habitat loss and fragmentation. Paracoprids are the most diverse group among dung beetles in Neotropical forests (e.g., Navarrete and Halffter 2008; Sánchez-Hernández et al. 2018; Gómez-Méndez et al. 2023), and such diversity is associated with their wide variety of strategies and behaviors (Scholtz et al. 2009). Also, this high proportion of paracoprids might be connected to the supply of food resources in the area, especially to the presence of cattle that could support a high diversity of burrowing species (Arellano et al. 2013). However, this predominance contrasts with patterns found in other studies indicating that the presence of these species decreases drastically in disturbed environments, particularly open areas. Small-sized paracoprids replaced them, because they are more resistant to high daytime temperatures, as well as to the hardness and compaction of the soil (Barragán et al. 2011; de Oliveira Ribeiro et al. 2022), while large paracoprids are particularly susceptible to these conditions (Davis 1996). These characteristics are usually more evident during the dry season due to the lack of humidity (Barraza et al. 2010; Miranda-Flores et al. 2020).Thus, our results could be explained by the high rainfall during the sampling period, as it lessens these impacts.

The data obtained in this work concur that the presence of arboreal habitats, such as live fences, can be important elements for wildlife within fragmented landscapes, thus compensating for the loss of forest cover, as they help to maintain the physical and functional connectivity of the landscape, acting as connectors between isolated fragments of vegetation and as biological corridors for species to move through the agricultural matrix (Harvey et al. 2005). So, these systems offer an alternative to support biodiversity in conventional livestock production systems. However, more information is needed to assess the role of different types of live fences (i.e., simple vs. multi-strata) as quality habitats for the persistence of Scarabaeinae assemblages over the long term and at diverse scales, as the structure and configuration of the tree composition of these habitats may be factors that also contribute to the diversity of species they can support (Garbach et al. 2010; Tobar and Ibrahim 2010; Zamora Pedraza et al. 2022).

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Declarations

Ethical approval The experimentation was not invasive and complied with Mexican law. At the end of the experiment, the specimens were deposited in the Entomological Collection of El Colegio de la Frontera Sur (ECOSUR), Mexico, following standard procedures.

Human participants and informed consent There were no human participants in the study and thus, no 'informed consent' was required.

Conflict of interest There are no conflicts of interest (financial and non-financial) among authors.

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