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Different habitat condition proportions on farms affect the structure and diversity of dung beetle (Coleoptera, Scarabaeidae, Scarabaeinae) communities

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Abstract: The continuous changes and increase of land use into ranching and agriculture have caused shifts in the composition and structure of dung beetle communities due to the modification of vegetation structure. The impact of these changes can be approached using dung beetles as ecological indicators. Agricultural, ranching, and forestry are often integrated into the same farm in different proportions (landscape level), and their degree of integration with habitats changes over time and space. We assessed if different habitat proportions of crop, pasture, and forest land on three farms affect the structure and diversity of dung beetle (Coleoptera: Scarabaeinae) communities. Farms included from three to four habitat conditions each (plantations of timber species, banana-coffee plantation, living fences, pastures, secondary and riparian forest). Pitfall traps with dung and carrion as bait were placed across each habitat condition of each farm during three different sampling periods. Across all samplings, 1,198 dung beetle individuals belonging to 21 species were captured. Species diversity and composition vary according to the type of farm and the main factor that modifies this tendency is the proportion of pasture land composing the farm. Farms with a lower proportion of grazing land (11.96% for forestry farms and 32.19% for agricultural farms) and denser vegetation canopy, which cast more shadows, had greater beetle diversity. Conversely, farms having a greater proportion of grazing land had low diversity and a dominant tendency in the species abundance curve. Umbraphile species dominated the forest farm, indicating a strong affinity for shaded environments such as the one provided there, while species displaying no habitat preference exhibited higher abundance in the ranching farm. Additionally, a notable prevalence of small-sized species was observed in the ranching farm, contrasting with a relatively even distribution of sizes in the remaining landscapes. These tendencies suggest that shade positively influences biodiversity conservation. Riparian vegetation, living fences, and banana-coffee plantations are important connectivity elements in agricultural landscapes for shade-adapted dung beetle species.

Key words: Agriculture; cloud forest; plantations; ranching; transitional zone; Veracruz.

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Introduction

The land use shift from forests to pastures and agriculture has changed vegetation structure affecting biodiversity (Hansen et al. 2012), mostly due to the species' capacity to adapt to new conditions in the local environment (Turner 1996). The type of crop or fodder cultivated is associated with the composition and diversity of species in different scales (Emmerson et al. 2016). Monospecific pastures are known to cause the biggest negative impacts on biodiversity due to the poor vegetation coverage they offer (Filazzola et al. 2020). Agriculture varies according to the crop and management implemented; some crops maintain a microclimate that allows biodiversity to be sustained (e.g., shade coffee plantations), while others do not (e.g., monocultures) (Udawatta et al. 2019). Forestry activities, such as timber plantations, may contribute to the restoration of biodiversity in degraded areas, especially when native trees are managed (Bremer and Farley 2010). Also, some agricultural and livestock practices (e.g., silvopastoral systems) integrate plant species that allow the presence of some elements associated with the natural forest, such as live fences (Pulido-Santacruz and Renjifo 2011) and fodder trees (Broom et al. 2013).

In Mexico, agricultural, ranching, and forestry activities are often integrated into the same farm in different proportions (landscape level), and their degree of integration with habitats changes over time and space (Ortiz-García et al. 2022). Forestry is generally considered less important (Bray 2005), but it has great potential for commercial and sustainability purposes (Cubbage et al. 2015). Woody vegetation often coexists with ranching since cattle farming is mostly practiced extensively. Forestry can also be integrated into agriculture through associations with shade-tolerant crops such as coffee and cocoa polycultures (López-Cruz et al. 2021; Imron et al. 2022). However, agriculture and cattle ranching generally avoid using woody vegetation due to concerns over the potential reduction in crop and pasture yield caused by shading and the management challenges it imposes (Romero-Alvarado et al. 2002; Tsonkova et al. 2018).

The effect of different land uses on species diversity can be evaluated through monitoring (Andonegi et al. 2021). One of the most common monitoring strategies is the use of biodiversity indicators, which are biological groups that can be used in a variety of habitat conditions. Choosing a biological indicator depends on the condition to be evaluated (Abas 2021). Dung beetles (Coleoptera: Scarabaeinae) are suitable organisms as indicators of land use changes in the tropics, since they are sensitive to environmental changes related to each land use (Martínez-Falcón et al. 2018) and are widely distributed. Favila and Halffter (1997) mention that the Scarabaeinae group meets the ideal characteristics to be biological indicators since they are a group that includes a rich and well-defined guild, that has been widely studied, its capture is relatively easy, and its collection does not compromise conservation. In addition, dung beetles play an important role in the structure and functioning of ecosystems because they contribute to nutrient recycling from dung, thereby improving soil fertility and promoting higher plant yields. The presence of these organisms also contributes to parasite suppression and fly control in dung pats (Nichols et al. 2008).

Most studies conducted on dung beetle diversity have focused primarily on the loss of vegetation cover caused by livestock systems (e.g., Halffter and Arellano 2002; Macedo et al. 2020). These studies have shown that the complete conversion of natural Neotropical areas into exotic pastures negatively affects dung beetle assemblages and alters species composition in open areas with cattle presence. In recent decades, the effect of vegetation gradients (e.g., Favila 2005; Andresen 2008; Arellano et al. 2008a,b; Martínez et al. 2009; Hernández et al. 2013) and management practices have been considered in studies about dung beetle communities (e.g., França et al. 2017; Alvarado et al. 2019; Gómez-Cifuentes et al. 2022). These studies have shown that species-specific abundances vary along vegetation gradients, and that the excessive use of agrochemicals and degree of disturbance negatively influence dung beetle species diversity in cattle pastures. Management decisions play an important role in improving the conservation of dung beetles. Some studies have evaluated the effect of agriculture on dung beetle diversity, but they do not distinguish between different types of crops (Estrada and Coates-Estrada 2002; Horgan and Fuentes 2005; Avendaño-Mendoza et al. 2005). However, there are studies that specifically analyze the diversity in certain agricultural land uses, such as shaded coffee plantations (Arellano et al. 2005; Halffter et al. 2007; Noriega et al. 2012; Villada-Bedoya et al. 2017), mango plantations (Paiboon et al. 2018; Arellano and Gómez-Bautista 2021), oil palm plantations (Gray et al. 2014; Harada et al. 2020) and silvopastoral systems (Giraldo et al. 2011; Farias et al. 2015; Montoya-Molina et al. 2016; Lopes et al. 2020) among others. Additionally, there are studies that focus specifically on forest plantations (Reyes-Novelo et al. 2007; Beiroz et al. 2019; Ruiz Pérez et al. 2019; Levia and Sobrino-Mengual 2022). In this sense, the studies have shown that these habitats or productive systems harbor significant diversity of dung beetles, maintaining connectivity between patches of native vegetation in landscapes with the presence of human activities.

In general, dung beetles exhibit either positive or negative changes in their diversity, distribution, and development due to human intervention (Halffter and Favila 1993; Halffter and Arellano 2002). Additionally, given the heterogeneity of landscapes, it has been found that integrating aspects of taxonomic diversity (richness, abundance and species composition), as well as functional diversity through the set of functional traits of dung beetle species, defined as all those physiological, phenological and morphological attributes that are related to the performance of their functions in ecosystems, provide us with an approximation of the consequences of human activities on the functioning of ecosystems (Tilman 2001; Violle et al. 2007; Arellano et al. 2023).

In this paper, we analyze their response across three farms with different habitat conditions such as conventional banana and coffee association crops, pastures with introduced grasses, plantations of timber species, secondary or riparian vegetation, and the presence of live fences. We evaluated changes in the diversity and composition of dung beetle species as well as the composition of functional traits at a local level and among farms (landscape). Our hypothesis was: the different habitat conditions implemented on farms and their proportions, which define the vegetation structures within agroecosystems, have an impact on the diversity and composition of dung beetle (Coleoptera: Scarabaeinae) communities, expecting to find a low diversity in farms with less proportion of shade or arboreal elements, i.e., less diversity in less heterogeneous habitat conditions. For functional traits, we would expect to find considering vegetation structures within agroecosystems that in less heterogeneous habitat areas there is less trait variability, with certain traits dominating over others.

Materials and methods

Study area, description of the farms, and habitat conditions

The study was conducted in the border area of two Mexican municipalities, Tlapacoyan in the state of Veracruz, and Hueytamalco in the state of Puebla (19º56′37″N, 97º15′42″W). The elevations in this region range from 700 to 900 m. The climate of the area is described as semi-warm with a temperate humid climate classification of (A)Cf, in the Köppen climate classification system modified by García (2004). The average annual temperature in the region ranges from 20 to 22ºC, and the annual precipitation is between 2000 mm and 2500 mm

(INEGI 2009a, INEGI 2009b). The study area is a mosaic of predominantly banana plantations, often associated with coffee plantations and scattered citrus trees. Pastures and small fragments of secondary subtropical perennial forests are also present, but the forest is located primarily in higher altitude areas or locations with limited access. One of the farms included in the study, which was previously used only for cattle ranching, was converted into a commercial forest plantation 20 years ago (Castillo-Gallegos et al. 2018) combined with ranching.

We identified the most representative options of land use within the ranches in the study area (we found 3 different ones) and we selected those properties that had a similar size and could be viewed structurally as a gradient in order to analyze the response of the dung beetles to that gradients and be able to recommend the productive system that best conserves the diversity and function of dung beetles.

The sampling was conducted across the three selected farms, each located at least 1 km apart and with a dominant land use dedicated to forestry, agriculture, or ranching and different habitat conditions for dung beetles. We included in habitat condition the type of land use prevailing in each farm, the woodlands (riparian and mature secondary vegetation), the living fences, and the pasturelands with isolated trees in different densities or terrain in slope.

The first farm (F) had the highest proportion of forest land covered by the timber species (*Melia azedarach* and *Ocotea puberula*). Four types of habitat conditions were identified on this farm in the following proportions: Low-Density (FL) (42.3%) and High-Density (FH) (31.8%) arrangement of timber trees, an abandoned field with mature secondary vegetation (FSV) (13.96%) and low-density timber tree area with Grazing (FG) (11.96%). The second farm (A) had a higher percentage of agricultural land and three habitat conditions in the following proportions: a conventional banana plantation (*Musa paradisiaca* var. *sapientum*) associated with coffee (*Coffea arabica*) (AB) (60.77%), pastures with Steep Slopes (15-30°) (AP) (32.19%), and Live Fences (ALF) (7.04%). The third farm (R) had the highest percentage of grazing land and featured four different habitat conditions in the following proportions: Pastures with Steep Slopes (45-60°) (RSP) (53.84%), Riparian Areas (RR) (23.08%), Living Fences (LLF) (15.38%) and Flat Pastures (RFP) (7.70%). Both living fence areas held the species *Bursera simaruba*.

Dung beetle trapping and taxonomic identification

Dung beetles were collected in the study area from 15.V.2021 to 15.III.2022. Sampling was conducted for each habitat condition identified on each farm; traps were placed at a minimum distance of 50 m from each other (Larsen and Forsyth 2005), following the shape of the sites, covering a 1-ha area, approximately. Baited pitfall traps were used, these are the most common traps for dung beetle collection (Lobo et al. 1998). The traps consist of a 1 L plastic container (11 cm x 14 cm) buried at ground level. An inverted suspended plate was placed over the container to protect it and to reduce the entry of sunlight or rainwater.

Three types of bait were used: cattle dung, sheep dung, and fish. For the sheep dung and fish traps, a triangle-shaped perforated lid was used, and the containers were filled halfway with soil. In traps for cow dung, the bait was placed on a nylon mesh suspended inside the trap. The containers were filled with water to approximately one-third of their capacity, and, approximately, 1/8 teaspoon of detergent was added to break the surface tension and facilitate the collection of beetles. Approximately 50 g of bait was placed on each trap. Nine traps were used to sample each habitat condition, resulting in a total of 99 traps with three replicates on different representative periods of the seasons. The traps were placed from May 28th to May 31st, 2021, representing the windy season and rainy season; from September 29th to October

2nd, 2021, representing the rainy and dry season; and from March 1st to March 4th, 2022, representing the dry and 'nortes' season. This sampling design covered the 11 identified habitat conditions on the farms, with each one having nine traps. All traps were open after 48 hours, and the dung beetles captured were fixed in 70% diluted alcohol. Organisms were identified at the species level, and the material was deposited in the Red de Ecoetología of Instituto de Ecología A.C. (Mexico).

Data analysis

The sample coverage (Chat) was calculated for each farm and habitat condition to assess the extent to which the species inventory approached the potential number of species. The diversity profiles of order q were estimated based on the Hill series, which includes q0 for species richness, q1 for the number of equally common species, and q2 for when dominant species have more weight (Hill 1973; Moreno et al. 2011). The interactive online R-based version of the iNEXT software (Chao et al. 2016) was used. The species diversity profiles, represented by the Hill series (q0, q1, and q2), we compared using Confidence Intervals (CI) at 95%.

Rank-abundance curves were done to analyze the abundance relationships between the species prevailing in the habitat conditions of each farm, using the BiodiversityR package (rank abundance function) (Kindt and Coe 2005).

Principal Component Analysis (PCA) was conducted to analyze the species composition of dung beetles across farms and habitat conditions. The analysis was performed using the FactoMineR package (Lê et al. 2008) and the factoextra package was used to extract and visualize the results (Kassambara and Mundt 2020). PCA is commonly employed as a suitable method to distinguish species abundance patterns among habitats (Scheffler 2005), particularly when sites exhibit short gradients (Ramette 2007).

To assess the abundance percentage of functional groups (defined by the combination of functional traits used) in each ranch, a Chi-squared analysis was performed, considering the percentage abundance of five biological attributes that influence the performance of dung beetles in ecosystems when handling and removing dung, which allowed determining the dependence of each in each grazing environment. Analysis was conducted, enabling the determination of the dependence of each group. The study encompassed five key functional groups: food relocation, which included paracoprids (tunnellers), endocoprids (dwellers), and telecoprids (rollers) (Halffter and Edmonds 1982; Tonelli 2021); activity period (according to literature), comprising diurnal, nocturnal, and flexible species (see Lobo and Cuesta 2021); food preference: proportion of food generalists (species in which at least 80% of the individuals were collected in both copro- and necrotraps) to specialists (species in which more than 80% of the individuals were collected in either copro- or necrotraps): coprophagous and necrophagous (Halffter and Arellano 2002); habitat preference, including umbraphiles, heliophiles, and species with no habitat distinction (habitat generalist) (according to literature); and size, categorized as small (<9 mm), medium (9-17.99 mm), and large (18-28 mm) (Halffter and Arellano 2002). Specifically, a generalist species makes no distinction considering any specific attribute, i.e., there is no differentiation or preference for a type of habitat or resource use as a source of food or nesting by dung beetles in ecosystems. These species have a broader environmental tolerance, able to be found in a variety of natural and disturbed habitats (MacArthur and Levin 1964; Devictor et al. 2010).

The community-level weighted mean (CWM; Lavorel et al. 2008) was used to see the composition of five functional traits across farms and habitat conditions. CWM was computed with function functcomp of the FD package (Laliberté et al. 2015), combining the trait matrix weighted by species abundances. The use of the packages was made in R software, version 4.3.1. (R Core Team 2022).

Results

A total of 1,198 dung beetles belonging to 21 species from six tribes of the subfamily Scarabaeinae were collected and analyzed (Table 1). The highest abundance was observed on the Ranching Farm (R) with 491 individuals, followed by the Agricultural Farm (A) with 386 individuals, and the Forestry Farm (F) had the smallest abundance with 321 individuals. Each farm held three exclusive species, *Ateuchus illaesum*, *Eurysternus magnus*, and *Onthophagus asperodorsatus* in the forestry farm; *Digitonthophagus gazella*, *Canthon cyanellus*, and *C. leechi* in the agricultural farm; and *Deltochilum carrilloi*, *Deltochilum mexicanus*, and *Onthophagus longimanus* in the ranching farm.

The rank-abundance curves at the farm level indicate a strong dominance of the most abundant species (Figure 1A). In the Ranching Farm (R), the three most abundant species, in order of importance, were *Onthophagus incensus*, *O. corrosus*, and *Copris incertus*. In the Agricultural Farm (A), the dominant species were *Copris incertus*, *Dichotomius colonicus,* and *Onthophagus corrosus*. Likewise, the Forestry Farm (F) showed the highest abundance of *Dichotomius satanas*, *Onthophagus belorhinus,* and *Coprophanaeus corythus*.

The rank-abundance curves performed for habitat conditions show a significant dominance of dung beetles on living fences in both L and A farms (Figure 1B, C). However, on the F farm (Figure 1D), the overall abundance is relatively low, with *D. satanas* being the most abundant species on Low-Density (FL), High-Density (FH) arrangement of timber trees and low-density timber tree areas that allow grazing (FG), and *O. belorhinus* being the most abundant on Secondary Vegetation (FSV). Nevertheless, *O. belorhinus* also ranks among the top three most abundant species in the remaining conditions. In the R farm, *O. incensus* emerges as the most abundant species across all conditions, except for Pastures with Steep Slopes (RSP), where it ranks second behind *O. corrosus*. Conversely, in the A farm, the most abundant species varies across the different conditions, with *D. satanas* prevailing on banana-coffee plantation (AB), *C. incertus* on live fences (ALF), and *D. colonicus* on pastures with steep slopes.

The diversity profiles at the farm level (Figure 2A) do not show significant differences at the species richness level (q=0). Both, the R and A farms had 14 species, while the F farm had 15 species (Figure 2A). However, there is a disparity in diversity observed at the next order (q=1), with farm R exhibiting lower diversity compared to A and F farms. Furthermore, at the q=2 order, farm F displays the highest level of diversity, followed by A, while R maintains the lowest level of diversity.

The estimated diversity profiles indicate no differences among habitat conditions in the R farm (Figure 2B) and poor diversity across all orders for the ASP at the A farm. For the remaining habitat conditions, the AB condition exhibits greater diversity at the q=2 order (Figure 2C). Finally, only the FG condition at the F farm showed greater diversity (q=2) (Figure 2D).

Based on the PCA, two primary components were extracted that collectively explained 88.5% of the total variance in the dataset (Figure 3). On the negative side of Axis 1, a distinct separation of the habitat conditions for farm F is observed, characterized by a higher shade coverage. On the negative part of Axis 2, habitat conditions with a moderate level of shading are shown (Riparian, Banana and coffee plantation, and live fences).

Table 1. Dung beetle Scarabaeinae species observed in forestry, agricultural, and ranching farms in Tlapacoyan, Veracruz and Hueytamalco, Puebla, Mexico.

Tribe	ID	Species	Functional groups	Forestry					Agricultural				Ranching					Total
				FG	FA	FH	FL	Total F	ALF	AB	ASP	Total A	RLF	RSP	RFP	RR	Total R	
Ateuchini	Aill	*Ateuchus illaesum* (Harold, 1868)	P,N,C,U,S	1			1	**2**										**2**
Coprini	Cpse	*Canthidium pseudopuncticolle* Solis & Kohlmann, 2004	P,D,C,HG,S	7	5	7		**19**	2			**2**		1		4	**5**	**26**
	Dcol	*Dichotomius colonicus* (Say, 1835)	P,N,C,H,L	1				**1**	41	15	25	**81**	18	5	1		**24**	**106**
	Dsat	*Dichotomius satanas* (Harold, 1867)	P,N,C,U,L	17	10	24	15	**66**	25	16		**41**	4				**4**	**111**
	Cinc	*Copris incertus* Say, 1835	P,N,C,I,M	11	1	3	1	**16**	70	10	15	**95**	39	25	12	6	**82**	**193**
	Clae	*Copris laeviceps* Harold, 1869	P,N,C,U,M	9	14	6	9	**38**		1		**1**				1	**1**	**40**
Deltochilini	Ccya	*Canthon cyanellus* LeConte, 1859	T,D,N,U,S						5	11		**16**						**16**
	Clee	*Canthon leechi* Martinez, Halffter & Halffter, 1964	T,D,C,U,S							1		**1**						**1**
	Dcar	*Deltochilum carrilloi* González-Alvarado & Vaz-de-Mello, 2014	T,N,FG,U,L										1	1			**2**	**2**
	Dmex	*Deltochilum mexicanum* Burmeister, 1848	T,N,Ne,U,L													1	**1**	**1**
Oniticellini	Emag	*Eurysternus magnus* Castelnau, 1840	E,D,C,HG,M			1		**1**										**1**
	Emex	*Eurysternus mexicanus* Harold, 1869	E,D,C,U,M	8	16	7	6	**37**	3	1		**4**	2			1	**3**	**44**
Onthophagini	Oasp	*Onthophagus asperodorsatus* Howden & Gill, 1993	P,NA,C,U,S			1		**1**										**1**
	Obel	*Onthophagus belorhinus* Bates, 1887	P,TG,FS,U,S	12	24	15	10	**61**	18	7		**25**	3	3	1	11	**18**	**104**
	Ocor	*Onthophagus corrosus* Bates, 1887	P,N,C,H,S	9	3	1	3	**16**	41	3	19	**63**	69	44	2	1	**116**	**195**
	Oinc	*Onthophagus incensus* Say, 1835	P,D,C,HG,S	7	5	1	9	**22**	28	8	7	**43**	113	41	19	15	**188**	**253**
	Olan	*Onthophagus landolti* Harold, 1880	P,D,FG,HG,S	1				**1**	2			**2**						**3**
	Olon	*Onthophagus longimanus* Bates, 1887	P,N,C,U,S										5	1			**6**	**6**
	Dgaz	*Digitonthophagus gazella* (Fabricius, 1787)	P,D,C,H,S								2	**2**						**2**
Phanaeini	Ccor	*Coprophanaeus corythus* (Harold, 1863)	P,N,Ne,U,L	13	15	2	9	**39**	1	4	5	**10**	13	7	11	2	**33**	**82**
	Psal	*Phanaeus sallei* Harold, 1863	P,N,C,H,S			1		**1**					6	2			**8**	**9**
		Total species		12	9	12	9	**15**	11	11	6	**14**	11	10	6	9	**14**	**21**
		Total individuals		108	93	81	63	**321**	247	77	73	**386**	284	140	46	42	**491**	1198
		C. hat		0,97	0.99	0.93	0.97	**1**	0.99	0.96	1	**0.99**	1	0.99	0.98	0.91	**0.99**	

Feeding relocation: P, Paracoprid; E, Endocoprid, T, Telecoprid. Diel activity: D, Diurnal; N, Nocturnal; FS, flexible species. Diet: C, Coprophagous; Ne, Necrophagous; FG, Food Generalist; NA; Not Available. Habitat preferences: U, Umbrophile; H, Heliophilous; HG, Habitat Generalist. Size: S, Small; M, Medium, L, Large. Forestry farm: FL, low-density arrangement of timber trees; FH, high-density arrangement of timber trees; FSV, abandoned area with advanced secondary vegetation; FG, low-density timber tree area that allows grazing. Agricultural farm: AB, banana-coffee plantation; ASP, pastures with steep slopes; ALF, live fences. Ranching farm: RSP, pastures with steep slopes; RR, riparian forest; RLF, living fences; RFP, flat pastures.*

Figure 4 shows a correlation between the habitat condition variable and some species types. For example, *Eurysternus mexicanus* and *Copris laeviceps* are associated with the Low-Density (FL) and High-Density (FH) arrangement of timber trees of the F farm, and *Dichotomius colonicus* is associated with the living fences of the R farm.

The abundance of each functional group across all landscapes exhibited significant dependence on specific landscape characteristics: food relocation (X^2=488.29, p<0.0001, df=20), activity period (X^2=189.44, p<0.0001, df=30), food preferences (X^2=166.84, p<0.0001, df=20), habitat preferences (X^2=477.29, p<0.0001, df=20), and body size (X^2=134.24, p<0.0001, df=20). The CWM of each trait shows us that paracoprids dominated in all farms and habitat conditions (Figure 5A). For the activity period, nocturnal species dominated, followed by diurnal and flexible species (Figure 5B), and for diet coprophagous species dominated (Figure 5C). Umbraphile species dominated the forest farm (Figure 5D), indicating a strong affinity for shaded environments such as the one provided there, while species displaying no habitat preference exhibited higher abundance in the ranching farm. Additionally, a notable prevalence of small-sized species was observed in the ranching farm, contrasting with a relatively even distribution of sizes in the remaining landscapes (Figure 5E).

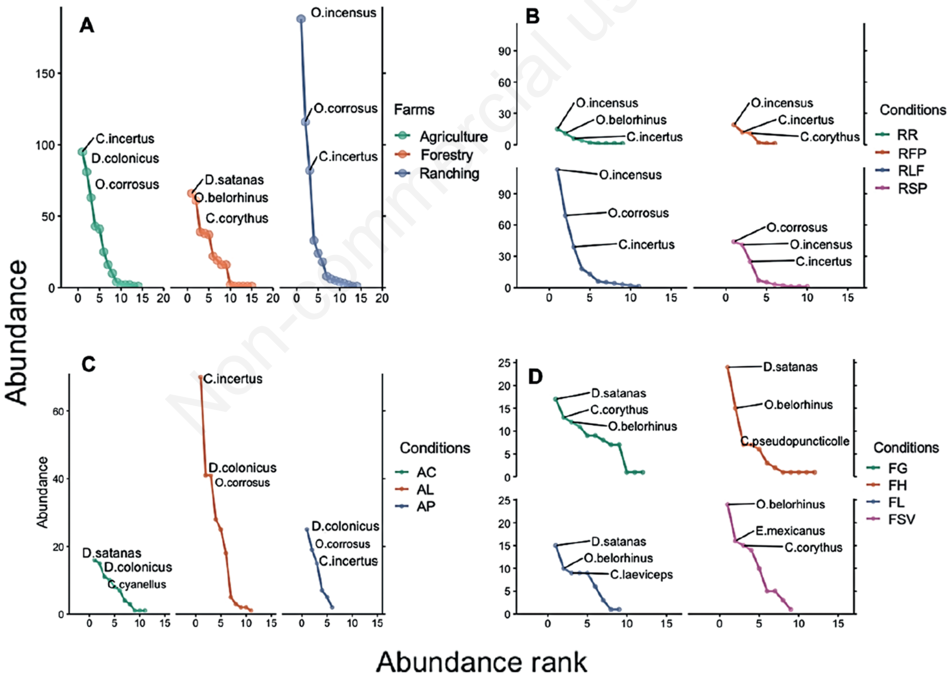

Figure 1. Rank-abundance curves (Whittaker's plots), comparing dung beetle abundance distribution in three farms in Veracruz, Mexico: A) at farm level, B) by habitat conditions in the Ranching Farm, C) by habitat conditions in Agriculture Farm, D) by habitat conditions in Forestry Farm.

Forestry Farm: FL, low-density arrangement of timber trees; FH, high-density arrangement of timber trees; FSV, abandoned area with advanced secondary vegetation; FG, low-density timber tree area that allows grazing. Agriculture Farm: AB, banana-coffee plantation; ASP, pastures with steep slopes; ALF, live fences. Ranching Farm: RSP, pastures with steep slopes; RR, riparian forest; RLF, live fences; RFP, flat pastures.

Discussion

Although historically the study area was covered mainly by subtropical perennial forest, its dung beetle species richness and composition correspond to a mix of species of different landscapes. The total species richness found (21 species) falls within the typical range observed in cloud forests (11-27 species) (Arellano et al. 2005; Rös et al. 2012; Barragán et al. 2014; Díaz-García et al. 2020), but lower than that in the tropical rain forests (24-55 species) (Navarrete and Halffter 2008; Díaz and Favila 2009; Santos-Heredia et al. 2018). Moreover, the most abundant species *Onthophagus incensus* and *Copris incertus,* are predominantly associated with this type of vegetation (Martínez et al. 1996; Huerta et al. 2010; Huerta and García-Hernández 2013). However, species associated with tropical rain forests were observed, but in lower abundances, such as *Copris laeviceps* (Klemperer 1986), *Canthidium pseudopuncticolle* (Kohlman and Solís 2006), *Canthon cyanellus* (Favila 1993), *Eurysternus mexicanus* (Capello and Halffter 2019), and *Phanaeus sallei* (Edmonds 1998). The presence of species associated with both ecosystem types suggests that the study area is a transitional zone for dung beetle fauna, because of the altitudinal ranges and the mixture

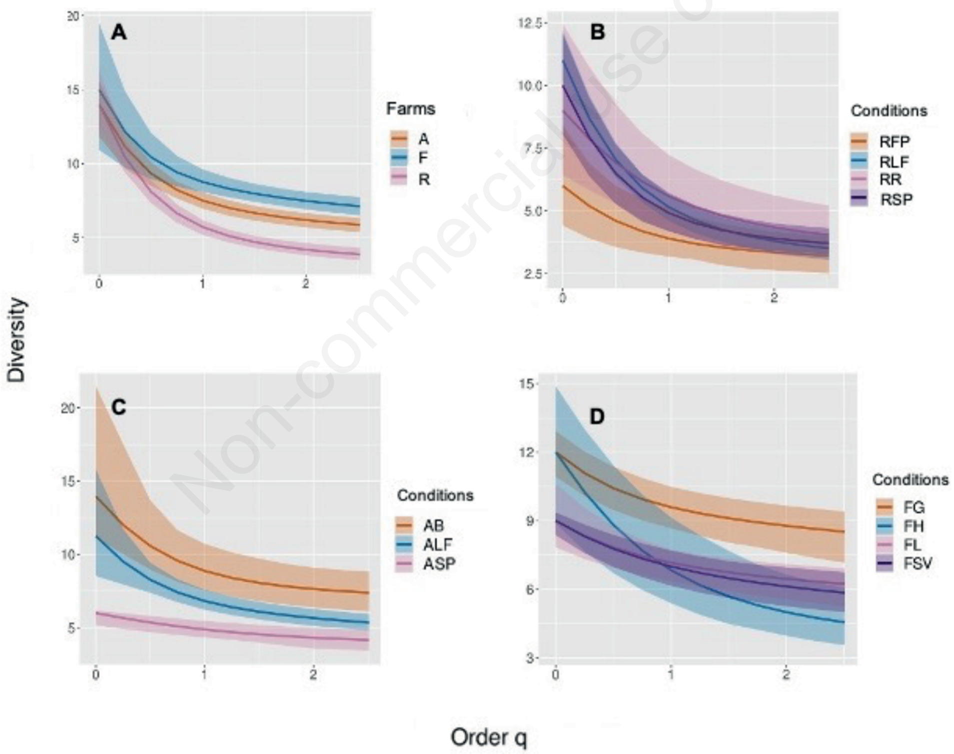

Figure 2. Diversity profiles (q0, q1, q2) of dung beetles in three farms from Veracruz and Puebla, México: A) at farm level, B) ranching farm (L), C) agricultural farm (A), D) forestry farm (F).

Forestry farm: FL, low-density arrangement of timber trees; FH, high-density arrangement of timber trees; FSV, abandoned area with advanced secondary vegetation; FG, low-density timber tree area that allows grazing. Agriculture farm: AB, banana-coffee plantation; ASP, pastures with steep slopes; ALF, live fences. Ranching farm: RSP, pastures with steep slopes; RR, riparian forest; RLF, live fences; RFP, flat pastures. At all diversity orders, the Confidence Interval (CI) is 95% (shaded area), The over position indicates no significant differences in the values of the different diversity orders.

of species of different biogeographic affinities and representative of both vegetation types; however, species richness and the dominant species observed suggest a greater affinity with the cloud forest.

The observed low diversity in the q1 and q2 orders seems to be related to the shade decrease, which is evident in R farm, where pastures account for up to 61.5% of the farm area.

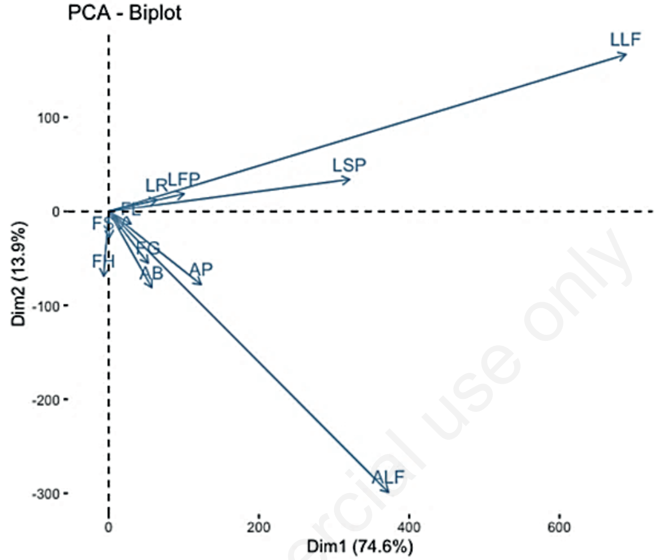

Figure 3. Principal Components Analysis (PCA) of habitat conditions found in three farms in Veracruz and Puebla, Mexico. See abbreviations in Figure 2.

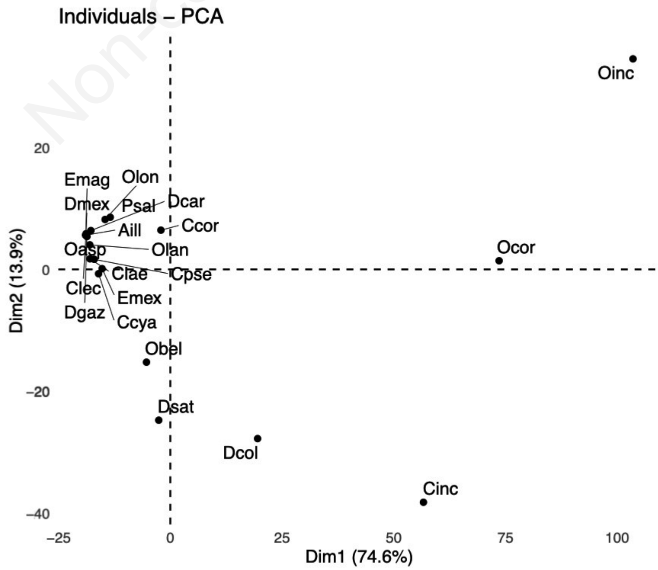

Figure 4. Principal Components Analysis (PCA) of dung beetle species in different habitat conditions found in three farms in Veracruz and Puebla, Mexico. See abbreviations in Table 1.

In contrast, the A farm consists of only 32.3% of pastureland, while the F farm allows cattle access only to a small area FG (12%). Despite the R farm featuring scattered trees and being surrounded by live fences (15.4%) and riparian vegetation (23.1%), the harsh conditions resulting from increased temperatures due to the lack of vegetation may create conditions for some dung beetle species but not for others (Navarrete and Halffter 2008; Niino et al. 2014). These results agree with our hypothesis that the different habitat conditions implemented on farms define the vegetation structures within agroecosystems, since as found a low diversity in farms with less proportion of shade or arboreal elements. Thus, farms with less diversity of dung beetles have less heterogeneous habitat conditions.

Arellano et al. (2005) investigated the abundance of dung beetles in coffee plantations

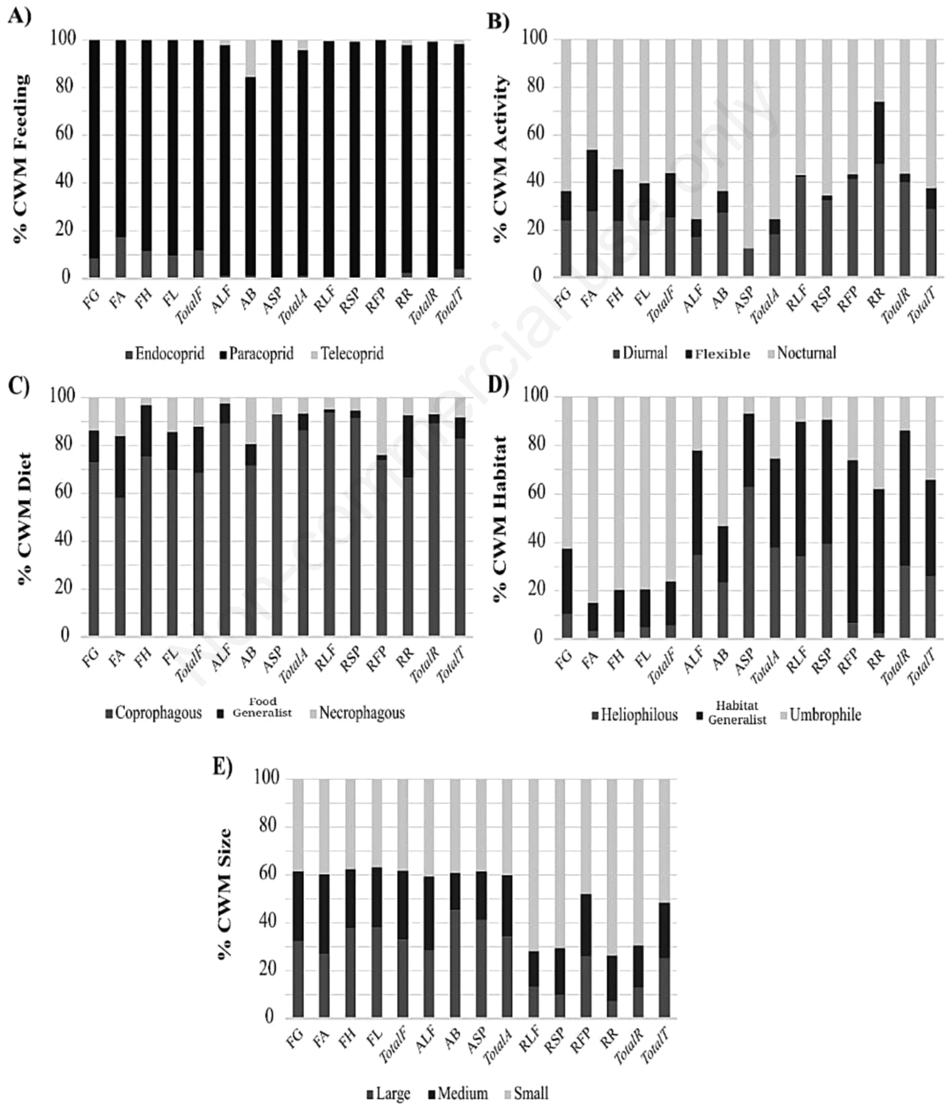

Figure 5. Community-Level Weighted Mean (CWM) by feeding type, activity, diet, habitat, and size type in different habitat conditions found in three farms. See abbreviations in Table 1.

within cloud forest landscapes and restored areas. They showed a higher abundance of dung beetles in environments characterized by greater heterogeneity. On the other hand, Díaz-García et al. (2020) found a higher species richness in pasturelands, primarily consisting of habitat generalist species, with a very low presence of forest species. Rös et al. (2011), in similar conditions in Puebla, also observed higher diversity, q0 and q1, in disturbed areas. The relationship between diversity and disturbances is complex, dependent on factors such as the extent, frequency, and intensity of disturbances (Hall et al. 2012), a pattern can be identified, where disturbed areas with specific elements, in this case, vegetation coverage, tend to support a wider range of species. For example, in the Neotropics has been observed species became locally extinct with the loss of trees or canopy cover (Arellano et al. 2023). This pattern is particularly evident in the grazing area (FG) of the F farm, where the presence of cattle and timber trees might be creating favorable conditions for both forest and habitat generalist species.

Patterns of species diversity and composition can be attributed to various mechanisms, one of these is niche relationships, which are imposed by the availability and quantity of resources (Shmida and Wilson 1985). Dung beetles display a wide range of feeding preferences such as dung, carcasses of small animals, and decomposing material, which are ephemeral and heterogeneously distributed in space and time (Inward et al. 2011). However, the introduction of cattle and the conversion of natural areas to pastures have significantly increased the abundance of manure, leading to changes in dung beetle resource selection patterns (Bourg et al. 2016).

Native species such as *Onthophagus incensus, O. corrosus, Copris incertus,* and *Dichotomius colonicus* among other abundant species in this study have a strong preference for cattle dung. Despite being an ephemeral resource that loses freshness and odor, important features for dung beetle attraction (Halffter and Edmonds 1982), this preference may explain the higher abundances of these species in areas with living fences. The presence of vegetation cover in these areas allows these characteristics to persist for a longer period compared to open areas, where direct exposure to sunlight dries the dung.

Differences in habitat conditions have an impact on the distribution and coexistence of dung beetle species (Shmida and Wilson 1985). Environmental factors such as soil type (Doube 1983; Daniel et al. 2022), humidity, and temperature (Verdú et al. 2006, 2007; Lobo et al. 2019) strongly influence these organisms. The concept of thermal niches, which refers to the temperature ranges that species can tolerate over time, explains the ability of some dung beetles to thrive in disturbed environments like grasslands.

Endothermy and body mass are traits that allow dung beetles to exploit anthropic sites with low tree cover, where some small size species with diurnal habits and low endothermy capacity have been able to colonize areas with such conditions (Verdú et al. 2007; Giménez-Gómez et al. 2020). These characteristics agree with the two most abundant species in the cattle landscape, *Onthophagus incensus* and *O. corrosus,* belonging to a genus characterized by a wide ecological valence and whose species can live in wooded and open conditions. However, there is a relationship between body size and thermoregulatory capacity in beetles, thus individuals of small size have a lower thermoregulatory capacity than larger ones. This pattern is observed in two necrophagous beetles found in this study, *Coprophanaeus corythus* and *Canthon cyanellus*. The first is a large beetle that displayed relatively high abundances across all habitat conditions. In contrast, the second is a smaller beetle, exhibited lower abundances, and was only found in the shaded habitat conditions of farm A.

Further investigation is needed to determine with greater detail the physiological capacities by dung beetle species (Verdú et al. 2006, 2007; Shepherd et al. 2008). Giménez-Gómez et al. (2018) attribute the impoverishment of grasslands to these physiological constraints, which could explain the low diversities found in the ranching. Many tropical grasslands are inhabited by *Digitonthophagus gazella* and *Euoniticellus intermedius*, two exotic species of Indoafrican origin. These species are adapted to heliophilous zones and feces of large animals, such as cows, and have successfully colonized tropical open areas through the Gulf and Pacific coastal plains. However, in the farms studied we only recorded two individuals of *D. gazella* and none of *E. intermedius*. This could be attributed to the surrounding matrix predominantly composed of banana and coffee associations that do not favor the colonization and persistence of these species.

In the context of functional groups and their interaction with environmental conditions, a noticeable tendency has been observed among dung beetles. However, the integration of functional groups considering variation in habitat preferences, relocation strategies, body size, daily activity, and food preferences has been little studied in different conditions of habitat (Arellano et al. 2023). Specifically, a clear connection exists between the size of individual beetles, primarily due to factors such as thermal stress and the quality of available resources (Gardner et al. 2008). Within degraded ecosystems, an interesting observation arises larger beetles show greater sensitivity to disturbances in their habitat, and the relationship between larger and smaller beetles decreases as land-use intensity increases (Shahabuddin et al. 2009). Based on the findings, this pattern is noticeable in Farm R, which has the largest proportion of pastures, implying a more intense land use and this agrees with our hypothesis since considering vegetation structures within agroecosystems there is less variability of traits in less heterogeneous areas although in general, we founded varies composition of functional traits in farms. Meanwhile, in the other two farms, the range of sizes (large, medium, and small) is more evenly distributed. In addition, replacing forests with cattle pastures not only modifies diversity, and species composition but also modifies resource food selection patterns, which could affect ecosystem function provision by dung beetles (Alvarado et al. 2021) since the richness of functional groups was seen to decrease in perturbed forests compared to conserved forests (Noriega et al. 2021).

Within each studied farm, the identified habitat conditions are a result of management decisions made by the owners, tailored to each agroecosystem. One notable element that occurs in agricultural and ranching farms is living fences. While the main purpose of this practice is to serve as boundaries and enclosures, they also offer additional benefits that can have positive impacts on biodiversity. They serve as shade and provide fodder for livestock, as well as offering protection for birds (Pulido-Santacruz and Renjufo 2011) and plants (Harvey et al. 2005; Zamora et al. 2022). Estrada et al. (1998) found that live fences, along with other anthropogenic vegetation types, contribute to the conservation of dung beetle species by enhancing landscape connectivity, since species composition is very similar between forest areas and living fences. Moreover, facilitates the movement of some species that avoid open areas (Hernández-Molina et al. 2023). For example, Arellano et al. (2008b) demonstrated that living fences allow the movement of species such as *Canthon cyanellus,* which occurs in the agricultural farm, across low deciduous forest landscapes, enabling resource search and mate interactions. However, at the level of dung beetle communities, Arellano et al. (2008a) did not find a significant effect of live fences on beetle diversity or abundance. Nonetheless, live fences influenced species composition by allowing the presence of forest-adapted species, thus fostering connectivity among fragments within the landscape. Giraldo et al. (2011), in a transition zone between humid low mountain and pre-mountain vegetation in the Colombian Andes, showed that there is no difference in richness (q0) but there is a difference in the abundance of beetle species in live fences. In this study, live fences had the highest abundance than the other habitat conditions of all farms. In the ranching farm, live fences are like the other habitat conditions such as steep slope pasture and riparian fragments but are richer than the flat pasture. In the agricultural farm, the live fence is more diverse in the q1 and q2 diversity orders and the pastureland use is less diverse, it may be that, again, the thermal niche explains the diversity patterns observed, and a gradient of shade cover can be appreciated, where the banana-coffee plantation has the greatest shade, the live fence is intermediate, and the pasture presents open conditions. Another factor that might explain the greater diversity in the banana-coffee plantation is the spatial heterogeneity and availability of resources for beetles, such as fruits, carcasses, and excreta of different animals, including humans. *Onthophagus belorhinus* is a species that includes banana in its diet.

A remarkable observation in this study is the high abundance of *Onthophagus corrosus* in the farms, despite being a species that has been associated with more preserved portions of vegetation. Martínez et al. (2017) emphasize that records of this species are rare, with a strong preference for higher tree cover areas. Therefore, they attribute its collection in grassland conditions to the loss of original vegetation. Although the highest abundances of this species occur along living fences and pastures in slopes, it is the second most dominant species observed along living fences and the most dominant species in pastures of the ranching farm. In the agricultural farm, it is the third most dominant species found in living fences and the second most dominant in pastures. In the plantation farm, it is present in all habitat conditions, but compressing very low abundances. The high abundances of this species do not correspond with the records in previous studies, however, Arellano and Halffter (2003) described a transitional landscape where there were no clear distinctions between dung beetles associated with pastures and those found in forests. This could potentially explain the presence of *O. corrosus* in these open conditions.

Finally, we recognize the methodological bias related to the focused sampling carried out in order to identify production system options with structural arrangements that could be friendly to the biodiversity of the dung beetle and to recommend the best production system. We identified in the study zone the most representative forms of land use within the agricultural ranches and we selected those properties that had a similar size and could be visualized, in group, as a gradient. As a result, there were no replicates of the farms with the same conditions as well as variations that may exist in production practices in the study area. In future studies, we recommend expanding the number of ranches to have a more representative sample and thus be able to establish with greater certainty the better arrangement inside every property to support diversity and functionality by dung beetles. We propose to involve other farms in the studied area to promote the care, expansion, and connectivity of wooded habitats, developing conservation programs for these ecosystems.

Further studies are needed that incorporate both the effect of different production systems and native habitats on dung beetle diversity. Future studies should consider a methodological guideline that can be replicated in other works at local scales in different regions, evidencing a more robust sampling scheme for ecological studies of dung beetles (Rivera and Favila 2022; Mora-Aguilar et al. 2023).

Conclusions

The effects of vegetation coverage are replicated across different habitat conditions in all farms. The agricultural farm displayed a higher incidence of species associated with conserved portions of cloud forest. On the other hand, in the pastures, there are a greater number of species associated with grasslands. Even in the FG, where cattle are grazing, there is a convergence of both species' types. Species diversity and composition vary according to the type of farm and the main factor that modifies this tendency is the proportion of pastureland composing the farm. The greater the proportion of pastures, the lower the diversity is, and this could be attributed to the effect of resource diversity and quality, which influences the diversity patterns of beetles across space. Specifically, the loss of shade decreases the quality of the habitats and limits the capacity of dung beetle species to establish themselves in the site, due to their physiological adaptation to temperature and humidity. In contrast, a lower proportion of grazing land and denser vegetation canopy, which cast more shadow support higher diversity and functionality by dung beetles. Riparian vegetation and banana-coffee plantations are also important connectivity elements in agricultural landscapes for shade-adapted dung beetle species.

Implementing diverse habitat conditions in a farm has consequences on the composition of dung beetle species, that is why decisions made in agroecosystems can influence the conservation of these organisms. Habitat conditions integrating trees promote connectivity between forest remnants across landscapes. Living fences enhance connectivity within the landscape and provide shaded microhabitats, which facilitate a greater diversity of some dung beetle species by creating favorable habitats, such as shaded areas, which can support the diversity and presence of these organisms.

Authors' contributions

LA, RT, and SL contributed to the conception and approach of the text and LA coordinated the progress of the document. RT, LA, SL, IO, and JJ were responsible for the results, design of the final figures and methods. All authors participated in the content of the manuscript, review of papers, synthesis of ideas, and general redaction and writing of the document. All authors have read and approved the final version of the manuscript, and agreed to be held accountable for all aspects of the work.

Conflict of interest

The authors declare no potential conflict of interest.

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Availability of data and materials

All data generated or analyzed during this study are included in this published article.

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