



Soil invertebrate diversity in a traditional livestock agroforestry landscape in southeastern Mexico †

[Diversidad de invertebrados del suelo en un paisaje agroforestal ganadero del sureste de México]

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SUMMARY

Background: Soil invertebrates play an active role as ecosystem engineers in physical, chemical, and biological processes, and are therefore important bioindicators of the health of natural and agroecosystems, such as pastoral landscapes, where these organisms have been poorly studied. **Objectives:** To evaluate the abundance, richness, and diversity of soil invertebrates and their importance as bioindicators in a livestock agroforestry landscape in southeastern Mexico. **Methods:** We used 45 pitfall traps placed in three production units (PU1, PU2 and PU3). Each PU's maintain similarly grazing areas, with grass monocultures and dispersed native trees, and natural vegetation patches within the same area. Sampling was performed across three periods (the dry season, the transition between the dry and rainy seasons, and the rainy season) to account for seasonal variation. **Results:** We obtained a total abundance of 12,342 invertebrates and a richness of 26 orders (taxa). The most abundant taxa were Hymenoptera (52 %), Coleoptera (15 %), Diptera (11 %), and Orthoptera (5%), and the remaining 17 % corresponded to 22 taxa. Taxon diversity was higher in PU3 compared to the other production units. **Implications:** Maintaining a livestock landscape with habitat heterogeneity can contribute to the conservation of biodiversity and the sustainability of production systems. **Conclusions:** The presence of indicator taxa was heterogeneous among the production units, which shows that, at the livestock agroforestry landscape scale, are able to maintain a functional structure that preserves the ecosystem services provided by the diversity of soil invertebrates.

Key words: indicator groups; soil fauna; pitfall traps; richness; traditional agroforestry.

RESUMEN

Antecedentes: Los invertebrados del suelo participan activamente en procesos físicos, químicos y biológicos, como ingenieros del ecosistema, lo que los convierte en importantes bioindicadores de la salud de sistemas naturales y agroecosistemas, como los paisajes ganaderos, donde estos organismos han sido poco estudiados. **Objetivos:** Evaluar la abundancia, riqueza y diversidad de los invertebrados del suelo y su importancia como bioindicadores en un paisaje ganadero del sur de Quintana Roo. **Métodos:** Se utilizaron 45 trampas de caída o pitfall colocadas en tres unidades de

† Submitted April 24, 2026 – Accepted August 5, 2026. <http://doi.org/10.56369/tsaes.6986>



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ISSN: 1870-0462.

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producción (UP1, UP2 y UP3). Las trampas fueron distribuidas equitativamente en zonas de monocultivo de pasto, en zonas con pasto que incluyen árboles nativos, y en parches de vegetación natural, dentro de la misma unidad de producción. El muestreo se realizó en tres ocasiones (secas, inicio de lluvias y lluvias), considerando la variación estacional. **Resultados:** Se obtuvo una abundancia total de 12,342 invertebrados y una riqueza de 26 órdenes (taxones). Los principales taxones fueron Hymenoptera (52 %), Coleoptera (15 %), Díptera (11 %) y Orthoptera (5 %), y el 17 % restante corresponde a 22 taxones. La diversidad de taxones fue mayor en la UP3 comparada con las demás unidades de producción. **Implicaciones:** Mantener un paisaje ganadero con heterogeneidad de hábitats puede contribuir a la conservación de la biodiversidad y a la sustentabilidad de los sistemas productivos. **Conclusiones:** La presencia de taxones indicadores fue heterogénea entre todas las unidades de producción, lo que demuestra que, los ranchos son capaces de mantener una alta diversidad de invertebrados del suelo y su estructura funcional, lo cual proporciona importantes servicios ecosistémicos a escala del paisaje.

Palabras clave: agroforestería tradicional; fauna edáfica; grupos indicadores; riqueza; trampas pitfall.

INTRODUCTION

Biodiversity plays a fundamental role in controlling crop pests and maintaining the stability, function, and services of agroecosystems (Sunderland and Samu, 2000; Letourneau *et al.*, 2009); however, intensified land use is one of the main causes of biodiversity loss worldwide (Raven and Wagner, 2021; Gaëtane *et al.*, 2021). In this scenario, agricultural systems could be an ally not only in stopping the processes of ecosystem degradation and biodiversity loss, but also in sustainably improving productivity. Hence, designs that incorporate trees, such as agroforestry systems, have been shown to serve as biodiversity and agrobiodiversity reservoirs, landscape connectors, and biological corridors between protected natural areas and human-controlled areas (Villanueva-López *et al.*, 2019; Mamabolo *et al.*, 2024).

In agroecosystems, and even more so in livestock systems, assessment of soil diversity as a functional component is scarce; in fact, livestock systems are often viewed negatively, due to cattle ranches, traditionally widespread in the tropics, are productive systems that substitute natural vegetation by grass (López-Santiago *et al.*, 2019; Villanueva-López *et al.*, 2019; López-Santiago *et al.*, 2023). Nevertheless, in the southeastern Mexico, these livestock systems are diverse, ranging from those that use extensive pastures for livestock to those that utilize agroforestry systems (Casanova-Lugo *et al.*, 2014; Villanueva-Partida *et al.*, 2016; Villanueva-López *et al.*, 2019); also include other animal and plant species, mostly with dual or multiple purposes (Villanueva-Partida *et al.*, 2019). Therefore, as the complexity of the system increases (crops, trees, shrubs), so does species diversity and the sustainability of agroecosystems (Goldman, 1995; Marja *et al.*, 2022; Vaupel *et al.*, 2025). Use of multiple crops or woody components such as trees and shrubs, instead of monocultures, provides greater richness of associated species, which contributes to increasing the soil invertebrate diversity of the system, improving connectivity, natural regeneration, and soil productivity, further ameliorating micro-climatic conditions within the pasture matrix (Esquivel-

Mimenza *et al.*, 2011; Villanueva-López *et al.*, 2019; Villanueva-Partida *et al.*, 2019; Vaupel *et al.*, 2025).

In general, soil invertebrates play an active role as ecosystem engineers in physical, chemical, and biological processes at different spatial and temporal scales, which provides soils with self-organizing characteristics, making soil invertebrates some of the best indicators of soil quality and a resource that, if managed properly, may increase the ecosystem services provided by agroecosystems (Lavelle *et al.*, 2006). Therefore, investigating their taxa, functional diversity, and abundance is essential to assess ecosystem resilience, detect environmental stress, and guide conservation efforts (Korobushkin *et al.*, 2025). Given the importance of systems more complex to the presence of soil organisms in the agroecosystems, the present study aimed to evaluate soil invertebrate abundance, richness, and diversity in a livestock agroforestry landscape in southeastern Mexico. Richness, diversity, and functional group structure of soil invertebrates can reveal the soil health in livestock agroforestry systems and landscape complexity and thus serve as bioindicators of conservation.

MATERIALS AND METHODS

Study area

The study was conducted in the livestock community of Río Verde, in the municipality of Bacalar, located in the south of the state of Quintana Roo, Mexico, between the geographic coordinates 18°40' N and 88°23' W, at an altitude of 53 to 69 masl. The livestock production of this municipality is one of the most important in the state and is dual-purpose (meat, milk and dairy products; Agricultura/Quintana Roo, 2018). The climate of the region is classified as warm sub-humid Aw₁, with rainfall in summer (García, 2004). The mean annual temperature ranges from 24 to 26 °C and the warmest month is May, with daily maximum temperatures typically ranging between 43 and 45 °C. Annual precipitation is 1200 to 1500 mm, with the highest levels occurring in September and the lowest in May. The predominant soil types in the region are gleysol and leptosol, according to the FAO (IUSS Working Group WRB, 2015).

Sampling design

We selected three animal production units (PU1, PU2 and PU3) with main characteristics of the landscape of the study area (Table 1), that is, ranches with grazing areas without trees, with dispersal native trees, and natural vegetation remnants (i.e., preserved areas of medium-height semi-evergreen rainforest), which compose the regional pastoral landscape (Table 1; Agricultura/Quintana Roo, 2018).

We established a total of nine 50-m-long transects distributed where the landscape was heterogeneous but representative of a productive regional scale. The transects were separated by a minimum distance of 50 m to ensure spatial independence; a distance of 50 m is the approximate activity radius of epigeal

invertebrates, which ensures the spatial independence of samples and transects (Guo *et al.*, 2020; Rivera and Favila, 2022). In each transect, five stations containing a pitfall trap were placed every 10 m, resulting in a total of 15 traps per agroecosystem and 45 traps for the whole study area (Boetzl *et al.*, 2018). Collections were made considering an ethical sampling intensity based on a cost-effective approach to avoid oversampling (Rivera and Favila, 2022). We conducted two surveys during the dry season, from February to May, two during the intermediate season, from June to July, and two during the rainy season, from August to September, resulting in a total of six surveys during 2023. We obtained a total of 270 samples, corresponding to 90 samples in the dry season, 90 in intermediate conditions, and 90 in the rainy season in the three sites in one year.

Table 1. Characteristics of production units (PU1, PU2 and PU3) in the south of Quintana Roo, Mexico.

Characteristics	PU1	PU2	PU3
Age of the systems (years)	20 – 30	16 – 20	20-25
Total area (ha)	106	160	50
Pastoral zone (ha)	60	40	15
Pastoral zone with trees (ha)	15	22	7
Natural vegetation (ha)	7	35	10
Purpose of natural vegetation patch	Conservation	Conservation	Conservation
Production purpose	Milk and beef production	Milk	Milk and beef production
Cattle breeds	Simmental × Gyr	Brown Swiss × Gyr	Brown Swiss × Gyr
Herd size	70-75	100-127	35-40
Stocking rate (AU ha ⁻¹)	1 – 4	1 – 4	1 – 4
Grass species	<i>Megathyrus maximus</i> cv. Mombasa, <i>Urochloa brizantha</i> Stapf.	<i>M. maximus</i> cv. Mombasa, <i>U. brizantha</i>	<i>M. maximus</i> cv. Mombasa, <i>U. brizantha</i>
Grazing system	Rotational	Rotational	Rotational
Days of grazing	10 – 15	15 – 30	15-30
Days of pasture recovery	15 – 20	15 – 20	15-20
Technical level	Medium*	Medium*	Medium*
Soil bulk density (Mg m ⁻³)	0.89 (±0.03)	0.85 (±0.04)	0.83 (±0.03)
Soil moisture (%)	11.8 (±1.4)	10.5 (±1.6)	11.3 (±0.6)
Organic material (%) MO)	15.4 (±2.5)	18.6 (±6)	17 (±2.2)

*Farmers apply animal health management (i.e., vaccination and deworming), artificial insemination for cattle, and the use of electric fences. (±) Standard deviation.

Pitfall trap design

For the present study, we used pitfall traps modified according to Galindo-Rojas *et al.* (2017) and Boetzel *et al.* (2018), which were made of 500-ml disposable plastic cups with dome lids. Each lid had four lateral windows (approximately 4 cm wide by 3 cm high) for the epigeal invertebrates to enter. Each trap was buried at ground level with only the dome exposed. Two 60-cm-long wooden rods were crossed perpendicularly through the windows at the level of the ground to increase the trap catchment area and ensure a higher sampling effort (Boetzel *et al.*, 2018). No baits were included in the pitfall traps to ensure a non-targeted capture of invertebrates and avoid bias due to the attraction of specific groups (i.e. scavengers, detritivores, coprophagous organisms) (Hosaka *et al.*, 2014). The traps contained water with detergent and salt to preserve the organisms (Brown and Matthews, 2016). The traps were active for a minimum of 48 h (2 days) and then taken to the laboratory to fix, count, and identify the morphospecies at the order or “taxon” level (Rivera and Favila, 2022; Mathieu *et al.*, 2022; Lara-Pérez *et al.*, 2023).

Sample collection and processing in the laboratory

The content of each sample from the pitfall traps was sieved with a 0.5-mm mesh and emptied into vials with fixative (70 % ethanol; Miller *et al.*, 2013). Each vial was properly labeled with the following information: collection date, place, collector’s name, site, transect, sample, coordinates, etc.

The collected invertebrates were transported to the laboratory, cleaned, and fixed in 70 % ethanol (Miller *et al.*, 2013). The collected material was observed and identified using a Leica S9i® stereoscopic microscope equipped with a Stereozoom® camera and the Leica Application Suite software. Large taxonomic groups were classified at the order or taxon level. We considered all soil invertebrates that met the criterion of a minimum size ≥ 0.5 mm according to a size visible under a stereoscopic microscope and/or to the naked eye (*meso and macrofauna, sensu* Decaëns, 2010; Lavelle *et al.*, 2022 and Brown *et al.*, 2024). The collected specimens were stored in the facilities of the Laboratorio de Estudios Avanzados en Agroecosistemas of the Instituto Tecnológico de la Zona Maya.

Diversity analysis

We estimated the diversity of the soil invertebrate taxa (qD) in terms of true diversity (effective number of species or taxa), also known as Hill numbers, where q is the order of the diversity (Jost, 2006) and $q = 0$ indicates richness, while $q = 1$ and $q = 2$ refer to the exponential of Shannon entropy and the inverse of

Simpson’s index, respectively. When $q = 1$, each species is weighted by its proportional abundance, and when $q = 2$, greater weight is given to the dominant species and is less influenced by rare species (Jost, 2006; Chao *et al.*, 2014).

To evaluate and compare sample completeness and expected richness and diversity in the three production units, we used the protocol proposed by Chao *et al.* (2020), where sample completeness profiles were estimated using the abundance data of the taxa in each treatment or production unit (Chao and Jost, 2012). The analysis was performed using the online program *iNext4steps* (<https://chao.shinyapps.io/iNEXT4steps/>). To determine if the data were sufficient to estimate true diversity (qD), we constructed extrapolation and rarefaction curves based on abundance, as well as asymptotic and empirical diversity profiles to assess the extent of undetected diversity in the dataset of the different treatments. Rarefaction and extrapolation based on incidence were carried out with Hill numbers that double the number of individuals in the reference sample.

To compare diversity, we constructed extrapolation and rarefaction curves based on the maximum coverage (C_{max}) of the reference sample (dataset) to make a fair comparison of species diversity estimates for equally complete samples (Chao *et al.*, 2014; 2020). Profiles with a steeper slope indicate a more uneven distribution because of rare and dominant species. We used a bootstrap method with 100 replications to estimate the 95 % confidence intervals. Significant differences between treatments were evaluated by the overlap between confidence intervals (Chao and Jost, 2012).

Data analysis

Taxon composition was visualized using a non-metric multidimensional scaling analysis (nMDS) to obtain the distribution of the taxa among the three production units (Clarke, 1993). We performed an analysis of similarities (ANOSIM) to compare the distribution between and within the three production units (Clarke, 1993). We also applied a permutational analysis of variance (PERMANOVA), using the Bray-Curtis dissimilarity matrix, to determine whether there was an effect of the production units on the community structure (Anderson, 2001). Finally, we conducted an indicator species analysis (IndVal; Dufrêne and Legendre, 1997), which combines measures of species specificity (the uniqueness of a particular habitat) and fidelity (frequency of occurrence in that habitat). To identify and evaluate the most prominent taxa in each production unit, the significance of the indicator value (IndVal $p < 0.05$) was tested using random permutations (9999 permutations; Dufrêne and Legendre, 1997; Hammer, 2001). To identify the

shared and unique species in the ranches or PU's, we construct a Venn diagram (Heberle *et al.*, 2015) in the program *Integrative Venn* (<http://www.interactivenn.net/index2.html>). The methods for the ordination, indicator species, and comparisons were carried out in PAST version 2.02 (Hammer, 2001).

RESULTS

Abundance of soil invertebrate taxa

We collected 12,342 soil invertebrates belonging to 26 orders (taxa) in three production units in the livestock agroforestry landscape; of which, 5,090 invertebrates were collected in PU1, 3,963 in PU2, and 3,221 in PU3. Of the individuals found, 97 % corresponded to the following eight taxa: Hymenoptera (52.3 %), Coleoptera (15.1 %), Diptera (11.1 %), Orthoptera (5.4%), Acaridae (4.4 %), Araneae (3.3 %), Collembola (2.8 %), and Hemiptera (2.7 %), which were the main taxa, and the remaining 2.4 % was distributed among 18 taxa (Blattodea, Opiliones, Lepidoptera, Psocoptera, Polydesmida, Thysanoptera, Ixodidae, Pulmonata, Isoptera, Pseudoscorpion, Isopoda, Embioptera, Archaeognatha, Mantodea, Dermaptera, Neuroptera, Phasmida, Trichoptera; Figure 1).

Richness, diversity, and sample completeness

According to the diversity analysis (qD), we obtained sample completeness ($C_{\max}$) and sample coverage higher than 99 % in all production units (Figure 2a and d). In the case of species richness ($q = 0$), even though PU3 exhibited lower taxon richness ($n = 19$ taxa) than PU1 and PU2 ($n = 22$ and 24 taxa, respectively), the three production units showed statistically similar values according to the overlap between curves (Figure 2b). However, in terms of abundance and dominance (diversity of order $q = 1$ and $q = 2$; respectively), PU3 showed the highest diversity (Figure 2b). Furthermore, PU3 showed the highest evenness in terms of taxon abundance ($C_{\max} = 99\%$) (Figure 2c).

Indicator taxa and community composition

Taxon abundance varied by PU, but given their higher abundance in the three production units, the most prominent taxa were Hymenoptera, Coleoptera, Diptera, and Orthoptera. However, some taxa were more abundant in PU3, such as Orthoptera, Araneae, Acaridae, and Collembola, whereas other groups, such as Hymenoptera, were notably more abundant in PU1 and PU2 (Figure 3).

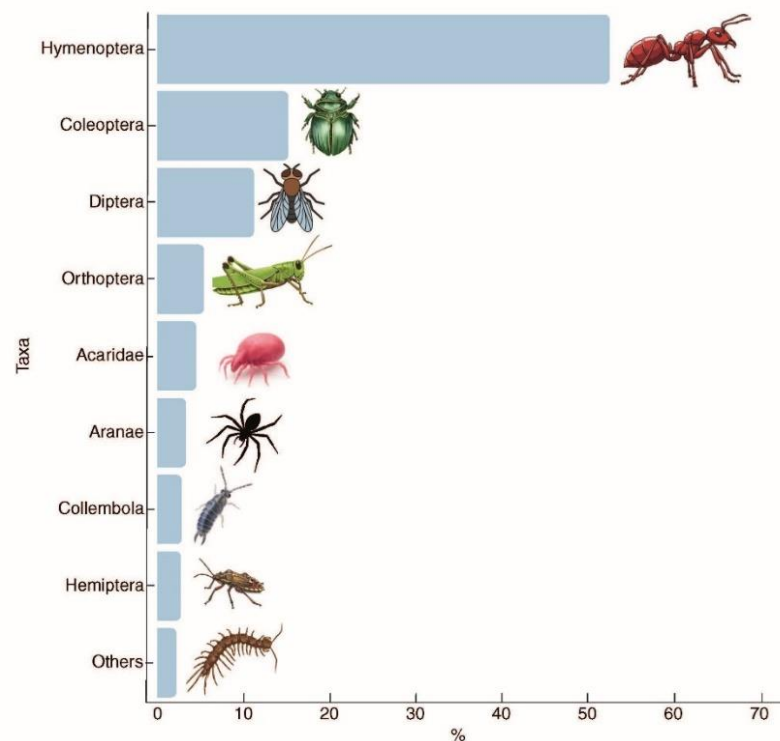


Figure 1. Total abundance percentages of the main taxa found in the livestock agroforestry landscape in southeastern Mexico.

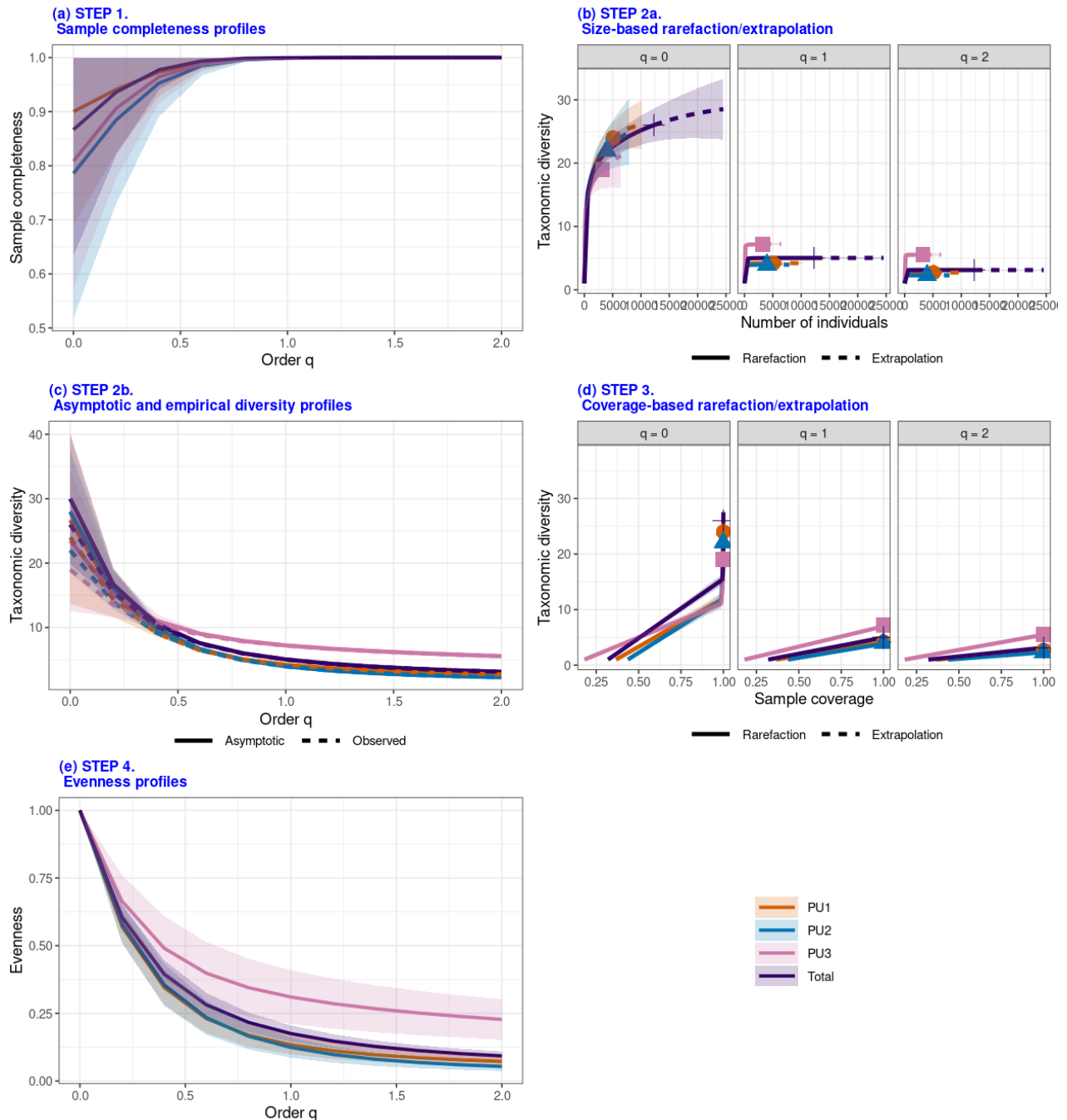


Figure 2. Completeness, rarefaction, diversity of order $q = 0, 1, 2$, and coverage curves of the samples obtained in three production units (PU1, PU2 and PU3) in livestock agroforestry landscape in the southeastern Mexico ($C_{max} > 99\%$).

According to the indicator species (i.e., taxa) index by production units, the most notable taxa as indicator groups in the PU3 were Acaridae, Araneae, Blattodea, and Orthoptera ($\text{IndVal } p < 0.05$), while Psocoptera was the most notable taxon in PU2 ($\text{IndVal } p < 0.05$). Finally, in PU1, the most notable indicator groups were the taxa Coleoptera, Lepidoptera, and Opiliones ($\text{IndVal } p < 0.05$).

Seventeen taxa (65.4 %) were shared among the three production units, while PU2 and PU1 had two unique taxa each (Phasmida-Trichoptera and Dermaptera-Neuroptera, respectively) and PU3 had no unique taxa (Figure 4).

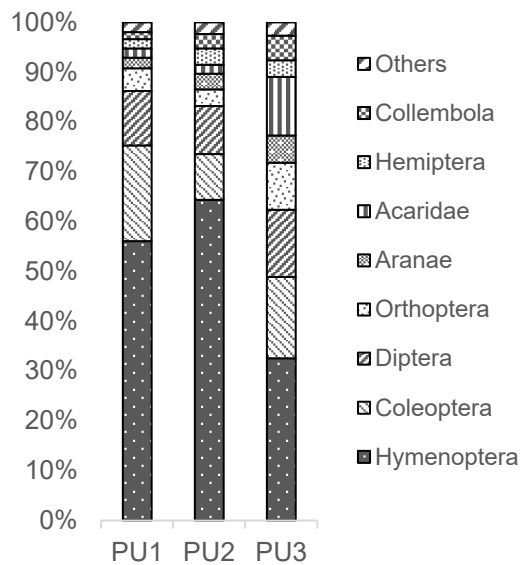


Figure 3. Relative taxon abundance (number of individuals) in three production units (PU1, PU2 and PU3) in livestock agroforestry landscape in southeastern Mexico.

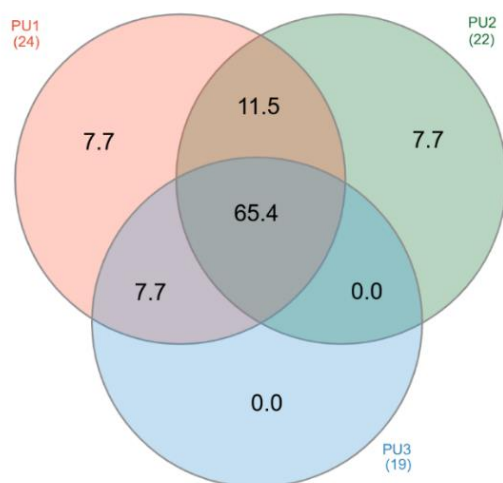


Figure 4. Venn diagram of shared and unique taxa in three production units (PU1, PU2 and PU3) in livestock agroforestry landscape in southeastern Mexico.

The composition of the taxon assemblages in the community appeared to be similar according to the overlap in the ordination (nMDS) and the similarity test (ANOSIM; $R = 0.014$; $p = 0.005$). However, the comparisons by the permutational analysis showed differences between PU3 and PU1 (PERMANOVA, $F = 2.107$; $p = 0.0058$).

DISCUSSION

Abundance, richness, and diversity of soil invertebrate taxa

The soil invertebrate abundance reported in the present study ($n = 12,342$) is lower (almost one third) than that found in other studies in similar land-use systems ($n = 42,269$; Villanueva-López *et al.*, 2019), but it is relatively similar ($n = 10,271$) when compared with a seasonal study (Lara-Pérez *et al.*, 2023). However, it is important to note that the sampling effort in the present study was substantially lower (270 samples) compared to the studies mentioned above (490 and 480 samples obtained with traditional pitfall traps, respectively).

We carried out collections considering seasonality and found 26 taxa, representing 65% of the 42 macroinvertebrate taxa (at the order level) present across different land-use systems in the Neotropics (Brown *et al.*, 2024). Between 7 and 15 taxa were recorded in the studies by Lara-Pérez *et al.* (2023) and Villanueva-López *et al.* (2019), and thus taxon richness in the present study was 3.7 and 1.7 times higher, which may be attributed to the modifications made to the pitfall traps to maximize capture efficiency with a lower sampling effort (Work *et al.*, 2002; Galindo-Rojas *et al.*, 2017; Boetzel *et al.*, 2018; Villanueva-López *et al.*, 2019; Rivera and Favila, 2022). Moreover, given that we did not use attractants or baits targeting specific groups and the defined size of the individuals collected (i.e. epigeal invertebrates ≥ 0.5 mm), it was possible to collect and include other soil invertebrate groups, such as Acaridae and Collembola, that are usually underrepresented (Lavelle *et al.*, 2022; Brown *et al.*, 2024).

Richness, diversity, and sample completeness

While taxon richness ($q = 0$) was relatively similar among the three production units, soil invertebrate diversity ($q = 1$ and 2) was similar only between PU2 and PU1, since PU3 exhibited higher diversity, even though all production units share the same landscape components (i.e., grazing areas and preserved vegetation patches). This demonstrates that, even at this observational scale, differences can be found from a soil invertebrate perspective. Heterogeneity in the system structure provides differential ecological niches for soil invertebrates with low mobility (i.e., Acaridae, Collembola) and others with greater mobility (i.e., Araneae, Hymenoptera and Coleoptera; Ekroos *et al.*, 2016; Eckert *et al.*, 2022; Romero-Díaz *et al.*, 2024). This may also be related to other landscape elements, such as more areas of preserved vegetation (such as in PU3), leaf litter production, shade, and soil moisture, which is a combination of elements that, at the local and landscape structure scale, maintains overall diversity (Ekroos *et al.*, 2016;

Eckert *et al.*, 2022). This type of production unit, as a small-scale form of land use, has a high spatial complexity and high density of agroecosystem elements, which promotes increased edge effects in the landscape, with a higher effect on the configuration of functional traits and ecosystem services of the taxa that inhabit them, as well as the dispersal of source populations of invertebrates that are found in non-cultivated habitats (Gallé *et al.*, 2020; Wang *et al.*, 2024). The above differs from intensive livestock and monoculture systems, which contribute to the global decline in the diversity and abundance of soil invertebrate (insect) populations due to habitat loss, fragmentation, and degradation (Didham *et al.*, 2020; Hallmann *et al.*, 2017; Wang *et al.*, 2024), and where a consistent decrease in soil invertebrate diversity has been observed compared to more complex and managed systems, such as agroforestry systems that have a higher density and diversity of woody species (Ramírez-Barajas *et al.*, 2019; Villanueva-López *et al.*, 2019).

Indicator taxa and community composition

In PU3, there were several notable groups that serve as indicators of conservation because of their function in the system as decomposers and consumers of organic matter, predators, and herbivores (Acaridae, Blattodea, Araneae and Orthoptera, respectively), all with particular habitat preferences. For example, several studies report that mite diversity (Acaridae) shows a positive response to plant and microhabitat diversity (Dacaëns, 2010), and spider (Araneae) richness is strongly related to the edge effects of internal and external landscape elements, larger habitat patches, and more complex landscape structures (Gallé *et al.*, 2020). On the other hand, according to Brown and Matthews (2016), the presence of cockroaches and crickets (Blattodea and Orthoptera) is important because they are related to geophagy, decomposition, and bioturbation, and because of their detritivorous, phytophagous, and fungivorous feeding habits. Another important finding is the presence of the taxon Psocoptera in the three production units, but it is particularly notable as an indicator taxon in PU2. This is an order that is generally found in live and dead foliage, tree bark and trunks, the surface of rocks, and even human living spaces and bird nests, and feeds on epiphytic and epigeal algae, lichen, eggs, and insect remains (García-Aldrete, 2014); thus, it requires environmental conditions rich in organic matter and humidity. In the case of PU1, Coleoptera, Lepidoptera, and Opiliones are taxonomic groups with a broad range of functions in agroecosystems, where beetles probably perform the highest number of functions, which range from bioturbation to a broad-spectrum diet (plants, organic matter, fungi, meat, etc.), while Lepidoptera are characterized by being phytophagous or crop pests and Opiliones by their geophagous,

predatory, and bioturbation habits (Brown and Matthews, 2016).

The abundance structure and taxon composition of soil invertebrates were similar in the three production units; that is, there was no statistical evidence showing any dissimilarities, since 65 % of the taxa were shared and only 0-8 % were unique. However, some noteworthy details should be mentioned: the highest diversity was observed in PU3, as well as different specialist functional groups sensitive to the conditions of the habitat, such as Acaridae, while PU1 was the most contrasting unit and had the presence of more generalist taxa such as Coleoptera and Lepidoptera, where the latter may be considered crop pests (in the case of the rice grain moth). The presence of indicator groups at a local (production units) or landscape level reflects the complexity of the habitat from a soil invertebrate perspective (Eckert *et al.*, 2022; Vaupel *et al.*, 2025). Given the scarcity of documented evidence of the movement of diversity from natural to transformed regions (van der Mescht *et al.*, 2023), it is essential to maintain and preserve patches of conserved vegetation and the presence of trees in productive management systems such as the production units in the region (Vaupel *et al.*, 2025). This will make it possible to preserve a higher functional diversity, such as specialist species and indicator species of the conditions of the habitat (Eckert *et al.*, 2022; van der Mescht *et al.*, 2023). This would be the case of the presence of taxa such as Collembola in all the production units, which, due to their lower mobility, sensitivity to soil moisture, and polyphagous habits (feeding on fungi, algae, and detritus), reflect the conditions of the habitat where they are found. They are also indicators of suitable conditions for their persistence in the landscape (Scheu and Folger, 2004; Auclerc *et al.*, 2009; Lessel *et al.*, 2011), which emphasizes the need to maintain small-scale heterogeneity in the landscape of productive systems (Eckert *et al.*, 2022). Another taxon that was always present and abundant in all the ranches was Hymenoptera, distinguished by the presence of various ant and wasp species (families Formicidae and Vespidae), which generally shows a stronger preference for open areas, higher mobility, and a broader diet spectrum than Collembola (Heil *et al.*, 2001; Gollan *et al.*, 2011; Eckert *et al.*, 2022).

CONCLUSION

The diversity of epigeal invertebrates, as a live soil component, is fundamental for maintaining the fertility of the system, making them important bioindicators of agroecosystem health. The soil invertebrate diversity, found in the production units in the livestock agroforestry landscape of southeastern Mexico (PU1, PU2, and PU3), provides an insight into the regional diversity that maintains these types of land-uses and

agroecosystems. We found a relatively high diversity of taxa at the order level, which is the opposite of what is expected in extensive conventional livestock systems, mainly due to the type of production units' management and a higher landscape structural complexity. Also, this heterogeneity in the landscape promotes less homogenization in the diversity of soil. The presence of the functional groups found indicates various ecosystem services, from bioturbation, organic matter recycling, to pest control, and predation, among others, which shows the complexity and functionality of the taxa found in livestock agroecosystems in southeastern Mexico.

Acknowledgements

We thank the Secretaría de Ciencia, Humanidades, Tecnología e Innovación (SECIHTI) for supporting the postdoctoral research stay of PJRB (11200/320/2022), and the Tecnológico Nacional de México for infrastructure support throughout this project. To the community of Rio Verde, Quintana Roo and the ranchers Gerardo, Héctor, and Javier for allowing us to conduct the field work, and to the students: Raúl, Gaudencio and Ruth, for their support in the field work.

Funding. Research was financed by authors.

Conflict of interests. The authors declare no conflicts of interest.

Compliance with ethical standards. Does not apply

Data availability: Data is available from P. J. Ramírez-Barajas, pjrbarajas@gmail.com, upon reasonable request.

AI disclosure statement: We declare that no generative artificial intelligence tools were employed in the preparation of this manuscript.

Author contribution statement (CRediT). **P.J. Ramírez-Barajas** - Writing–review and editing, Writing–original draft, Resources, Project administration, Conceptualization, Visualization, Software, Methodology, Investigation, Formal analysis, Data curation. **L.A. Lara-Pérez** - Writing – review and editing, Methodology, Investigation, Conceptualization, Supervision, Validation. **L. Macario-González** - Writing – review and editing, Investigation, Conceptualization, Validation. **F. Casanova-Lugo** - Writing–review and editing, Visualization, Resources, Project administration, Methodology, Investigation, Formal analysis, Conceptualization, Supervision. **N. Torrescano-Valle** - Writing – review and editing, Investigation, Conceptualization, Validation. **M. Ojeda-Chi** - Writing – review and editing, Investigation, Conceptualization, Validation.

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