Research Topics

Neotropical dung beetle diversity: Ecological, historical, and anthropogenic perspectives

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Neotropical dung beetle diversity: Ecological, historical, and anthropogenic perspectives

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Cover image
Cover image of *Oxysternon conspicillatum* (Weber, 1801) looking for food in a neotropical forest, courtesy of Jorge Ari Noriega

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Editorial: Neotropical dung beetle diversity: ecological, historical, and anthropogenic perspectives

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Editorial on the Research Topic
Neotropical dung beetle diversity: ecological, historical, and anthropogenic perspectives

The Neotropical region hosts the highest diversity of dung beetles worldwide, linked to the diversity of mammals that thrive in the ecosystems of this region, particularly in its extensive tropical forests. The large amount of feces produced by herbivorous and omnivorous mammals in the natural and modified ecosystems of the Neotropical region is used by dung beetles for feeding and reproduction, but many species consume carrion and decomposed fruits including mushrooms, and even are predators of insects. Therefore, Neotropical dung beetles provide one of the most critical ecosystem services: organic waste recycling. However, our understanding of their behavior, biology, ecology, and taxonomy in this region still needs to be improved. We invite researchers from different countries of Latin America who are investigating various aspects of the biology, behavior, ecology, evolution, and taxonomy of Neotropical dung beetles to participate in our Research Topic.

In the Neotropical region, forests are being converted to grasslands. As a result, the species composition of dung beetles is also changing, and the dung deposited by cattle in pastures is consumed and recycled into the soil by these new dung beetle communities. The ecological roles of dung beetles that contribute to human ecosystem services in these transformed ecosystems encompass improved soil nutrient cycling, bioturbation, plant growth promotion, secondary seed dispersal, control of fly populations, and parasite suppression. Arellano et al. have reviewed the available literature on taxonomic diversity, functional diversity, and ecological functions of dung beetles in Neotropical grazing lands. They highlight the current knowledge gaps regarding the impact of livestock management practices, forms, and the historical context on dung beetle diversity. To enhance ecological studies in these lands, they have proposed a standardized data collection format that distinguishes among the diverse tropical grazing lands documented in the literature.

Andresen and Urrea-Galeano have reviewed one of the most studied ecosystem services of dung beetles in the Neotropical region: secondary seed dispersal. These authors have analyzed the current knowledge on the influence of dung beetles on the structure and dynamics of seed banks and their impact on tropical forest plants through the dispersal of defecated seeds. They have also explored the crucial role of secondary seed dispersal in the performance of understory seedlings. They believe that this comprehensive review will inspire further investigation into the fascinating interactions between dung beetles and plants in tropical ecosystems.

The methodology used for collecting and monitoring dung beetles to evaluate their communities has recently been questioned, as the conclusions drawn can change depending on the methods used. Mora-Aguilar et al. analyzed the various methodologies employed in dung beetle biodiversity studies in the Neotropical region, ranging from pitfall traps to supplementary techniques. They have proposed a standardized protocol for dung beetle sampling tailored to specific research objectives, including a fundamental methodology for generating comprehensive local inventories. In their review, Rivera and Favila explored the interaction between sampling intensity, sampling coverage, habitat type, and the journal-impact factor in peer-reviewed research in the Neotropical region. From this review, they have suggested sampling guidelines to ensure robust dung-beetle diversity assessments while preventing oversampling.

Studies of dung beetle diversity have been carried out primarily in natural and modified tropical forests. The research by Simões-Clivatti and Hernández addressed the complex dynamics influencing dung beetle metacommunities in native subtropical forests and *Pinus* monocultures. Their analysis evaluated factors such as habitat type, vegetation, mammalian presence as a food resource, and temperature, shedding light on the drivers shaping these assemblages. The metrics they used did not reflect the difference in the environmental quality of the areas with respect to species richness and diversity in different habitats. They suggest supplementing the assessment with composition analysis methods. Villamarin-Cortez et al. examined diversity and distribution patterns of dung beetles in Ecuador. Their research underscores the crucial role of elevation and precipitation in shaping the distribution of dung beetle assemblages in the country, providing a framework for assessing dung beetle habitats and diversity at various scales within the broader Neotropical region.

The association between mammals and dung beetles in the Neotropical region has been consistently recognized, but needs a more in-depth analysis. Halffter and Favila addressed the intricate relationship between dung beetles and primates in Neotropical forests. In South America, the diversity of arboreal dung beetles associated with monkeys exceeds that observed in tropical forests in Mexico and Central America. These authors suggested a systematic and comparative methodology to shed light on the foraging behaviors of arboreal beetles and their role in recycling arboreal dung.

Dung, carrion, and other wastes consumed by dung beetles are recycled into the soil via the reproductive behaviors of dung beetles. Huerta et al. outlined a comprehensive summary of field and laboratory studies on the reproductive behavior of Neotropical dung beetles. Their review identified geographic and habitat gaps in the current knowledge on the nesting behavior of these beetles. To address these gaps, they have proposed future research objectives and suggested alternative methodologies for analyzing the behavioral responses of Neotropical dung beetles facing the impact of human activities.

Dung beetles are a suitable model for examining the historical and contemporary factors associated with the speciation process in the Mexican Transition Zone (MTZ), where the Nearctic and Neotropical regions converge. Within the MTZ, dung beetles inhabit diverse environments that promote *in-situ* and vicariant allopatric differentiation of their populations. Nolasco-Soto et al. analyzed the most well-studied dung beetle species of the Neotropical region, *Canthon cyanellus*, which is actually a species complex, focusing on its ecological and evolutionary aspects. They examined the current understanding of divergent patterns that have defined the speciation process within this species complex. Their conclusion underscores the significance of merging traditional morphological taxonomy with phylogeography to gain insight into the speciation dynamics of *C. cyanellus* and other dung beetle species.

Finally, Cupello et al. have highlighted a pivotal period in dung beetle research in the Neotropical region. The “Taxonomic Revolution of New World Dung Beetles” began in 1988 and marked a significant surge in taxonomic studies of Scarabaeinae dung beetles in the New World. Simultaneously, an “Ecological Revolution of Dung Beetles” is characterized by the expansion of ecological studies on these organisms. These authors have stressed the importance of collaboration between ecologists and taxonomists in advancing the scientific understanding of the natural history of Neotropical dung beetles.

As a continued effort to summarize and expand the understanding of the natural history of dung beetles, we are pleased to dedicate this Research Topic to Prof. Gonzalo Halffter, a pioneer in investigating the natural history of dung beetles.

These contributions will catalyze new research and inspire young students and researchers to investigate dung beetles in the Neotropical region and tropical regions worldwide.

Author contributions

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Good news! Sampling intensity needed for accurate assessments of dung beetle diversity may be lower in the Neotropics

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Ecological studies with Scarabaeinae dung beetles have increased exponentially over the past 30 years, using lethal pitfall traps baited with mammal feces or carrion as the preferred sampling method. Different studies have determined the distance between pitfall traps for effective sampling, but the number of traps is often subjective, leading to excessive or poor sampling. This study provides quantitative guidelines for establishing the sample size for optimal completeness of dung beetle diversity by systematically reviewing the relationship between sampling intensity and sampling coverage, habitat type, and the journal impact factor in peer-reviewed research. We gathered 94 studies covering a range from México to Argentina. Sampling was conducted mainly in forested habitats, followed by treeless agriculture and agroforestry systems, with a median value of 50 pitfall traps per sampled habitat. Sampling completeness was above 0.9 in 95% of the studies. Oversampling ranged from 1 to more than 96,000 individuals, and sampling deficit varied between 2 and 3,300 specimens. Sampling intensity and the journal impact factor were significantly and positively correlated with oversampling, but these variables did not explain the sampling deficit. The positive correlation between journal impact factor and oversampling may reflect a publication bias where high-impact journals and researchers seek more generalizable information obtained with a higher sampling intensity. Dung beetle oversampling was not homogeneous between habitats, being highest in old-growth forests and lowest in disturbed habitats such as pastures and forest edges. Our results show that the collection intensity used in dung beetle studies should be reconsidered carefully. By incorporating ethical principles used in animal science, we suggest sampling guidelines for a robust sampling scheme of dung beetle diversity, which would also prevent oversampling. Consciously reducing sampling intensity will make resource use more cost-effective. We suggest increasing the number of independent sampling units rather than intensifying subsampling, thereby increasing the predictive power of statistical models to obtain more robust evidence of the phenomena under study.

KEYWORDS

sampling effectiveness, *Neotropics*, animal ethics, cost-effective sampling, precautionary principle, R′ principles

Introduction

Scarabaeinae dung beetles are among the most studied and best-known insect groups (Nichols et al., 2007; Fuzessy et al., 2021). Although globally distributed, they are most abundant in the tropics (Gill, 1991). Dung beetles provide vital ecosystem functions, including nutrient recycling, soil removal, secondary seed dispersal, and control of livestock parasites (Nichols et al., 2008). Environmental disturbances that affect mammalian communities — the primary resource suppliers for dung beetles — rapidly cause alterations in dung beetle communities (Nichols et al., 2009; Bogoni et al., 2019). Microclimatic changes in humidity, temperature, and soil conditions may also negatively affect dung beetles (Giménez Gómez et al., 2020; Pessôa et al., 2021). Besides, dung beetles are highly effective biological indicators of habitat quality, given their stable taxonomy and quick response to habitat disturbances, in addition to our deep understanding of their ecology (Favila and Halffter, 1997; Nichols et al., 2007; Tarasov and Dimitrov, 2016; Fuzessy et al., 2021).

The ease and relatively inexpensive collection of dung beetles make them an extremely popular model group in ecology (Gardner et al., 2008). Ecological and biodiversity studies with dung beetles have increased exponentially over the past 30 years (**Figure 1**). Although several methods have been proposed for the systematic collection of dung beetles, such as NTP-80 (sensu Morón and Terrón-S, 1984) and flight interception traps (Davis et al., 2001), pitfall traps baited with mammal feces or carrion are the most popular sampling method (Price and Feer, 2012). Pitfall traps consist of a plastic container buried flush with the ground, usually filled up to one-third of its capacity with an aqueous solution that prevents dung beetles from escaping while preserving the specimens fresh (Iannuzzi et al., 2020).

Several studies have evaluated the factors involved in conducting a comprehensive and statistically rigorous sampling of dung beetle communities using pitfall traps. The effective sampling area of pitfall traps in tropical habitats is well documented (Larsen and Forsyth, 2005; da Silva and Hernández, 2015). The effectiveness of different bait types (Filgueiras et al., 2009; Whipple and Hoback, 2012; Marsh et al., 2013; Bogoni et al., 2014), the effective activity time for pitfall traps according to bait type (Flechtmann et al., 2009; Price and Feer, 2012), and the efficacy of different liquid preservatives (Aristophanous, 2010) have also been evaluated. However, much remains to be understood regarding the sampling effort (e.g., the number of traps) needed to obtain a representative sample of dung beetle diversity. Some authors recommend a minimum of 30 pitfall traps per habitat type, distributed in two or three linear transects (Villarreal et al., 2004); others proposed using seven or ten pitfall traps per sampling site (Larsen and Forsyth, 2005; Krell, 2007), whereas Feer (2000) suggest that the number of traps is not as significant as the sampling time. These suggestions are based on empirical field experience. While the few systematic approaches for establishing an appropriate number of traps are very valuable (i.e., Price and Feer, 2012; Ferrer-Paris et al., 2013; Tocco et al., 2017), these derive from local and highly contextual studies, making it difficult to generalize their results.

A method to assess and compare diversity through sampling coverage instead of sampling size was proposed by Chao and Jost (2012). Coverage estimates the proportion of individuals in a community that belongs to the species observed in the sample. As completeness increases, the proportion of individuals of

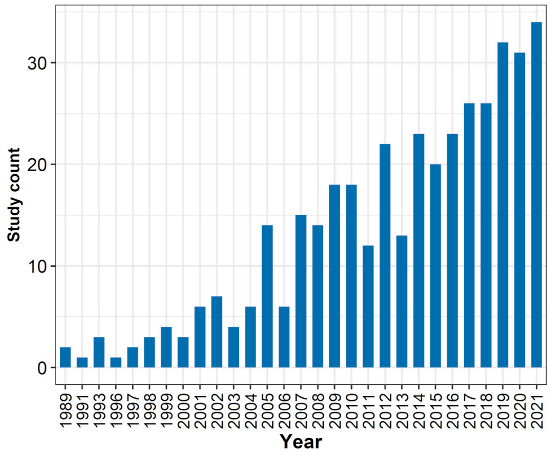

FIGURE 1
Ecological studies addressing dung beetles throughout the years. Data gathered from a search on Web of Science using the following terms: ((“Dung Beetle*” OR Scarabaeinae) AND Tropic* AND (Disturb* OR “Land-use change” OR modific* OR fragmenta* OR Ecolog*)).

undetected species in the community decreases. Comparing samples robustly without discarding information through the rarefaction process helps design sampling schemes that ensure a representative community sample (Bonar et al., 2011; Montes et al., 2021; Roswell et al., 2021). Insufficient species sampling restrains effective diversity comparisons between communities, while oversampling is less pragmatic as it wastes time and money and leads to the unnecessary population extraction of hundreds to thousands of specimens, including non-targeted ones (Tocco et al., 2017). A substantial decline in species abundance in animal communities can ultimately lead to impaired ecosystem functioning (see Gaston et al., 2018).

Recent studies have shown the accelerated decline of terrestrial insects due to habitat loss and climate change (Sánchez-Bayo and Wyckhuys, 2019; Wagner et al., 2021). These environmental pressures are arguably more intense on organisms susceptible to habitat disturbances, such as Scarabaeinae dung beetles, characterized by their relatively low reproductive and growth rates, making this group more vulnerable to extinction (Horgan and Fuentes, 2005; Larsen et al., 2005). Nevertheless, we expect an increasing demand for field data on dung beetles for future ecological studies, given their proven effectiveness as an ecological model (Brischoux and Angelier, 2015). Given the discouraging environmental scenario for insect populations and the continuous need for dung beetle field data, our main objective is to provide quantitative guidelines that establish the sample size for optimal completeness of dung beetle diversity. To this end, we have systematically reviewed and analyzed the relationship between sampling effort and the degree of coverage completeness of species richness, the journal impact factor, and the habitats surveyed in ecological studies of Neotropical dung beetles. Our guidelines aim to lead to more practical, cost-effective, sustainable, and ethical dung beetle sampling without under- or oversampling individuals and species.

Materials and methods

Literature search

To construct the database, we systematically searched published literature on the Web of Science website (WoS)[1]. The search covered articles published from 1980 to 2021. We employed the search terms ((“Dung Beetle*” OR Scarabaeinae) AND (“Disturbance gradient*” OR “Habitat disturbance*” OR “Land-use change” OR Anthro* OR Modification OR Fragmentation OR Agriculture OR Pasture*) AND (“Species richness” OR Diversity OR Abundance*) AND (Communit* OR Assemblage*) AND (“Tropical forest” OR Tropic*)).

We included only those articles that met the following criteria: (1) the study should address the ecology and diversity of Scarabaeinae; (2) the study should be conducted within the Neotropics (sensu Morrone et al., 2022); (3) the study should report the abundance of collected dung beetles; (4) abundance data should be reported separately for each species, habitat, or locality; (5) each dataset should be unique, i.e., not having been used previously in a different publication.

Data extraction

From each selected article, we extracted the number of individuals collected by species, habitat type, and number of replicate samples collected in each habitat (n); the Scopus impact factor of the journal where and when each paper was published; the species collection method; the total number of traps per habitat; the bait type; geographic information regarding the sampling sites, including the locality, municipality, and country; the climatic season when samples were collected; and the Neotropical dominion zone (sensu Morrone et al., 2022) where the study was carried out (**Supplementary Tables 1**, **2**). Dominions are part of a hierarchical system that categorizes geographic regions according to their extant biota (Morrone, 2014). We omitted biogeographic provinces — a spatially finer biogeographic division in Morrone’s scheme (2022) — because the poor representativeness of some provinces would have created a significant imbalance between categories.

Habitat recategorization

Considering the heterogeneity of habitat classifications in each paper, we decided to recategorize them into broader land-use types, pooling those habitats with similar characteristics (**Table 1**). Our new classification scheme could not include some habitat types because of their unique characteristics, low representativeness, or location in transition zones between Neotropical and Nearctic ecosystems. Such categories in our new classification scheme were altitudinal gradients ($n = 8$), landscape types ($n = 6$), Nearctic/tropical transition zones ($n = 5$), shrublands ($n = 3$), and pine forests ($n = 2$).

Data analysis

All analyses were performed using the statistical environment R v.4.1.1 (R Core Team, 2021). We determined the sampling coverage and the abundance needed to reach 99% of sampling completeness based on the number of individuals collected per species and habitat type in each study with Chao and Jost’s (2012) coverage estimator using the “iNEXT” package in R (Hsieh et al., 2016). We selected 99% completeness to

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[1] https://www.webofknowledge.com

TABLE 1 Habitat types and sampling size.

	Habitat	Definition	n
A	Old-growth forest	Tropical forests composed mainly of evergreen tree species. Complex vegetation structure and characteristically lush canopy. Little or no human disturbance. These are typically used as a control group.	53
B	Deciduous forest	Forests composed chiefly of deciduous tree species. Located in areas with a climate characterized by a marked dry season.	9
C	Cloud forest	Forests characterized by the presence of clouds at the altitude of the vegetation. The presence of clouds depends on the proximity to the ocean or altitude.	7
D	Forest fragments	Tropical forest fragments ranging from 5 ha to 300 ha.	23
E	Second-growth forest	Tropical forests under different stages of secondary succession due to anthropogenic disturbances. These forests usually lack a dense canopy compared to old-growth forests, and their understory tends to be denser.	37
F	Forest Edge	Edge of a forest or forest fragment.	12
G	Shaded agroforestry	Agricultural production systems characterized by keeping native trees for shade provision. These systems include cacao, coffee, and rubber crops.	14
H	Lowly-shaded agroforestry	Similar to shaded agroforestry systems but with a sparser use of shade. These systems include some banana varieties and silvopastoral systems.	7
I	Tree plantation	Tree monocultures plantations, such as African palm and eucalyptus.	9
J	Live fence	Treelines used as natural boundaries between landholdings, typically found in tropical agroecosystems.	4
K	Crop	Monoculture of annual plants, such as corn, beans, pumpkin, or watermelon.	11
L	Pasture	Plant communities of natural or anthropogenic origin composed mainly of native or exotic grasses. Little to no presence of trees or shrubs.	47

perform a more conservative assessment of the abundance needed to achieve a near-complete sampling of species richness in the habitats sampled in each study. We also quantified the number of individuals exceeding (oversampling) or required (sampling deficit) to achieve 99% coverage. Oversampling and sampling deficit were represented by positive and negative values, respectively.

Linear mixed models were used to evaluate the correlation of sampling intensity and the journal impact factor with dung beetle oversampling and sampling deficit. To control for potential confounding factors caused by variations in the dung beetle trapping efficiency observed with different traps (Ong et al., 2022; **Supplementary Table 2** and **Supplementary Figure 1**), we restricted the analysis to only those studies that used pitfall trapping as the primary collection method. We did not control for sampling season (SS) and bait type (BT) as linear mixed models showed no significant relationships between these independent factors and dung beetle sampling (SS: $F = 1.09$, $P = 0.34$; BT: $F = 1.82$, $P = 0.15$; **Supplementary Table 3**).

Sampling intensity was represented by the number of pitfall traps used in each habitat of each study. We adjusted the number of traps to the number of resamplings conducted at each study site ($Sampling\ intensity = No.\ of\ pitfall\ traps^{*}No.\ of$ resamplings) to obtain a less biased value of sampling intensity. We defined resampling as the number of times the researcher sampled a particular site during each study. Due to the high heterogeneity observed between response and predictor variables, the data were log-transformed to normalize the distribution of trap numbers and dung beetle oversampling. Thus, we modeled sampling deficit as log-transformed positive values. The identity of each study and the biogeographic dominion were employed as nested random variables (Biogeographic dominion/study ID) to control for the lack of independence of the predictor factor derived from the intrinsic characteristics of each study (researcher, sampling site, and design) and environmental similarities within biogeographic dominions. We eliminated dominions whose data did not significantly correlate with dung beetle oversampling to increase model fit. Model simplification was supported by significantly lower Akaike information criterion values (Δ AIC > 2; **Supplementary Tables 4A,B**; Burnham and Anderson, 2002).

Exploratory analysis models showed no significant differences in dung beetle oversampling patterns between biogeographic dominions ($F = 0.54$; $P = 0.80$, **Supplementary Table 3**). Therefore, we pooled the data to model how sampling intensity determines dung beetle oversampling in each habitat (**Table 1**) using the study identity and its biogeographic dominions as random variables. All linear mixed models were constructed with the lme4 R package (Bates et al., 2015). Model fit and the assumptions of residuals normality, variance homoscedasticity, and independence between the response variables were checked with the Performance R-package (Lüdecke et al., 2021). The predicted parameters of the linear mixed models were obtained with the "ggeffects" package in R (Lüdecke, 2018).

Results

Dataset

Our search recovered 272 published papers, from which we selected 87 after applying the exclusion criteria mentioned above. We included seven additional articles from the authors' collection not captured by the systemized search (**Supplementary Table 1**; Study ID: 17, 29, 35, 55, 70, 81, 82). The studies covered ten countries: 32 in Mexico, seven in Central America, and 55 in South America; of these, 38 were conducted in Brazil (**Figure 2** and **Supplementary Table 1**). Sixty percent of the studies were located in the Mesoamerican, Pacific and Parana dominions (30.9, 17, and 17%, respectively), followed by the Boreal Brazilian, and South Brazilian dominions (**Supplementary Table 2**). The Southeastern Amazonian and Chacoan dominions were the least represented, comprising 10% of the study sites (**Supplementary Table 2**). Most sample sites belonged to forest habitats under varying degrees of disturbance (60%; see **Table 1**), followed by treeless agriculture systems (24%) and agroforestry systems, which were the less represented habitat types (13%; **Table 1**).

Because of the high heterogeneity and extreme outliers found in abundance and pitfall numbers, the data were described with median and mean values. We found a median of 52 traps and a mean of 247 traps per sampled habitat; sampling intensity ranged from four to 12,600 traps (**Supplementary Table 2**). Regarding studies with pitfall traps, 268 sampled habitats (73%) achieved 99% sampling coverage, 67 (18%) between 98 and 95%, and 33 (9%) showed a sampling coverage below 95%. The mean and median sampling coverage values per habitat and study were 98 and 99%, respectively; the lowest recorded value was 33%. Oversampling ranged from 1 to 96,464 individuals, with a mean of 2,928 dung beetle specimens and a median of 630. Sampling deficits varied between 2 and 3,329 dung beetles, with mean and median values of 248 and 103 dung beetles, respectively (**Supplementary Table 2**).

Overall sampling intensity

Dung beetle oversampling was significantly explained by sampling intensity and the journal impact factor (**Figure 3**). The total explanatory power of the linear mixed model was 0.71 (conditional R^2), of which 0.41 was due to the fixed effects alone (marginal R^2). According to our model parameters, oversampling increased by 0.98% and 0.55% for every 1% increase in trap number and journal impact factor, respectively (**Supplementary Table 4B**).

The transformed predicted values from our model show that oversampling increased from tens to hundreds of dung beetle individuals per site, in line with the number of pitfall traps placed (**Table 2** and **Supplementary Table 4C**). For instance, ten pitfall traps led to an excess of 54 dung beetles (min 22 and max 130), 50 traps to 265 (134 min, 518 max), and 300 traps to 1,033 (534 min, 2018 max) per site. The sampling deficit of dung beetles was not significantly explained by sampling intensity and the journal impact factor, and the model explanatory power was low (conditional R^2 = 0.12, marginal R^2 = 0.02; **Supplementary Table 4D**).

Sampling intensity per habitat

Dung beetle oversampling was significantly explained by sampling intensity in most habitats (**Figure 4**), except for the lowly-shaded agroforestry systems and crops (**Supplementary Table 5A**). The models based on forest edges and cloud forests showed the best fit (marginal R^2 = 0.90 and 0.74, respectively), followed by the shaded agroforestry systems (marginal R^2 = 0.66). Tropical deciduous and old-growth forest models showed an intermediate fit (marginal R^2 = 0.32 and 0.31, respectively), whereas the lowest fit values were obtained for the second-growth forest, pasture, and forest fragment models (marginal R^2 = 0.22–0.18; **Figure 4**). Dung beetle oversampling was not homogeneous between habitats. Old-growth forests showed the highest oversampling rates, followed by forest fragments (**Table 3** and **Supplementary Table 5B**). In comparison, oversampling rates were low in more disturbed habitats, such as shaded agroforestry systems, second-growth forests, pastures, and forest edges (**Table 3** and **Supplementary Table 5B**). Oversampling rates of cloud forests and tropical deciduous forests were intermediate between those of forest fragments and shaded agroforestry systems (**Table 3** and **Supplementary Table 5B**).

Discussion

Researchers are interested in practical, cost-effective, but statistically rigorous sampling methods when constructing biodiversity inventories. Robust sampling is especially critical when biodiversity monitoring is used for making management decisions such as terminating an allegedly harmful mining project or assessing the impact of a hydropower plant (Hayward et al., 2015; Kühl et al., 2020). Therefore, data accuracy and precision are essential. However, biological diversity cannot be accurately measured because the observed number of species is always a downward-biased estimator of the true species richness (Gotelli and Colwell, 2011). An appropriate sampling effort can help reduce such measurement errors and facilitate achieving asymptotic estimates of diversity (Bonar et al., 2011). Our data showed that 95% of the reviewed studies were effective at measuring dung beetle diversity (SC > 90%). The remaining studies obtained a sampling coverage between 88 and 33%.

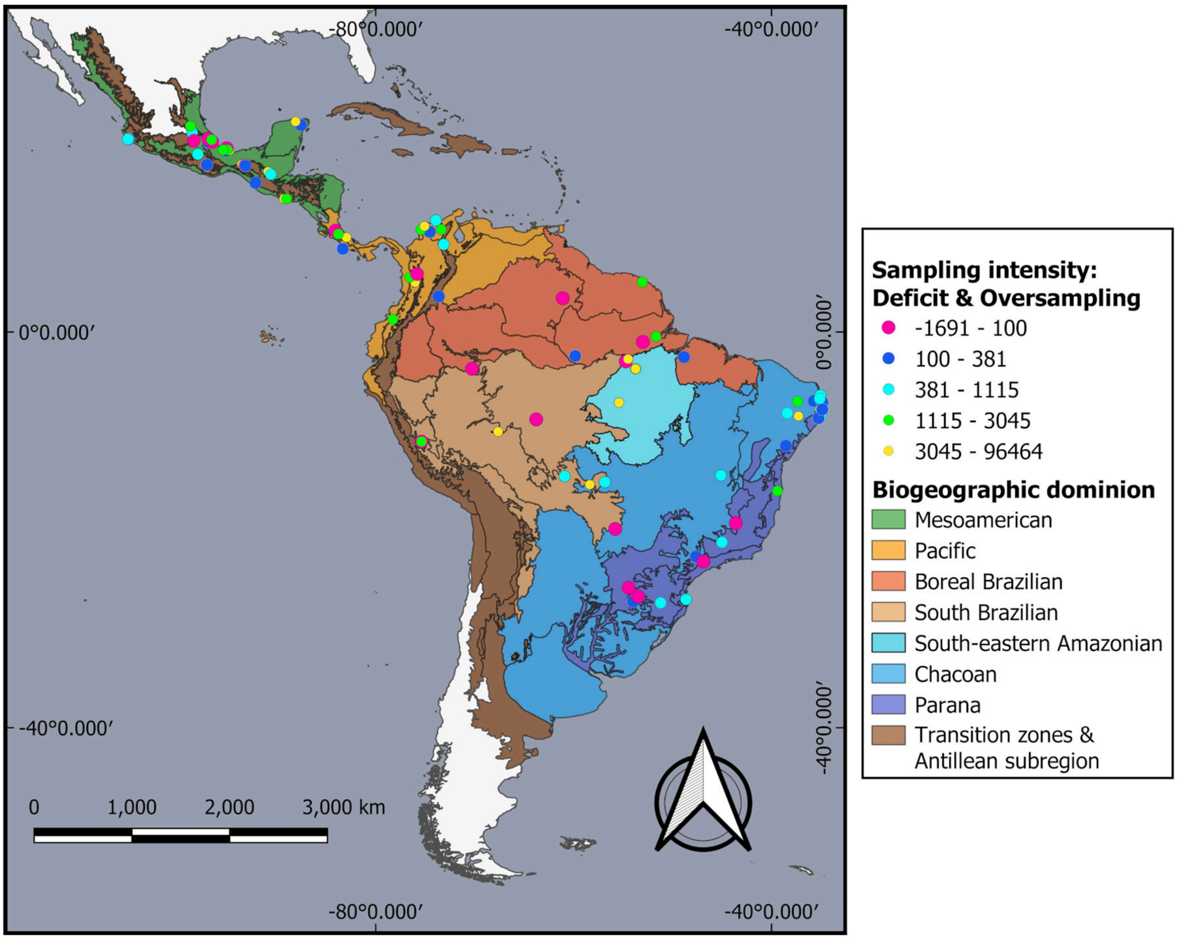

FIGURE 2
Geographic distribution of the sites studied. Sampling intensity is reported for each study site. The sampling deficit shows those sites where the sample did not reach 99% completeness, with negative values representing the effective abundance deficit per sampling site. Oversampling shows those sites where the sample exceeded 99% completeness, indicating the excess abundance per sampling site. Vector image from Morrone et al. (2022).

TABLE 2 Predicted dung beetle oversampling values (Predicted OS) on their original scale (i.e., natural log exponential) as a function of sampling intensity (SI, number of traps).

	SI	Predicted OS	95% LCI	95% UCI
1	5	27	10	75
2	10	54	22	130
3	15	73	36	183
4	20	108	50	233
5	30	159	77	327
6	40	213	107	424
7	50	265	134	518
8	100	523	276	1,002
9	200	781	403	1,495
10	300	1,033	534	2,018
11	400	2,039	982	4,273
12	500	2,540	1,188	5,432

The predicted values are adjusted to the mean impact factor of all studies (S-IF: 1.68). The lower and upper limits of 95% confidence intervals are shown (95% LCI and 95% UCI, respectively). The original non-transformed values are detailed in Supplementary Table 4C.

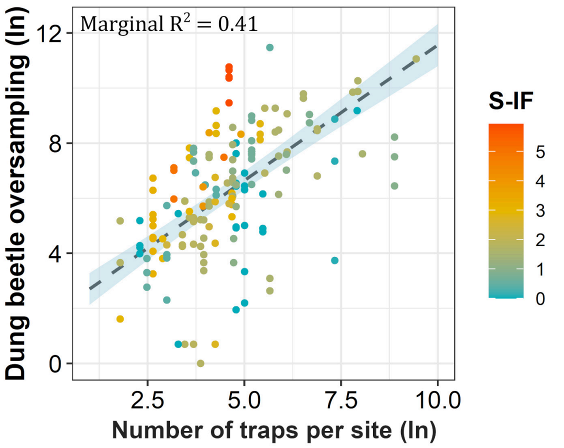

FIGURE 3
Correlation between log transformed (ln) number of traps per sampling site and dung beetle oversampling. Bar colors indicate the Scopus impact factor (S-IF) of the journal where the study was published. The complete model results are shown in **Supplementary Table 4B**. Model fit and assumptions are shown in **Supplementary Figure 2**.

Therefore, the likelihood of undersampling dung beetle diversity through pitfall traps is low.

Sampling intensity correlated significantly and positively with dung beetle oversampling. Although the relationship between sampling intensity and completeness is similar to that of the species-area (Hill et al., 1994), very few traps were needed to obtain (or exceed) the abundance required to achieve 99% species coverage. Sampling coverage above 90% using five pitfall traps was achieved in most cases, and studies with 20 or more pitfall traps per habitat reached 99.99% sampling coverage. Such a sampling scheme could lead to a less cost-effective use of research funds since there is a high possibility that additional sampling will only add dominant specimens rather than increase species richness (see Chao et al., 2014). The surprisingly low number of pitfall traps needed to obtain a representative sample of dung beetle diversity can be explained by the extremely high effectiveness of these baited traps in attracting and capturing dung beetles (Ong et al., 2022). For instance, studies involving several collecting methods and different Coleoptera families have consistently shown significantly higher capture rates and abundances for Scarabaeinae dung beetles (e.g., Caballero and León-Cortés, 2012; Ramírez-Ponce et al., 2019; Quinto et al., 2021).

Oversampling rates were also significantly and positively correlated with the impact factor of peer-reviewed journals. High-impact factor journals aim for generalizable ecological evidence that can be extrapolated and replicated to other locations (Barto and Rillig, 2012). Such data may require a high sampling intensity across extensive areas or over several years (Hughes et al., 2017), ultimately leading to oversampling, as shown by our models. The correlation between the journal impact factor and dung beetle oversampling may also be an indirect outcome of studies intended for publication in high-impact factor journals, which likely influences the overall research design and sampling intensity. The sampling deficit of dung beetle diversity was not explained by sampling intensity or the journal impact factor. Deforestation and land-use change possibly explain the poor explanatory power of the sampling deficit since these anthropogenic disturbances cause a significant decline in dung beetle diversity and abundance (Nichols et al., 2007; Fuzessy et al., 2021). As fewer dung beetles are present in a given habitat due to anthropogenic disturbances, the capture rate of pitfall traps will be reduced, hence increasing the likelihood of undersampling. Our results also suggest that no minimum effective number of traps could lead to incomplete sampling of dung beetle diversity. That is, as long as no environmental factor significantly affects dung beetle abundance and diversity, pitfall traps will likely capture a sample of reasonably good completeness (i.e., SC $\geq$ 90%).

Oversampling was lower in agroforestry systems and pastures than in forested habitats, including forest fragments and second-growth forests. The population dynamics of dung beetle assemblages differ significantly between forest inner areas and pastures (Horgan, 2008; Silva et al., 2017). Pasture habitats are typically diversity-poor because of their more extreme microclimatic conditions, which act as a natural barrier preventing the entry and establishment of the most susceptible species (Giménez Gómez et al., 2020; Rivera et al., 2022). Dung beetle populations may also be smaller in pasture systems than in forests due to more hostile environmental conditions that prevail in these systems, as suggested by differences in capture between the two habitats (e.g., Quintero and Roslin, 2005; Braga et al., 2013; Rivera et al., 2020; Salomão et al., 2020). Therefore, the asymptote of species richness is reached more rapidly in pastures than in forested habitats, while the supposedly small populations of pastures can also favor low oversampling rates.

Forest habitats, particularly old-growth forests, had high oversampling rates even with a relatively low sampling intensity. Old-growth forests possess more niches and resources for Neotropical dung beetle species, as most species in this region evolve within forested habitats (Halffter and Matthews, 1966; Gill, 1991). Also, dung beetle populations may grow faster under undisturbed conditions (Beiroz et al., 2017; Fuzessy et al., 2021), making it easier to obtain a large sample size with less effort. On the other hand, forest edges require more intensive sampling to exceed the abundance needed to achieve 99% completeness. This finding suggests that the sampling effort in this habitat type may need to be high. Forest edges are likely low-quality habitats for many dung beetle species, especially if the contrast between contiguous habitats is high (Spector and Ayzama, 2003; Martello et al., 2016; Villada-Bedoya et al., 2016; Martínez-Falcón et al., 2018). Besides, forest edges may be subject to continuous changes due to traditional land-use

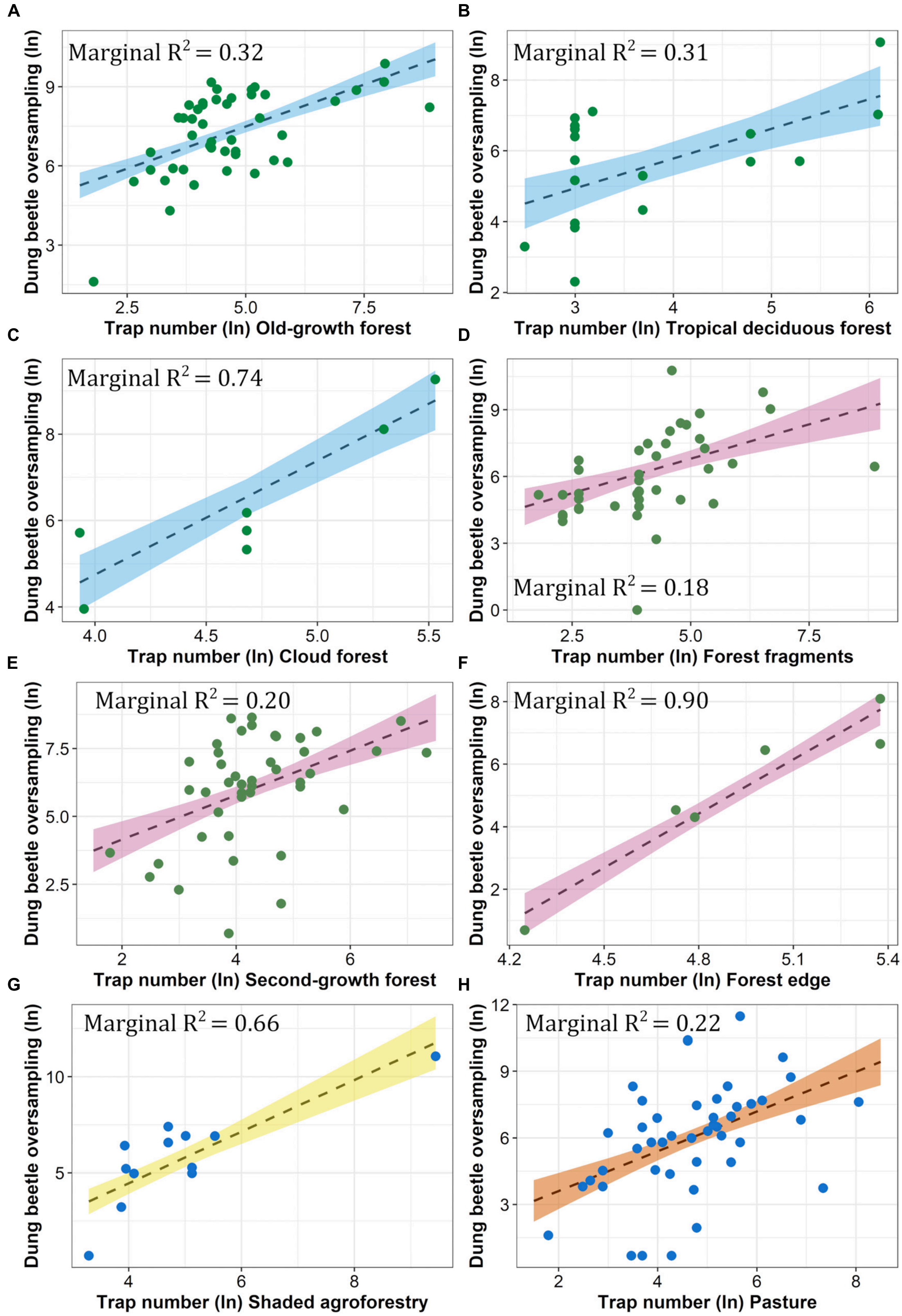

FIGURE 4
Correlation between the log-transformed (ln) number of traps and dung beetle oversampling across habitat categories. **(A)** Old-growth forest, **(B)** tropical deciduous forest, **(C)** cloud forest, **(D)** forest fragments, **(E)** second-growth forest, **(F)** forest edge, **(G)** shaded agroforestry, and **(H)** pasture. The complete model results are shown in **Supplementary Table 5A**. Model fit and assumptions are shown in **Supplementary Figure 3**.

TABLE 3 Predicted dung beetle oversampling values (predicted OS) on their original scale (i.e., natural log exponential) as a function of sampling intensity (SI, number of traps) in different habitat types.

A. Old-growth forest

SI	Predicted OS	95% LCI	95% UCI
5	206	81	523
10	321	150	692
15	503	270	925
20	508	265	973
30	781	478	1274
40	898	567	1422
50	1394	925	2122
100	1808	1176	2779

B. Tropical deciduous forest

SI	Predicted OS	95% LCI	95% UCI
5	44	7	290
10	78	18	347
15	110	31	395
20	140	45	437
30	196	73	528
40	250	100	626
50	302	125	728
100	545	209	1408

C. Cloud forest

SI	Predicted OS	95% LCI	95% UCI
20	8	1	79
30	24	4	144
40	51	11	226
50	91	26	324
100	578	252	1313

D. Forest fragments

SI	Predicted OS	95% LCI	95% UCI
5	111	23	528
10	169	47	608
15	219	72	672
20	262	95	721
30	334	138	812
40	399	178	898
50	459	215	982
100	706	351	1437

E. Second-growth forest

SI	Predicted OS	95% LCI	95% UCI
5	46	10	206
10	81	25	265
15	113	41	311
20	144	59	351
30	200	94	424
40	252	129	498
50	302	162	567
100	534	293	982

F. Forest edges

SI	Predicted OS	95% LCI	95% UCI
70	3	1	12
80	7	2	22
90	15	6	38
100	28	12	63

G. Shaded agroforestry

SI	Predicted OS	95% LCI	95% UCI
10	9	2	48
15	15	3	70
20	23	6	92
30	38	11	136
40	57	18	181
50	77	26	230
100	196	74	523

H. Pasture

SI	Predicted OS	95% LCI	95% UCI
5	26	4	154
10	48	11	206
15	69	19	250
20	90	29	284
30	129	48	347
40	167	69	407
50	34	89	464
100	380	189	765

The lower and upper limits of 95% confidence intervals are shown (95% LCI and 95% UCI, respectively). The original non-transformed values are detailed in **Supplementary Table 5B**.

dynamics such as crop rotation and abandonment, preventing beetle populations from reaching a more stable state (Barnes et al., 2014).

Should oversampling dung beetles matter?

The hypothesis that extracting individuals from their natural environment may adversely impact populations has been little studied in vertebrates (McCay and Komoroski, 2004; Sullivan and Sullivan, 2013; Poe and Armijo, 2014; Hope et al., 2018), but much less in invertebrates (Gezon et al., 2015). Nevertheless, the consensus is that the impact of scientific collections on animal populations is minimal (Rocha et al., 2014, but see Delibes et al., 2011; Minteer et al., 2014). Gezon et al. (2015) argued that removing invertebrates during scientific sampling may liberate ecological niches and reduce competition, leading to population growth. However, new niches can be colonized by new individuals or species as long as populations are not fragmented or spatially isolated (Thomas, 2000; Ricketts, 2001), which today is increasingly challenging because forest remnants are becoming more isolated from each other due to deforestation (Laurance et al., 2012). In addition, according to Gezon et al. (2015), lethal sampling probably exerts no effect if the individuals sampled have already reproduced. According to our systematic research, most studies collect dung beetles during the rainy season (49% rainy, 39% dry and rainy; see **Supplementary Table 2**) — the period of their highest activity rate (Correa et al., 2021) —, enabling efficient sampling of these insects. However, most Neotropical dung beetle species emerge, feed, and reproduce during the rainy season (Halffter and Edmonds, 1982), so it is challenging to assume that all the collected individuals have already reproduced. Finally, Gezon et al. (2015) focused on bee taxa, which includes multiple families, and collected 14,000 bees over five years of intensive sampling. Our database shows that with sufficient sampling effort, it is possible to collect and exceed 14,000 individuals of tropical Scarabaeinae in less than three months (**Supplementary Table 2**). Therefore, although Gezon's criteria are valuable, a more careful approach is needed for dung beetles because these criteria are not entirely applicable to them.

It is worth mentioning that we are not against using or collecting dung beetles in research since scientific collections represent a valuable register of biodiversity, whose importance for conservation has been reviewed in depth by several authors (Patterson, 2002; Suarez and Tsutsui, 2004; Rocha et al., 2014). Instead, we advocate a thorough discussion of the collection methods used for dung beetles, recalling the five Rs and Precautionary Principles. The R principles, proposed by Russel and Burch (1959), suggest that scientific research with animals should be guided by refinement, reduction, and replacement. We acknowledge the difficulty in refining or replacing lethal collection practices because identifying live dung beetles is highly challenging. Many species are sympatric and morphologically indistinguishable (Larsen and Forsyth, 2005), thus requiring specimen collection for correct identification. However, we can apply the reduction principle effectively because, as demonstrated in the present study, few pitfall traps are needed to obtain a representative and robust sample of dung beetle diversity. Two additional R principles — respect and responsibility — were proposed by Crespi-Abril and Rubilar (2021). These ethical-based epistemological practices highlight the importance of researchers respecting and showing empathy for life, recognizing its value regardless of its complexity, and taking responsibility for their actions, as animals are no longer a means but also an end for conservation.

Although growing evidence shows the decline of tropical insect populations in the Anthropocene (Lister and Garcia, 2018; Wagner, 2020), there is still no proof that oversampling affects dung beetle populations. However, "the absence of evidence is not evidence of absence" (Crespi-Abril and Rubilar, 2021). In this sense, we can also apply the precautionary principle, which aims to prevent or reduce damage even if the evidence is insufficient to determine the magnitude or probability of occurrence (Kriebel et al., 2001). Ethical sampling that consciously reduces the number of pitfall traps in each independent sampling unit following the Rs and Precautionary principles will improve the cost-efficiency of resource use in research while preventing specimen oversampling. Researchers can focus instead on increasing the number of independent sampling units using a smaller number of traps, thereby increasing the predictive power of statistical models and obtaining more robust evidence of the phenomenon under study (see Gotelli and Elllison, 2004).

Recommendations

Our models showed that a representative sampling of dung beetle diversity (i.e., SC >90%) could be achieved with no more than ten pitfall traps. Therefore, we recommend placing up to six pitfall traps per independent sampling unit when using only a single bait type (dung or carrion) and up to eight pitfall traps when using both bait types. We do not consider traps baited with fruit as the beetle capture rate is significantly low. If the research addresses forest habitats solely, the number of pitfall traps may be smaller, e.g., three to five traps per sampling unit (see Price and Feer, 2012). These recommendations can also apply to landscape-scale studies (see Arroyo-Rodríguez and Fahrig, 2014). For example, if a landscape-site design is used, six to ten traps can be distributed around the centroid of the landscape. In landscape-scale designs, pitfall traps can be distributed in five or six groups of three to four pitfall traps each. The number of pitfall traps in each independent sampling unit can be further reduced for longitudinal studies in which the same site is sampled several times. A presampling protocol may be the best way to assess the optimum number of traps per site, considering our suggestions as a starting point. In conclusion, a sampling scheme guided by ethical guidelines will make the research more economical, time-effective, statistically robust, and friendlier to dung beetle biodiversity.

Data availability statement

The original contributions presented in the study are included in the article/**Supplementary material**, further inquiries can be directed to the corresponding author/s.

Author contributions

JR and MF contributed to the conception and design of the study, and organized the database. JR performed the statistical analysis and wrote the first draft of the manuscript. Both authors contributed to manuscript revision, read, and approved the submitted version.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2022.999488/full#supplementary-material

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Ecological indication metrics on dung beetles metacommunities in native forests and *Pinus* monocultures

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Beetles of the subfamily Scarabaeinae are commonly used as ecological indicators in studies about the effects of environmental changes. We analyzed the influence of the type of habitat, vegetation, mammals (as food resource), and temperature on dung beetle metacommunities in subtropical native forests and *Pinus* monocultures to evaluate the factors driving these assemblages. In the summer of 2018/2019, we sampled 12 areas in Southern Brazil, six *Pinus* monocultures and six native forests. We performed a dispersal test, applying a marking-recapture method. Some recaptures occurred in different habitats, showing low dispersal between habitats. We recorded behavioral activities confirming the use of both native forest and *Pinus* areas. The metrics did not reflect the difference in the environmental quality of the areas regarding species richness and diversity in different habitats. This shows that these metrics are not the best when using dung beetle assemblages as ecological indicators of biodiversity loss resulting from land-use changes, requiring complementing the analysis with composition analysis methods. When we partitioned beta diversity between habitats, we observed a dissimilarity between *Pinus* monocultures and native forest assemblages due to species substitution, with many species contributing to the dissimilarity between habitats. In our structural equation models, the influence of environmental factors on metacommunities showed no predictor related to dung beetle richness, but several variables influenced their abundance.

KEYWORDS

alpha and beta diversity, biodiversity conservation, bioindicators, dispersion, ecology

Introduction

Beetles of the subfamily Scarabaeinae, commonly called dung beetles, have been used in several studies as ecological indicators of habitat disturbance since their first proposal by Halffter and Favila 1993 (Davis and Sutton 1998; Davis et al. 2001; Gardner et al. 2008; Audino et al. 2014; Sarmiento-Garcés and Hernández 2021). The advantages of using this taxon are many since they are abundant in a wide range of terrestrial ecosystems (Mcgeoch et al., 2002; Davis et al., 2004; Hernández et al., 2014), are easy to sample, have a quick response to environmental disturbance (Gardner et al., 2008), and, especially, because of their species specificity to different habitats (Hanski and Cambefort, 1991; Scholtz et al., 2009). They can also be used to explore species-functioning relationships (Sarmiento-Garcés and Hernández, 2021), as they provide ecosystem functions by actively participating in nutrient cycling, promoting soil aeration, and removal of decaying organic matter (Halffter and Matthews, 1966; Nichols et al., 2008).

We can interpret habitat fidelity of dung beetles as an evolutionary response to the high interspecific competition for resources, which are often limited and ephemeral (Hanski and Cambefort, 1991). These beetles use dung or other organic debris, such as carcasses and some decaying fruits, as food resources. High competition greatly influences their assemblage structure (Simmons and Ridsdill-Smith, 2011). Furthermore, there is also a correlation between dung beetles' richness and mammals abundance and richness because of the amount and diversity of available resources (Halffter and Matthews, 1966; Estrada et al., 1999; Davis et al., 2002; Andresen and Laurance, 2007; Nichols et al., 2009; Barlow et al., 2010; Bogoni et al., 2016). Dung beetles have developed foraging techniques by using their olfactory cues to rapidly locate and choose resources, depending on each resource's type, distance, and nutritional quality (Hanski and Cambefort, 1991). Nevertheless, most species of this group are generalist in feeding strategies (Larsen et al., 2008; Frank et al., 2018; Giménez Gómez et al., 2018).

In local assemblages, the high diversity of dung beetles is related to niche differentiation due to evolutionary pressures of interspecific competition, which led to behavior variation according to resource allocation, time of activity, body size, and other intraspecific differences such as sex and age (Hanski and Cambefort, 1991). The adaptive evolution inside the group allows the occupation and preference of many species for a specific type of habitat, with some exclusive to forest areas and others typical of open areas, like savannas and meadows (Hanski and Cambefort, 1991). These features of habitat partition allow dung beetles to occupy many types of environments, having a high degree of fidelity for a biotope or phytophysiognomy (Klein, 1989; Driscoll and Weir, 2005). Some studies show that some forest specialist species do not leave their habitat even with the supply of food resources in open areas nearby (Klein, 1989; Larsen et al., 2008).

The high competition and ephemeral nature of food resources suggest that dung beetles are probably good dispersers (Roslin and Viljanen, 2011). However, according to some studies, Scarabaeinae species with different sets of ecological traits differ in mean movement rate (Howden and Nealis, 1975; Peck and Forsyth, 1982), with only a few species traveling longer distances in the same habitat (Arellano et al., 2008; Da Silva and Hernández, 2015). This dispersion ability in searching for resources through poorly suited habitats and the tolerance to remain in sub-optimal environments can be an important factor in their species reproduction. Some species from open areas may even have a higher tolerance to microclimatic changes, being able to enter and inhabit degraded forests and vice versa, changing the assemblage composition of these areas. As a result, forested areas adjacent to open habitats can present a high turnover of species composition, where open habitat specialists increase the alpha diversity of these disturbed places (Arellano and Halffter, 2003; Gardner et al., 2008). Although remnants of native forests allow forest-associated dung beetles and other animals to survive in patchy landscapes (Halffter and Arellano, 2002; Arellano and Halffter, 2003; Andresen, 2005; Campos and Hernández, 2015), habitat modification is often related to species loss, especially the ones with larger body size (Gardner et al., 2008; Batilani-Filho and Hernández, 2017; Sarmiento-Garcés and Hernández, 2021).

When using dung beetles as ecological indicators, we hope to obtain reliable measurements and interpretations regarding changes in environmental conditions by their presence and abundances in a particular area (Nichols and Gardner, 2011). For that, richness and diversity indexes are often used as measures to assess assemblage changes, considering different species as equal in their contribution to ecosystem functioning (Barragán et al., 2011). However, when we try to understand how dung beetle assemblages vary between habitats (such as natural and anthropogenic), including species compositon, it is possible to better understand how human actions can transform its dynamics, structure, and behavior.

We also point here to the importance of considering the spatial scale when using dung beetles as ecological indicators since they can disperse between different areas. In this study, we try to look beyond the diversity of each location, seeking a better understanding of the dynamics of these assemblages and the metacommunities formed between them. In metacommunity ecology, the local scale and a combination of local and regional processes matter to understand patterns of species abundance, occurrence, composition, and diversity in different scales of space and time (Chase et al., 2020). The formation of dung beetle metacommunities is strongly marked by the habitat (model known as species sorting). Still, it can also follow the mass effect model, where the rescue of species from competitive exclusion is marked by dispersal of individuals between areas with different environmental qualities (Leibold et al., 2004). In this case, individuals depart from sites considered to be of better quality to areas of worse resource quality, resulting in some environments working as sources and others as sinks. The mass effect can be more significant in species with high dispersal capacity or smaller spatial extensions due to habitat proximity, regardless of environmental quality (Heino et al., 2015).

Many studies indicate the exotic trees from the genus *Pinus* as invaders and their potential to inhibit the growth of other plant species, negatively affecting local and regional biodiversity (Rejmánek and Richardson, 1996; Brewer, 1998; Ledgard, 2001; Buckley et al., 2005; Richardson, 2006; Essl et al., 2011; Gundale et al., 2014). Studies regarding the composition and dynamics of dung beetle assemblages in *Pinus* monocultures shows that some species can inhabit mature *Pine* plantation areas (Peyras et al., 2013; Pryke et al., 2013). Furthermore, when forestry plantations are connected to natural forest, a negative effect may not be registered (López-Bedoya et al., 2021). It is possible that certain aspects of the environmental characteristics of *Pinus* monocultures, such as temperature and canopy cover, may not show such discrepant microclimatic changes when compared to native forest areas, as occurs in open fields. There are studies that showed high diversity and abundance of dung beetles in land-uses that preserve tree canopy (Bustamante-Sánchez et al., 2004; Braga et al., 2012; Gómez-Cifuentes et al., 2017; Giménez Gómez et al., 2018). Therefore, in cases where habitats modified for forestry use present similar microclimatic conditions to native habitats, it would be important to understand under which conditions dung beetles can be used as ecological indicators.

This paper hypothesizes that the local assemblages of dung beetles in *Pinus* monocultures and the native forest remnants are connected by dispersion constituting metacommunities. The factors that allow dung beetles to inhabit both *Pinus* monocultures and native forest areas would be the presence of food resources, as a product of the transit of mammals and attendance of domestic animals, and similar microclimatic conditions suitable for their occurrence. Therefore, we aim to understand if the structuring of local dung beetle assemblages in *Pinus* monocultures resembles the nearby native forest dung beetle assemblages. We first verified the species' dispersal and fidelity to the different habitats. Then we looked for the factors that may drive them, relating dung beetle assemblages to factors known to influence their ecology, such as food resources availability, microclimate conditions, and vegetation structure variables (Halffter and Arellano, 2002).

Materials and methods

Study area

We developed this study in the microregion of Tabuleiro in the State of Santa Catarina, southern Brazil, which includes the counties of Anitápolis, Rancho Queimado, Alfredo Wagner, Águas Mornas, and São Bonifácio (27°54′25.25″ S, 49°10′48.3″ W). This region has rugged topography, with elevation ranging between 440 and 1,000 m a.s.l., and native vegetation mainly composed of a dense ombrophilous forest. The landscape is a heterogeneous mosaic of forest patches that vary in size, density, and connectivity, immersed in a matrix of forestry, pastures, and small crop fields. The climate is Cfa according to the Köppen-Geiger classification, with rainfall well distributed in average annual rainfall of 1,700 mm.

We selected six sample sites that presented two landscape components in this region, *Pinus* monocultures and a native forest area (Figure 1). Thus, sampling was performed in six areas with *Pinus* monocultures (P1, P2, P3, P4, P5, P6) paired with six native forest areas (F1, F2, F3, F4, F5, F6), totaling 12 sampling areas. We selected the sites based on their accessibility and degree of isolation of the *Pinus* monocultures in relation to the forest fragments. Thereby, three of the *Pinus* monocultures areas (P1, P2, and P3) were connected to the native forest and the other three monocultures (P4, P5, P6) were at least 60 meters away from the native forest areas. There were open fields with small bushes between the three areas apart. All six areas were at least 1 km apart from each other. We conducted the fieldwork during November–December of 2018 and January–February 2019.

Habitat use and dung beetle dispersal: Sampling and analysis

We placed 10 attraction traps in each area to test if dung beetles build nests for reproduction in both habitats and the dispersion between different habitats (*Pinus* monocultures and native forest). Those traps, named "nesting houses," consist of PVC pipes buried vertically on the ground, with an opening on top for free access of the dung beetles. The traps were filled with soil and dog feces as a food resource. The nesting houses were placed 10 meters from each other at 10 meters from the edge of the habitat (Supplementary Figure S1). We applied the following marking and release protocol after 48 h of exposure: first, we cleaned and identified the collected Scarabaeinae, then marked them with scarification on the pronotum using a dental drill added to a small battery, subsequently releasing them near the trap in the same areas where they were captured. The species were identified by comparison using a reference collection of regional species from the Entomological Collection Mítia Heusi-Silveira of the Universidade Federal de Santa Catarina (Hernández et al., 2019). The scarification marking technique used is considered noninvasive and does not risk being lost by the insect as some paints (Wuerges and Hernández, 2020). The mark had the shape of a line and allowed us to identify the habitat where the beetle was first found, *Pinus* monocultures on the left side of the pronotum, and native forest on the right. We marked only species with body lengths of 4 mm or higher. We replicated the marking-release protocol once after a month from the first sampling. After 3 weeks from that second sampling, we conducted one last attempt to recapture marked individuals.

With the nesting house data, we first confirmed the use of the different habitats (*Pinus* monocultures and native forest) by the dung beetle species found there. Afterward, we calculated recapture rates for each species with one or more recaptured individuals. We then analyzed the recaptures that occurred outside the original marking habitats to observe the dispersion of the dung beetles between the different habitats (*Pinus* monocultures and native forests).

Dung beetle metacommunities: Sampling and analysis

Parallel to the first experiment of the nesting houses, we installed 10 pitfall traps in the same 12 areas to capture dung

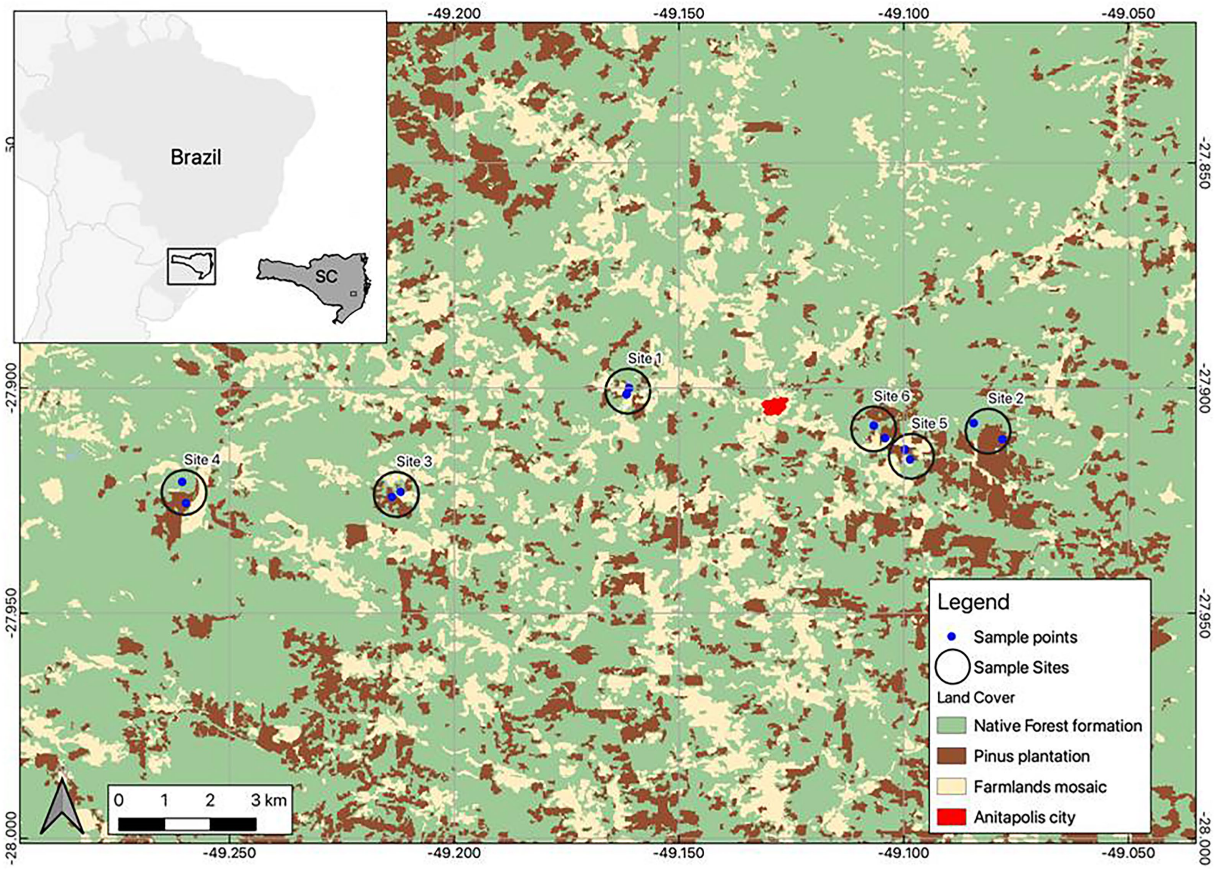

FIGURE 1
General view of the landscape and the six sample sites, each with two areas of different habitat (one of *Pinus* monocultures and one of native forest), in Santa Catarina, southern Brazil.

beetles (Supplementary Figure S1). We placed those pitfall traps 40 meters away from the nesting houses, remaining 50 meters from the edge of sampled areas. The sampling design consisted of 10 pitfall traps distributed in pairs into two parallel transects, one pair trap spaced 100 meters apart from the other to avoid pseudoreplication. Paired traps were spaced 10 m apart and had different types of bait, one with human feces (20 g) and the other with two-day rotten meat (20 g), for the attraction of both coprophagous and necrophagous species, respectively. The pitfall traps consisted of plastic containers (15 cm diameter × 20 cm depth), buried with the top edge leveled to the ground, allowing insects to fall in. All traps contained water (300 ml) and neutral detergent, with a plastic lid supported by wooden sticks placed approximately 10 cm above their opening for rain protection. The lid prevented overflow and supported the bait. We replicated sampling three times, once a month, during 3 months (December 2018 and January–February 2019) on all 12 areas. All traps remained in the field for 48 h, after which we took the collected material to the Laboratório de Ecologia Terrestre Animal (LECOTA/UFSC). There, we mounted dung beetle individuals on entomological pins, dried in an oven (40°C for 48 h), identified, and included them in the Coleção Entomológica Mítia Heusi-Silveira from the Centro de Ciências Biológicas of the Universidade Federal de Santa Catarina. The expert Dr. Fernando Vaz-de-Mello, from the Universidade Federal de Mato Grosso, Brazil, confirmed the identifications.

We classified species into generalists and specialists of the two habitats using a multinomial classification model based on an iterative program (CLAM). The program estimated the species' relative abundance in the two types of habitats (*Pinus* monocultures and native forest), allowing a robust statistical classification of habitat specialists and generalists without excluding rare species (Chazdon et al., 2011). We used the R package "vegan" for this analysis (Oksanen et al., 2020).

We used rarefaction and extrapolation curves with the effective number of species to compare and estimate species richness, diversity, and sample sufficiency between different habitats of each site. This method is based on Hill numbers and sets up intervals of confidence around species richness ($q = 0$), Shannon entropy ($q = 1$), and Simpson dominance ($q = 2$; Chao et al., 2014; Hsieh et al., 2016). The baseline sample size was the highest or double of the smallest sample size, the interval of confidence was 95%, and the analysis was performed using the R package "iNEXT."

To verify differences in composition among assemblages of native forest and *Pinus* monocultures, we used the Bray-Curtis index of dissimilarity, partitioned into two components: balanced variation in abundance and abundance gradients. The balanced variation in abundance is related to individuals of some species in one site substituted by the same number of individuals of different species in another site. The second component of the partition concerns the loss of individuals from one site to another (Baselga, 2013). We used the R package "betapart" for this analysis. Subsequently, we compared the dissimilarities between the sites with adjacent habitats and the ones with habitats apart using a *t*-test to see if there were major differences among the areas.

Finally, we partitioned total beta diversity into species contributions to beta diversity (SCBD), which is the degree of variation of individual species across the study area, to test the relative importance of each species affecting beta-diversity patterns per site. The analysis was based on abundance data (Legendre and De Cáceres, 2013). All analyses were performed in the R 3.6.3 program (R Core Team, 2020).

Environmental influence on the metacommunities

We used camera traps to record mammalian presence inside the areas for dung beetle resource availability. We placed one camera trap in the central point of each area during dung beetle sampling and checked the batteries every 20 days. The cameras were active for a minimum of 30 days and a maximum of 60 days. We only considered the records made during 1 month for all locations. After that period, we identified the mammals from the photographs. The mammalogist Dr. Mauricio E. Graipel from the Universidade Federal de Santa Catarina, Brazil, confirmed the species identification. After the mammals identification, we calculated an approximation on the abundance of mammals as a way of checking the resources available in each area. For that, we considered only records of mammals from the same species that had at least one-hour difference each and the number of individuals of the same species in each record when in groups.

We measured environmental variables on each area related to vegetation using an adapted point-centered quarter method (Cottam and Curtis, 1956). We placed a plastic pipe cross in the center of every two sampling points in each study area, dividing them into four quadrants: northwest, southwest, southeast, and northeast. Then, we measured the distance from the nearest tree, from the nearest shrub, and their height for each quadrant. Additionally, we visually estimated the percentage of vegetation cover and bare ground in 1m^2 plots in each quadrant. We considered the shrubs with a minimum height of 1 m and, for trees, the height over 1 m and the diameter at breast height over five centimeters. We measured the circumferences and distances with a tape measure.

Temperatures (in °C) were measured throughout the experiment using an environmental thermometer (datalogger) installed in the central point of each sampling site, buried in the ground. Geographical coordinate data (UTM) of each site and the sampled points were obtained using a manual GPS. We used the Google Earth Path software to measure the altitude and size of the sites and the distance between the isolated sites of *Pinus* monocultures and native forest.

We used structural equation models (SEM) to evaluate the relationships of environmental factors on dung beetle assemblages (Grace, 2006; Shipley, 2016). Thus, we built a conceptual model employing dung beetle richness and abundance as response variables. For the explanatory variables, we had temperature, vegetation structure (trees for tall vegetation structure, shrubs for middle vegetation structure, and herb cover for the ground level), and the number of times mammals were recorded (as a form to measure the amount of food resources available to dung beetles). This model could determine which explanatory variables would influence other variables, with hierarchical submodels influencing the final result. The regressions between variables were performed using Piecewise SEM in the R 3.6.3 program (R Core Team, 2020). All variables with a probability below 0.05 were included in a structural frame, where we estimated the coefficient for each equation in the model. Then, we highlighted the positive and negative relationships using arrows, with sizes according to the coefficient value of each variable relationship.

Results

Habitat use and dung beetle dispersal

We marked and released 883 live individuals belonging to 19 species, all captured in the nesting houses (Supplementary Table S1). We recorded feeding balls from telecoprids and tunnels with paracoprids inside the traps, indicating that dung beetles use both native forests and *Pinus* monocultures to feed and bury resources for nesting. The species with the highest number of marked and released individuals were *Dichotomius sericeus* (Harold, 1867) (236), *Canthon rutilans cyanescens* Harold, 1868 (133), *Coprophanaeus saphirinus* (Stürm, 1828) (122), and *Dichotomius assifer* (Eschscholtz, 1822) (102). During 20 to 76 days, we recaptured 18 individuals from three species only: *Canthon rutilans cyanescens*, *Dichotomius sericeus,* and *Dichotomius assifer*, with an overall recapture rate of 3.82 (Table 1).

Of those individuals, 15 were recaptured in the same marking areas, 12 in *Pinus* monocultures and three inside native forests. Three individuals from two species were found in different areas from where they were marked, showing their ability to move between habitats, marked on *Pinus* monocultures and found in native forests (Table 1). One hundred and thirty-three individuals of the species *Canthon rutilans cyanescens* were marked five were recaptured. Among these, three were recaptured in the same marking area (*Pinus* monocultures P1) and one was found in a different habitat, being marked in the *Pinus* monocultures area and recaptured 2 months later 180 meters into native forest area

TABLE 1 Number of marked (Mk) and recaptured (Rc) individuals and total recapture rate (% Rc) per species.

Species	Mk	Rc	% Rc	Sm	Rc areas	Time	Diff	Disp	Time
Canthon rutilans cyanescens	133	5	3.76	4	3 in P1 and 1 in F4	20 to 58 days	1	P4–F4	65 days
Dichotomius assifer	102	4	3.92	4	3 in P1 and 1 in P5	20 to 39 days	0	-	-
Dichotomius sericeus	236	9	3.81	7	4 in P6, 2 in F3 and 1 in P3	37 to 76 days	2	P5–F5 F3–P3	29 to 76 days
Total	471	18	3.82	15			3		

Number of individuals recaptured in the same marking area (Sm) and recapture area (Rc Area). Number of individuals recaptured in different areas (Diff) and areas from where the individuals dispersed and were recaptured (Disp), P, *Pinus* Monocultures, and F, Native Forest.

(from P4 to F4). For *D. assifer*, 102 individuals were marked and four were recaptured, all in the same marking areas: inside *Pinus* monocultures (three in P1 and one in P5), of which one was recaptured in 20 days, another in 36, and the last two in 58 days. *Dichotomius sericeus* presented the highest number of individuals marked (236) and recaptured (9). Seven of these were found in the same marking areas, both in *Pinus* monocultures and native forests (four in P6, one in P3, and two in F3). The other two individuals were found in areas different from where they were first captured and marked, going from *Pinus* monocultures to native forest and *vice-versa* (from F3 to P3 at a distance of 180 meters, and from P5 to F5, at 130 m). One of the recaptures happened in a pitfall trap (from F3 to P3). These results show the species dispersion capacity inside and between both habitats.

Dung beetle metacommunities

We collected 3,222 dung beetles belonging to 41 species (Supplementary Table S2). The three most abundant species were *Dichotomius sericeus* (19.11%), *Eurysternus inflexus* (Germar, 1824) (14.83%), and *Deltochilum morbillosum* Burmeister, 1848 (13.22%), which together represented 47.16% of the total individuals captured. The rare species, with only one individual collected, were *Canthidium* aff. *taurinum* (Harold, 1867), *Canthidium femoratum* Boucomont, 1935 and *Canthon oliverioi* (Pereira and Martínez, 1956). *Scatonomus fasciculatus* Erichson, 1835 and *Sulcophanaeus radamanthus* (Harold, 1875) had two individuals captured each.

Seven of the collected species were found in all sampled areas: *Deltochilum morbillosum*, *Dichotomius assifer*, *Dichotomius sericeus*, *Canthidium* aff. *trinodosum* (Boheman, 1858), *Coprophanaeus saphirinus*, *Eurysternus inflexus,* and *Phanaeus splendidulus* (Fabricius, 1781). In contrast, we collected six species in only one of the 12 areas: *Dichotomius opalescens* (Felsche, 1910) (P4), *Canthidium* aff. *taurinum* (F3), *Canthidium dispar* (Harold, 1867; F2), *Canthidium femorale* (F2), *Canthon oliverioi* (F2), and *Sulcophanaeus radamanthus* (F2).

According to the multinomial classification analyses, only four species were native forest specialists: *Canthidium* aff. *trinodosum*, *Canthon angularis* Harold 1868, *Paracanthon* aff. *rosinae* Balthasar, 1942, and *Uroxys terminalis* Waterhouse, 1891, and seven were *Pinus* monocultures specialists: *Canthidium* sp.1, *Canthon lividus seminitens* Harold 1868, *Canthon rutilans cyanescens*, *Deltochilum multicolor* Balthasar, 1939, *Deltochilum rubripenne* (Gory, 1831), *Eurysternus inflexus,* and *Onthophagus tristis* Harold, 1873. This analysis showed 16 habitat generalist species inhabiting both *Pinus* monocultures and native forest habitats, reaffirming that many species occupy both habitats. Fourteen species were considered too rare to be confidently classified (Figure 2).

The abundance of dung beetles found per type of habitat was 1,351 individuals from 32 species in the *Pinus* monocultures and 1,844 dung beetles from 38 species in the native forest areas (Supplementary Figure S1). The extrapolated species accumulation curves for each area showed sampling sufficiency since all curves reached the asymptote (sample coverage over 95% for all the sampling areas). Species richness ($q = 0$) was similar between *Pinus* monocultures and native forests in all six sites, with overlapping intervals of confidence (Figure 3).

Including abundance data in the analyses (Shannon entropy exponential, $q = 1$), we can see that the number of typical species was the same in four of the six sites, with the same diversity measure between *Pinus* monocultures and native forest. Only Sites 2 and 3 presented opposite patterns, with the first having higher diversity in the forest (F2 with 15.12 typical species and P2 with 6.24) and the second in *Pinus* monocultures (P3 with 10.45 typical species and F3 with 5.51; Figure 4).

The areas of *Pinus* monocultures and native forest statistically presented the same number of dominant species in four of the six sites from this study (Site 1, 4, 5, and 6) based on the Simpson's dominance analyses ($q = 2$; abundant species). Site 2 presented more dominant species in the native forest habitat (F2 with 9.82 and P2 with 3.15), and Site 3 had more dominant species in the *Pinus* monocultures (F3 with 3.28 dominant species and P3 with 7.93; Figure 5).

Unlike the diversity analysis, which shows the two habitats with similar richness, beta diversity was very high between them. The Bray–Curtis dissimilarity index indicated a greater difference between the assemblages that inhabit *Pinus* monocultures and native forests, varying between 47% and 72% of dissimilarity (Supplementary Table S3). The partitioning of beta diversity showed that the dissimilarity due to balanced variation in abundance is higher in all areas (except in Site 3), showing that species composition and relative abundance of the assemblages in native forest areas differ from *Pinus* monocultures.

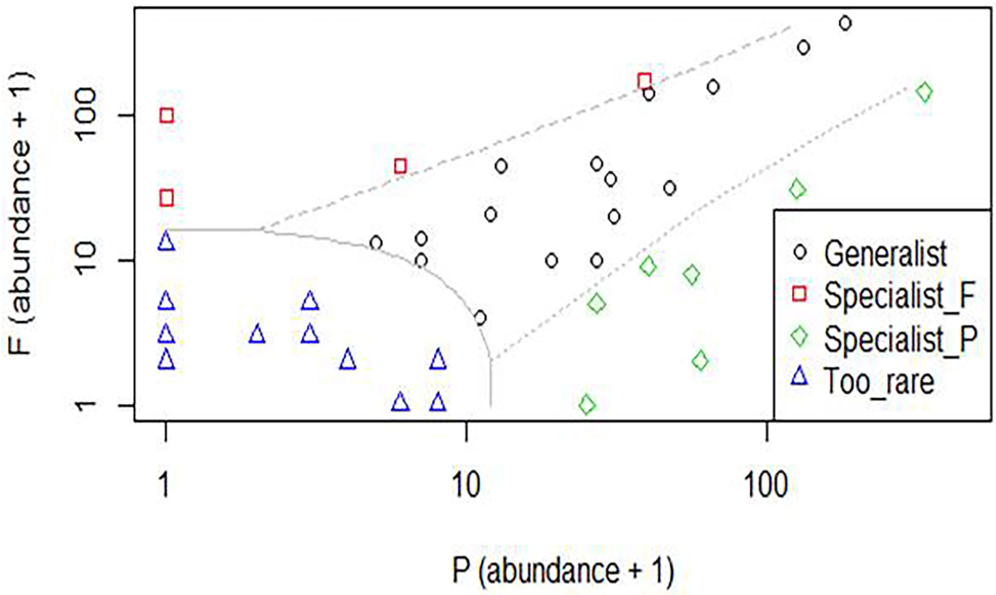

FIGURE 2
Species classification with data collected in habitats of native forest and *Pinus* monocultures in the State of Santa Catarina, southern Brazil. Specialist_F, native forest specialist; Specialist_P, *Pinus* monocultures specialist.

The dissimilarity did not vary according to the proximity of native forest and *Pinus* monocultures since both adjacent areas (Mean: 0.563, Sites 1, 2, and 3) and areas apart (Mean: 0.574, Sites 4, 5, and 6) had the same dissimilarity values when compared using a t-test ($t = 0.104$, $df = 3.99$, value of $p = 0.92$).

The analysis of species contribution to beta diversity (SCBD) indicated that 24 species are important contributors to beta diversity, whether for just one site or more (Supplementary Table S4). All SCBD values ranged from 0.035 to 0.299, and 14 species contributed to beta diversity above the overall mean (0.102). The species that most contributed to beta diversity were *Eurysternus inflexus* and *Onthophagus tristis*, more abundant in *Pinus* monocultures than in native forests, and *Canthidium* aff. *trinodosum* and *Paracanthon* aff. *rosinae*, more abundant in the native forest habitat (Supplementary Table S4). All 11 species classified as specialists are present in the SCBD results, reinforcing the multinomial classification analysis previously carried out (Figure 4). However, the SCBD analysis had 13 more species contributing to overall beta diversity, identified as generalists or too rare in the multinomial classification analysis.

Environmental influence in the metacommunities

As a result of camera trap records, we obtained 92 records of mammals belonging to 13 species (Supplementary Table S5). Nine species were native, with few records, occurring mainly in native forests. Three exotic species showed a large occurrence in *Pinus* areas, demonstrating the large supply of food resources that these habitats offer to dung beetles. These are: *Bos taurus* Linnaeus 1758, *Equus caballus* Linnaeus 1758, and *Canis lupus familiaris* Linnaeus 1758, the first two considered large.

The result obtained in measuring environmental variables, temperature, altitude, and tree density assessment (calculated as the average distance between trees) were very similar between *Pinus* monoculture and native forests (Supplementary Table S6). In the shrubs density assessment, we got lower values of distance between shrubs in the native forests when compared to *Pinus* monocultures, showing greater density of shrubs in those areas (understory). Lastly, the green cover percentage of the soil varied widely between areas, without following any apparent pattern.

The overall SEM model showed that none of the environmental factors significantly affected dung beetle richness, but several influenced dung beetle abundances (Figure 6). The variables temperature, vegetation structure (trees and herbs), and mammal abundance positively influenced the abundance of dung beetles. Temperature, with the most significant relationship with dung beetle abundance. Vegetation structure (shrubs) and mammal richness also influenced dung beetle abundance but in a negative way. Trees, shrubs and mammal richness had positive effect on the amount of resources.

Discussion

The results from the marking-recapture experiment show a species sorting effect in dung beetle metacommunities, in which niche has more influence than dispersal, with low movement rates.

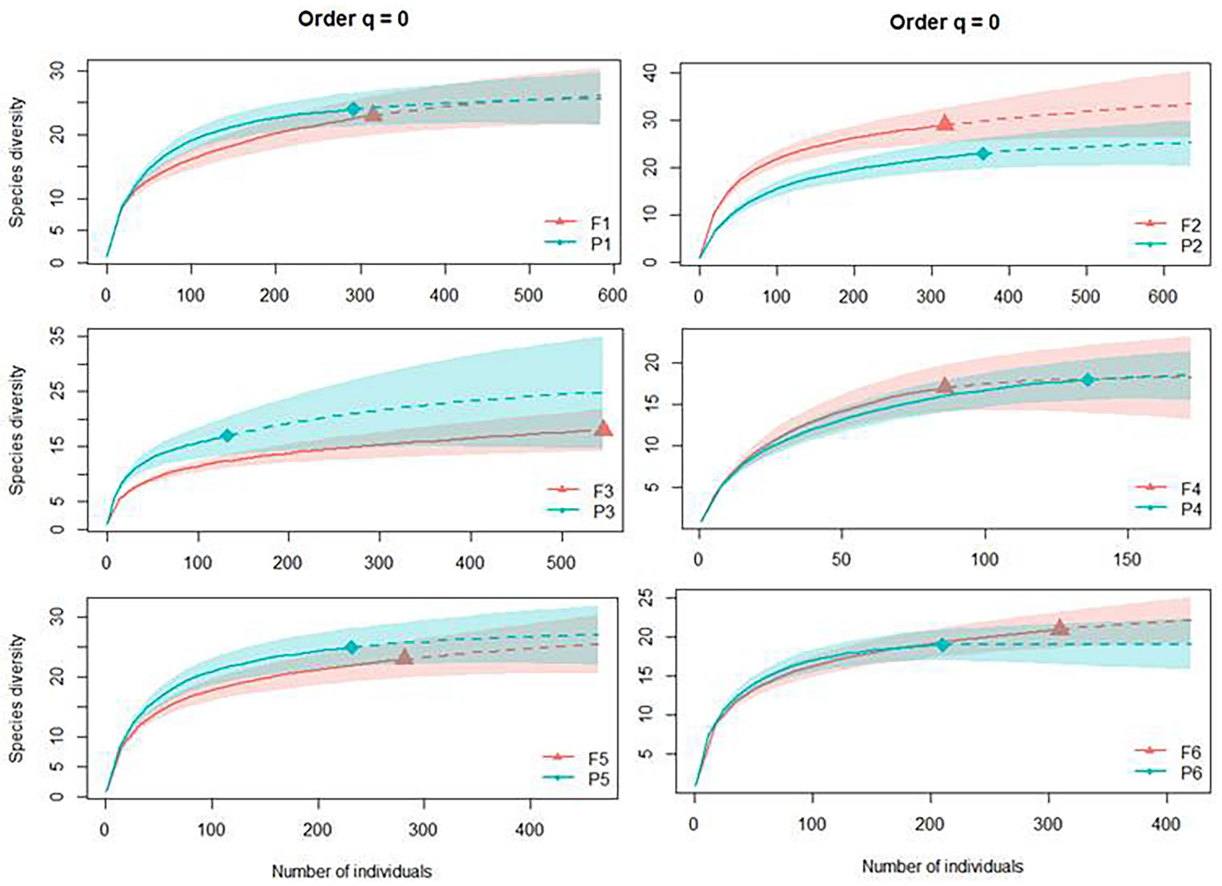

FIGURE 3
Individual-based rarefaction (solid lines) and extrapolation (dashed lines, up to double the smallest sample size) of dung beetle species richness for Hill number (q=0) for each site, where F represents native forests and P represents *Pinus* monocultures.

We observed some movement of individuals between the habitats. Still, most dispersions were inside the same habitat, showing that dung beetle dispersal was insufficient to highly expand their distributions but was enough for the individuals to track the alternative resources present in the *Pinus* monocultures. Although we have a low rate of individuals recaptured, the recapture rate was similar to results presented in other studies (Arellano et al., 2008; Noriega and Acosta, 2011; Da Silva and Hernández, 2015). In addition to the dispersal between areas, the species found inside the nesting houses were effectively using the habitats since we registered the presence of feeding balls and tunnels within those traps in both habitats (*Pinus* monocultures and native forest).

The transit of dung beetles between one habitat and the other shows that they move through areas of *Pinus* monocultures and native forests, interacting and connecting with those assemblages. We can state that the coexistence of species within a regional level occurred due to the niche differentiation between them, causing high beta diversity (Leibold et al., 2004), differences that were not pointed out by richness and diversity indices. The species richness and diversity of dung beetles had close values in both *Pinus* monocultures and native forest habitats. A study in areas close to those of the present work, related to dung beetle taxonomic and functional diversity among native forests and altered subtropical habitats, also showed that forests and *Pinus* monocultures have similar richness values, different from open habitats (fields), which presented a great decrease of species richness and individual abundance (Sarmiento-Garcés and Hernández, 2021). These results contrast with the severe decline in biodiversity observed in other studied areas that suffered higher alteration levels (Nichols et al., 2007; López-Bedoya et al., 2022).

Then, considering species abundance and richness, as shown in the extrapolation curve analysis, it is impossible to observe significant differences between assemblages of different habitats, not being a reliable and sufficient approach. Moreover, even in cases where these measures serve to assess changing patterns of diversity, they remain limited in describing which species are lost and how this loss can alter ecosystem dynamics (Nichols et al., 2007). That's because ecological indicators should provide reliable and interpretable information on the ecological consequences of human activities for a measured component of biodiversity (Nichols and Gardner, 2011). In the diversity partitioning analysis, we can see that there are differences in both assemblages, which are mainly due to the species variation in abundance. The Bray-Curtis index analysis shows that part of the dissimilarity between the areas of *Pinus* monocultures and native

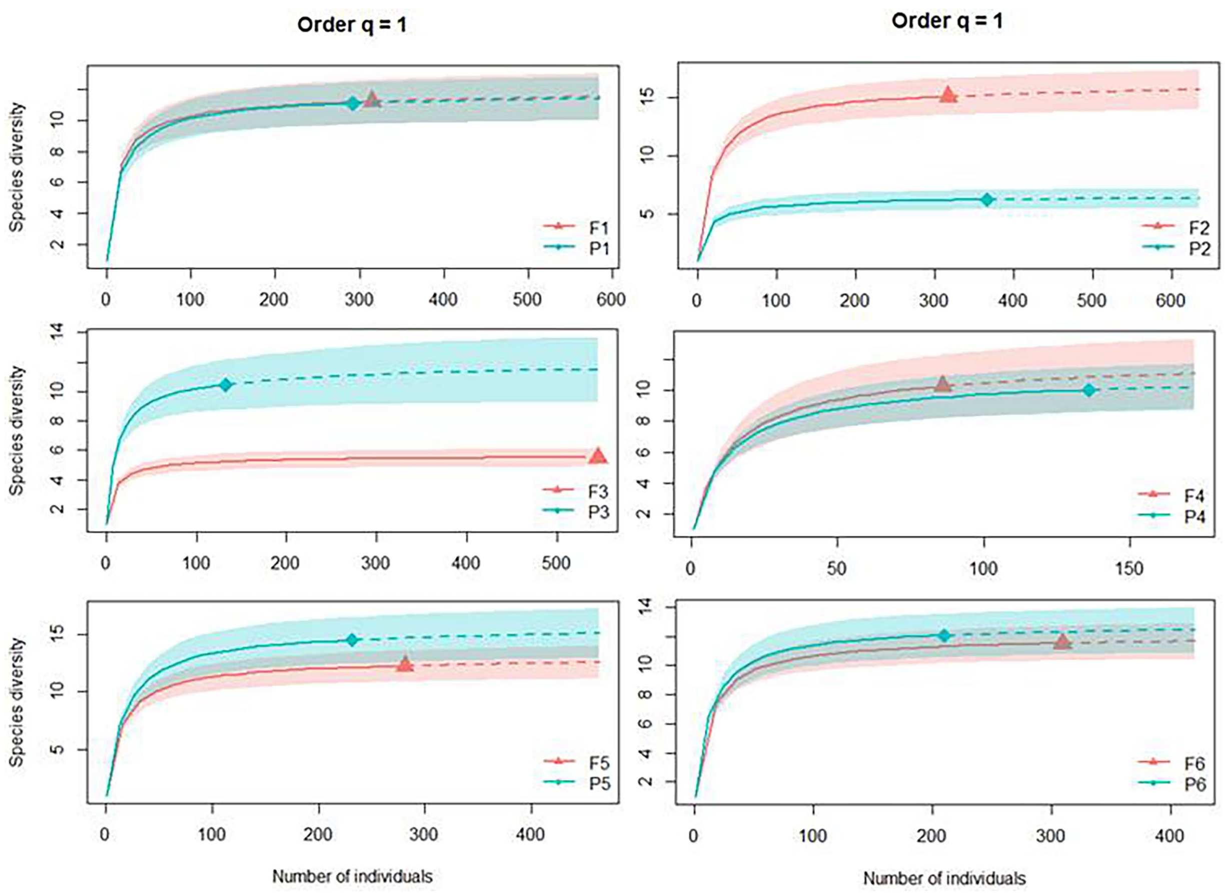

FIGURE 4
Individual-based rarefaction (solid lines) and extrapolation (dashed lines, up to double the sample size) of Dung beetle diversity for Hill numbers (q=1) for each site, where F represents native forests and P represents *Pinus* monocultures.

forests is due to the abundance of some species that prefer one or another habitat. This occurs because of the balance or shift of species between the areas. The composition of the assemblages is similar to a certain point, where some species become more specific to forest areas and others more linked to *Pinus* monocultures sites. These species, presented in the multinominal classification analyses as habitat-specific, are few compared to those considered generalists or too rare to be classified.

Furthermore, the structural equation models showed no influence of environmental factors or resource availability on dung beetle richness, with very close averages among habitats. On the other hand, many factors like habitat type, temperature, vegetation structure (trees and herbs), and mammal abundance positively influenced dung beetle abundance, with more emphasis on temperature. Thus, we can see important features for the maintenance of the dung beetles, such as proper temperature and the presence of resources. It is interesting to reflect on the presence of exotic animals, such as cattle, horses, and dogs, which greatly contributed to the occurrence and mammal richness, especially in the *Pinus* monocultures. These domestic animals can have a major effect on dung beetles assemblages, being an alternative as a potential source of resources, reflecting the mammal abundance in altered habitats. In this way, the dung beetle assemblage in the *Pinus* monocultures areas is affected by mammal composition, habitat structure, and spatial distance (Barlow et al., 2010; Bogoni et al., 2016).

The presence of exotic domestic mammal species mainly in monoculture areas reaffirms the anthropization of these areas. In addition, among all species recorded, two are large (*Bos taurus* and *Equus caballus*), contributing even more to the supply of resources. Many studies have shown that there is a positive relationship between dung beetles and the richness of omnivorous mammals, where the majority of the individuals being attracted by the feces of mammals from this trophic group (Estrada et al., 1993; Filgueiras et al., 2009; Bogoni et al., 2016). We took the opportunity to reflect on the limitations we found when analyzing mammal abundance as the amount of resources available because we know that the size of the identified mammals is not standard, with species of large, medium, and small size. Other points not included are the different trophic groups of mammals present in the areas (herbivores, carnivores, and omnivores) and necrophagous dung beetle preference for arthropod carcasses (Bogoni et al., 2016; Gimenéz Gómez et al., 2021).

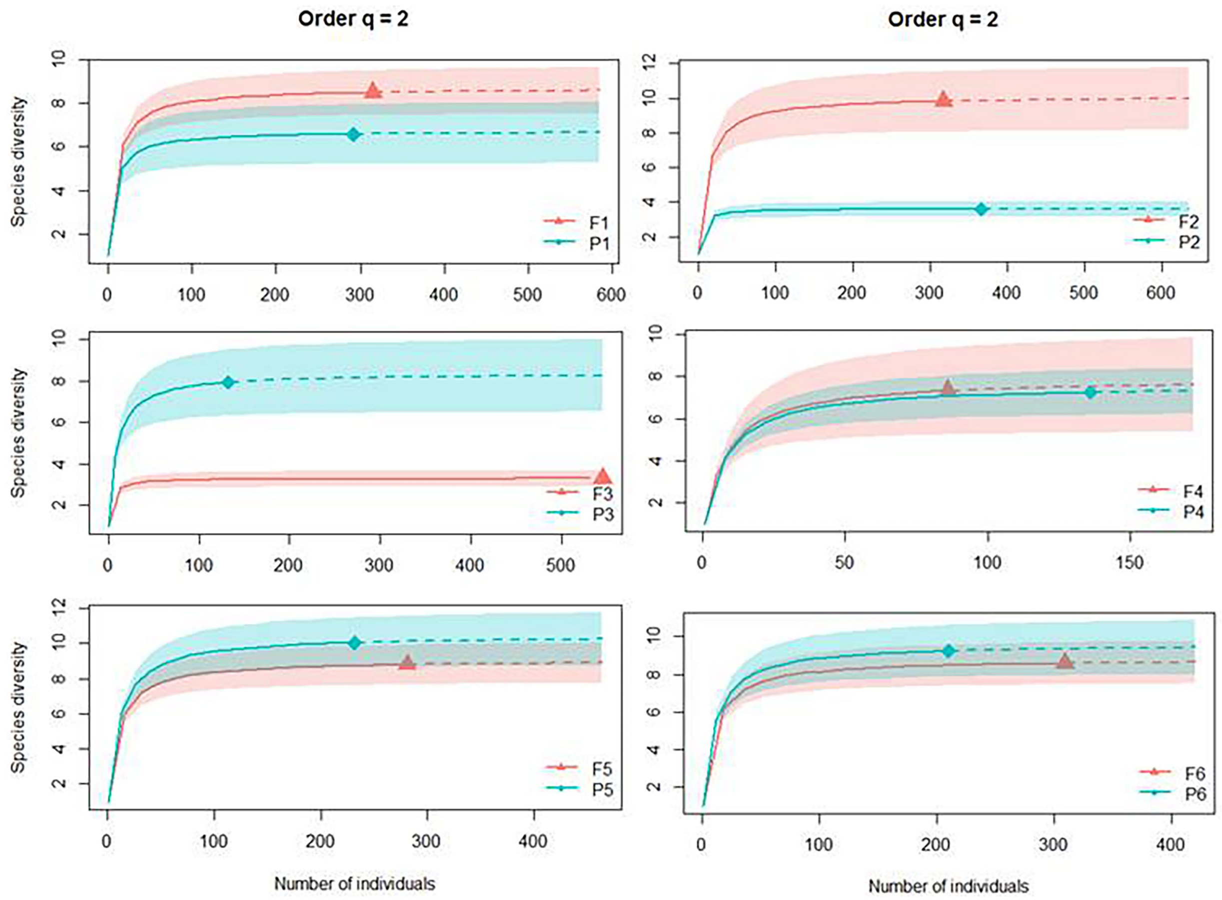

FIGURE 5
Individual-based rarefaction (solid lines) and extrapolation (dashed lines, up to double the sample size) of Dung beetle diversity for Hill numbers (q=2) for each site, where F represents native forests and P represents *Pinus* monocultures.

Some studies suggest that very few forest dung beetles can extend their activity into strongly altered forests or natural open habitats (Nummelin and Hanski, 1989; Halffter and Arellano, 2002; Gardner et al., 2008; Gries et al., 2011). However, our results suggest that *Pinus* monocultures provide habitat for forest dung beetles. Canopy openness is an influential variable that structures dung beetle assemblages across all habitats and types of plantation (Hernández and Vaz-De-Mello, 2009; Barlow et al., 2010; Da Silva et al., 2018). Canopy cover can influence both soil humidity and surface temperature, which might affect the survival and reproduction of dung beetles and food availability and attractiveness (Gries et al., 2011). Thus, the conservation of either native or exotic canopy can determinate whether highly diverse dung beetle assemblages and their ecological functions are preserved or not (Giménez Gómez et al., 2018).

We remember the risk that *Pinus* monocultures pose to biodiversity in Brazil, which has more than 7 million hectares in homogeneous reforestation, with *Pinus* being one of the most representative in the southern region of the country (Anuário estatístico de base florestal para o estado de Santa Catarina, 2019). In addition to being exotic, the species has a high invasive potential and is well documented worldwide (Richardson, 2006). Additionally, some of its features, such as short juvenile period and numerous small, winged seeds that characterize them as pioneers in their native range, are responsible for their invasiveness (Rejmánek, 1996; Richardson, 2006). This way, *Pinus* trees can severely impact the local biota and ecosystem processes, such as changes in water and fire regimes (Simberloff et al., 2010).

In conclusion, through this work, we observed the lack of indication of the approach of dung beetle richness and diversity in *Pinus* monocultures and native forest, and to reflect on the need to complement the method with other composition analysis when using dung beetles as ecological indicators. This is due to the differences in the composition of the assemblages (species that prefer different types of habitats) being demonstrated only when we calculate beta diversity. We must consider this when using dung beetles as ecological indicators since we found similar indices in very different areas in terms of biodiversity. Thus, our results demonstrate that the use of species richness and diversity indices alone may not show real differences between assemblages in areas with distinct habitats, not reflecting the real environmental quality of the sites. Therefore, we must consider the differences in

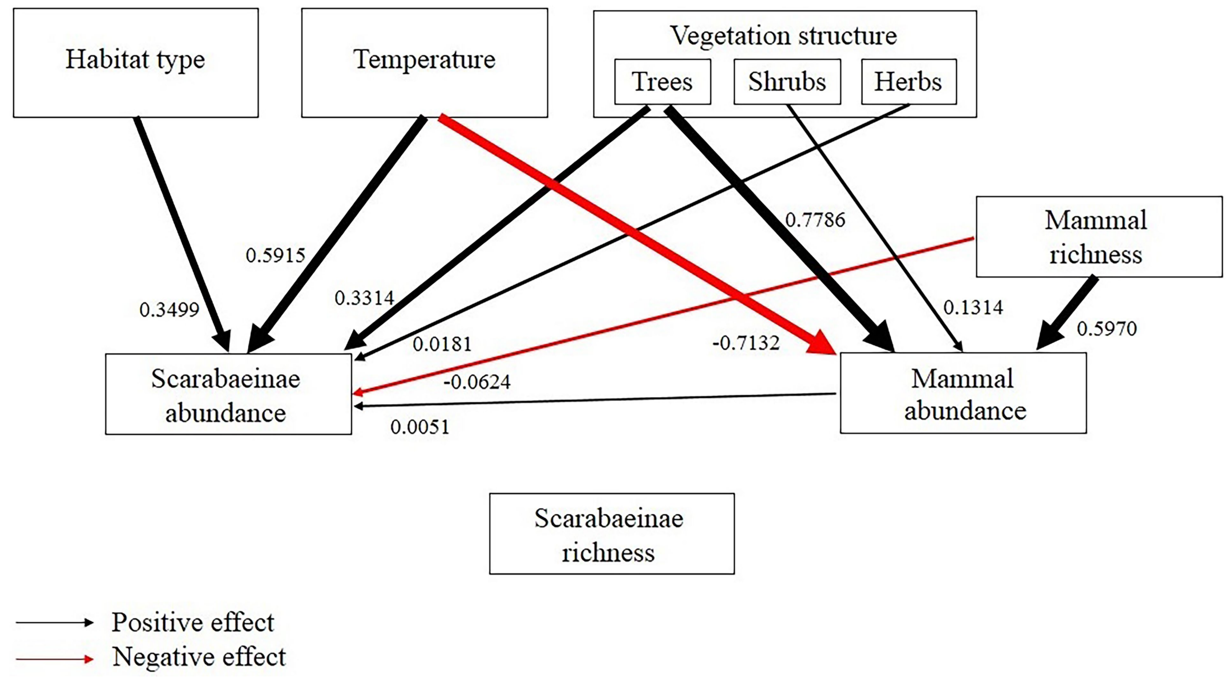

FIGURE 6
Structural equation model for dung beetle richness and abundance. The arrows indicate the significant influence of environmental factors and resources (with their respective coefficients) on dung beetle abundance. Black arrows denote positive relationships, and red arrows denote negative relationships.

species composition of the assemblages between habitats. In this case, analyses like the ones of dissimilarity, SCBD, and multinomial classification complement each other, contributing to better understanding the dung beetle metacommunities. Still, according to these results, our structural model overall SEM shows that dung beetle richness in both types of habitats is not influenced by environmental factors, although dung beetle abundance is. We also conclude that there was no relationship between the composition and abundance of dung beetle assemblages in monocultures to the distance of the native forest areas in this study. However, the presence of native forests and other habitats very likely provides individuals to the *Pinus* monocultures. On the other hand, these monocultures have characteristics similar to the native forests, such as temperature, humidity, canopy cover, and alternative food resources, which allow the permanence of the beetles. We also emphasize that even though the *Pinus* monocultures allow the permanence of dung beetle assemblages with a richness similar to those found in areas of native forests, we should consider the invasive potential of this exotic species and the inhibitory effect on native plants, as well as other possible negative impacts on animal species in the region. Also, the high availability of food resources in *Pinus* monoculture areas with domestic animals is not an exclusive feature of all monocultures. The monoculture areas in this study belong to small farmers, with some presence of shrubs of other plant species (understory) and are used for purposes other than logging (such as resin extraction and cattle raising). Thus, we can consider that other *Pinus* monoculture areas, which are larger, more isolated, and aimed only at logging, with high plantation turnover, can provide a much less suitable environment for dung beetles. In this case, the richness and diversity indexes would most likely be more effective.

Data availability statement

The original contributions presented in the study are included in the article/Supplementary material, further inquiries can be directed to the corresponding author.

Author contributions

All authors listed have made a substantial, direct, and intellectual contribution to the work and approved it for publication.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

Supplementary material

The Supplementary material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2022.972176/full#supplementary-material

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Diversity and distribution patterns of Ecuador's dung beetles (Coleoptera: Scarabaeinae)

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Introduction: Ecuador harbors an astounding number of ecosystems and species. However, anthropogenic land-use changes are the primary drivers of biodiversity loss in major taxonomic groups, especially insects. Among them, the Scarabaeinae subfamily containing dung beetles, is an excellent taxon for studying taxonomic and functional diversity, as they are relatively stable taxonomically and have a wide variety of ecological services. Their distribution is mainly influenced by biogeography and climate as their main ecological and environmental factors will allow us to quantify what aspects of diversity are being impacted under different circumstances and at different scales.

Methods: To understand the main of dung beetle distribution drivers, we analyzed a museum database from the National Institute of Biodiversity, Ecuador (INABIO) of over 5000 dung beetle specimens with 122 species collected throughout the country, we addressed the following questions: i) How does tribe distribution vary across climatic and elevational gradients? and ii) How does functional and taxonomic beta diversity vary across spatial scales? To address them, we focused on three main tribes: Canthonini, Coprini, and Phanaeini. We constructed GLM's and niche-based models to estimate Ecuador's distributions based on climate variables to explore potential predictor variables, using tree classification models, along with taxonomic and functional beta diversity across scales.

Results: The main variables influencing dung beetle distribution were elevation, and precipitation. The Phanaeini niche model is significantly better at predicting dung beetle presence throughout Ecuador than Canthonini and Coprini. We found high turnover in functional groups at larger scales, suggesting that dung beetles show high levels of habitat specialization, which associates to our findings where taxonomic beta diversity was higher in the Amazon basin compared to the coastal region. This may be due to the higher rate of dung production in Amazonia. Our findings also suggest that dung beetles are not found in areas above 2000m, mainly because dung beetles are well adapted to warmer and moist climatic regions. Precipitation and elevation are consistently essential variables for predicting Canthonini and Coprini presence, while temperature explains Phanaeini presence. Low levels of species turnover at the regional scale may be because the total species richness in Ecuador is different, where divergence in taxonomic beta diversity between the two regions is an artifact of such differences in richness in Amazonia versus the coast, the distinction is also due to nonrandomly low taxonomic beta diversity levels in the coastal region.

Conclusions: Our results provide an essential framework for evaluating potential dung beetle habitat and diversity at different scales; therefore, by identifying dung beetles' diversity, combined with considerations of habitat fragmentation, human land-use alteration, and climate change, will be an important next step to inform better and prioritize dung beetle conservation efforts in other countries.

KEYWORDS

Amazonia, biodiversity, distribution modeling, ecological niche modeling, functional beta diversity, Neotropics, Scarabaeidae, species turnover

Introduction

Ecuador is the smallest of the 17 megadiverse countries (Mittermeier et al., 1998) harboring an astounding number of ecosystems and species, with many endemic species occurring in small geographic ranges (Brooks et al., 2002, 2006; Bass et al., 2010). Unfortunately, the country has experienced profound changes to its natural habitats (Cuesta et al., 2017). In 2014, the country reported an estimated 1.83 million-hectare (14%) loss of forest area since 1990 (Sierra et al., 2021). The annual deforestation rate for 2008–2014 was – 0.37%, equivalent to an average annual loss of 47,000 hectares (Sierra et al., 2021). Due to these recent trends in habitat loss and extensive historical changes that occurred during the mid-20th century, only ~30% of the original natural vegetation remains in the coastal plains, 60% in the Andean region, and 88% in the Amazon lowlands. In this context, anthropogenic land-use changes are the primary drivers of global biodiversity loss in major taxonomic groups (Reid et al., 2005), and Ecuador is not the exception. Invertebrates are often particularly susceptible to landscape changes (Dunn, 2004; Samways, 2005), and because of the key roles they play in many ecosystem processes, their loss could produce cascading effects on the entire communities (Coleman and Hendrix, 2000). Despite this, our knowledge about the response of many insects to climate conditions and human activity is minimal (Nichols et al., 2008; Wagner, 2020). Understanding the response of insects to human activity and climate is necessary to support conservation policies and assess the functional consequences of human disturbance (Balmford and Bond, 2005; Halsch et al., 2021).

The order Coleoptera constitutes the richest group of species of any animal taxa, with more than 400,000 species described so far (McKenna et al., 2015; Zhang et al., 2018). Among this diverse order, dung beetles belong to the Scarabaeoidea superfamily, one of the largest superfamilies of beetles in the world, with approximately 150 families and 30,000 species (Carvajal et al., 2011). Scarabaeoidea is the most diverse group within the Coleoptera order in terms of its biology, ecology, and behavior (Woodruff, 1973). Dung beetles are an excellent taxon for studying both taxonomic and functional diversity. They are widely distributed, diverse, and abundant in tropical and warm temperate ecosystems. Additionally, the ecological roles of dung beetles are known (Hanski and Cambefort, 1991) and the group has a relatively stable taxonomy (Philips et al., 2004). Adults and larvae are part of a specialized group that feeds mainly on the feces of herbivorous mammals, thus playing an integral role in recycling nutrients, improving plant growth, reducing pests, bioturbation, pollination, and secondary seed dispersal (Nichols et al., 2008). In addition, this taxon has been proposed as an excellent bioindicator group of environmental processes, being very sensitive to anthropic disturbance events (Halffter and Favila, 1993, McGeoch et al., 2002, Spector, 2006, Otavo et al., 2013, Noriega et al., 2021).

Two principal ecological factors influence present tribal, genera, and species distribution patterns of Scarabaeinae dung beetles worldwide (Davis and Scholtz, 2001): suitable climate and the number of dung types. At the species and generic level, there is a strong correlation between dung beetle taxon richness and the area of suitable climate in each of the world's biogeographical regions. However, at the tribal level, taxon richness and composition strongly correlate to both climatic area and the number of dung types. Dung type diversity also varies between biogeographical regions according to the evolutionary history of mammals (Davis et al., 2002). However, their relative influence differs according to the two main components of biodiversity: overall numerical richness and taxonomic identity. In the first instance, current distributional variance in taxon richness is often correlated strongly with current ecological or environmental factors (Francis and Currie, 1998; Davis and Scholtz, 2001; Moura et al., 2016). Scarabaeinae dung beetles also show strong spatial specializations stemming from their Gondwana land origin (Halffter and Matthews, 1966; Halffter, 1974; Silva and Hernández, 2014) centered on warmer, moister, climatic regions (Halffter, 1991; Davis et al., 2002; Birkett et al., 2018). At a regional scale, climate type exerts a significant influence on dung beetle diversity (Kirk and Ridsdill-Smith, 1986; Davis and Dewhurst, 1993; Davis, 1997; Duncan et al., 2009), which appears to be a general rule in the large-scale distribution of any taxonomic group (Currie et al., 1999; Clark et al., 2011). At a local scale, soil and vegetation types, influence dung beetle distribution (Nealis, 1977; Doube, 1983; Cambefort, 1991; Davis, 1996; Daniel et al., 2021); which, could strongly affect ecosystem functioning and disrupt all ecosystem services provided by this group of insects. Potential distribution and/or niche models for this group of species in Ecuador are scarce.

To quantify the effects of this habitat alteration and climate change, we need to understand which roles, functions, and ecological services exist on the landscape. Understanding where, when, and how species change in relation with the environment will allow us to quantify what aspects of diversity are being impacted under different circumstances and at different scales of land-use change (Barragán et al., 2011). These patterns allow for more effective management of natural areas to avoid biodiversity loss in critical regions (Hayes et al., 2009). In this context, beta diversity may be a handy metric for elucidating the processes underlying dung beetle community assembly at a regional scale. Beta diversity, which measures how species composition changes across space, can allow us to evaluate how community structure and assembly processes change as a function of the environment (McKnight et al., 2007; Buckley and Jetz, 2008; Lepori and Malmqvist, 2009). At local scales, high beta diversity measurements can reflect a decisive role of environmental filtering and species interactions in community organization (Fukami et al., 2005). At regional scales, high beta diversity can reflect a strong role in trait evolution, habitat specialization, and speciation (Graham and Fine, 2008). Taxonomic diversity, however, is often sensitive to stochastic effects such as genetic and ecological drift due to dispersal limitations (Baiser and Lockwood, 2011). And, furthermore, the presence of functionally redundant species limits the ability of taxonomic diversity to reflect environmental filtering (Swenson et al., 2011; Siefert et al., 2012). To tease apart these processes, one solution is to compare taxonomic and functional beta diversity. In comparison to taxonomic diversity, functional trait diversity is highly responsive to deterministic environmental processes but not to the stochasticity caused by ecological drift and dispersal limitation (Villéger et al., 2012; Myers et al., 2013). When functional beta diversity and taxonomic beta diversity respond similarly to spatial or temporal changes, communities are likely to assemble deterministically, while opposed responses suggest that stochastic effects may be causing mismatches in functional and taxonomic levels (Condit et al., 2002; Chase and Myers, 2011; Leibold and Chase, 2017). The dung beetle assemblages of Ecuador span a large and heterogeneous area, making it is critical to also consider regional habitat type, which can affect beta diversity (Swenson et al., 2011). By measuring the correlation between taxonomic and functional beta diversity, we hope to understand whether dung beetle assemblages in Ecuador are organized *via* habitat filtration and species interactions, which act at the functional level, or dispersal limitation and ecological drift, which operate at the species level.

To understand distribution and biodiversity patterns among Ecuador's dung beetles, we conducted two analyses utilizing a database of over 5,000 dung beetle specimens collected throughout the country, addressing the following questions: (i) How does tribe distribution vary across climatic and elevational gradients? And (ii) How does taxonomic and functional beta diversity vary across spatial scales? We first examined the distribution of three widespread tribes that play distinct roles in ecosystem functioning (Canthonini, Coprini, and Phanaeini) using distribution models to evaluate which environmental and topographic variables are significant drivers of tribe presence. We hypothesized that elevation and temperature would be the most important drivers of these tribes' distributions because of the dung beetle's small body size and dependence on mammal populations, which likely vary according to vegetation assemblages driven by elevation and moisture. Second, to assess the relative importance of stochastic versus ecologically driven community assemblage processes throughout Ecuador, we compared the relationship between alpha and beta diversity at the taxonomic level (taxonomic alpha/beta diversity) and functional group level (functional alpha/beta diversity) using 20 different spatial scales. Spatial scale was represented here as 20 spatial grids which all covered the same extent of Ecuador, but which differed in grain size, ranging from a 4-bit grid to a 256-bit grid. Based on their sensitivity to climate and specialization to dung type, we hypothesized that dung beetle community assemblage processes are likely driven by ecological factors such as niche specialization and biotic interactions both at the local and regional levels. We thus expected functional beta diversity and taxonomic beta diversity to respond similarly to spatial scale and alpha richness. Finally, to assess the importance of habitat type on stochastic versus ecologically driven community assembly processes, we compared the response of taxonomic and functional beta diversities to scale in the northern coastal region to the northern Amazonian region of Ecuador. We hypothesized that highly productive and more environmentally stable regions, such as the Amazon basin, would show high beta diversity at a much finer scales than heterogeneous regions such as the northern Coast.

Materials and methods

Data were analyzed from the Coleoptera Collection of the National Institute of Biodiversity, Ecuador. This database includes adult dung beetle collections with records from the 1970s, with more than 5,000 entries, encompassing 122 species from three natural regions (Coast, Andes, and Amazonia), 19 provinces, and 11 vegetative formations. All the collections belong to more than 200 locations across Ecuador. All analyses focused on the three main tribes: Canthonini (42 species), Coprini (42 species), and Phanaeini (17 species), as they belong to groups with broad distributions and adapted to high percentage of canopy cover. Ecuador is divided into four unique geographical regions; the Coast, which has seven provinces ranging from 0 – 900 m and limiting with the western Andes cordillera; the Sierra region (Andes) has 10 provinces all in high elevations ranging from 900 to 6,263 m, the Amazon has six provinces all located in the Amazon Basin from the Eastern Andes foothills at 800 m towards the evergreen forests at 200 m.

The Coleoptera Collection was trimmed to include only one entry per species per location to account for sampling bias. We analyzed the data in two ways. First, to understand how different tribes are distributed across the landscape, we fitted distribution models using several climate variables and elevation data (Supplementary Table S1). Second, we analyzed how grain size affects β-diversity using taxonomic and functional approaches, where the largest grain size divides the region (Amazonia or Coast) into fourths, each plot about 22,000 km^2, and the smallest grain size divides the region into 256 plots each equal to 344 km^2. All data analysis was conducted in R (R Core Team, 2022).

Distribution modeling of dung beetle tribes

We constructed a niche-based model to infer climatic processes driving the species spatial distribution. To characterize the niche climatic space, we used 9 bioclimatic variables (Supplementary Table S1) obtained from the WorldClim database (Fick and Hijmans, 2017), including global monthly climate data from 1970 to 2000 at approximately 1 km resolution. We selected climate variables related to temperature and precipitation. These raster data and elevational data were imported in the statistical software R (R Core Team, 2022) as a raster stack for spatial analysis and the models were generated using the “sf” (Pebesma, 2018), “dismo” (Hijmans et al., 2022) and “raster” (Hijmans, 2022) packages. Since elevation data were available as spatial polylines, the data were converted to a raster using nearest-neighbor interpolation with the same extent and resolution as the climate data for ease of analysis. Global climate data were cropped to Ecuador, then extracted to the location of each dung beetle specimen. Although vegetation data were also available, we did not use these data in distribution modeling because of the large number of different vegetation classes for the number of observations available, then we performed distribution models separately for each tribe.

Because our data were presence-only, we generated pseudo-absences by randomly sampling background locations across Ecuador to produce approximately equal sample sizes of presence/absence data, as recommended by Barbet-Massin et al. (2012). Climate and elevation data were again extracted to these background locations.

In order to select the most appropriate climate variables, we used a classification and regression tree model (CART) (Lewis, 2000, de Ona and de Ona, 2012) to identify potential predictor variables for determining tribe presence/absence. Classification trees partition the response recursively into hierarchical subsets that are increasingly homogeneous in presences/absences (Urban et al., 2002). The model uses single predictor variables for partitioning at each branch of the tree. Classification trees were ‘pruned’ using a cost-complexity parameter that minimized the relative misclassification rate from 10-fold cross-validation to avoid overfitting. To evaluate each reduced classification tree, we fit a model on a training subset

TABLE 1 AIC and BIC data for model selection for each of the three tribe distribution models using binomial generalized linear regressions.

Model	AIC	BIC
Canthonini		
PA ~ Elev + MAT + MAP + PPT seasonality + PPT warmest quarter + PPT coldest quarter	462.00	489.91
PA ~ Elev + MAP + PPT seasonality + PPT coldest quarter	489.13	509.06
PA ~ Elev + MAP + PPT coldest quarter	494.27	510.21
PA ~ (Elev + MAP + PPT coldest quarter)^2	460.11	484.03
PA ~ Elev + MAP + PPT coldest quarter + Elev:MAP + MAP:PPT coldest quarter	456.08	483.99
Coprini		
PA ~ Elev + PPT driest month + PPT seasonality + PPT warmest quarter + PPT coldest quarter	496.48	520.52
PA ~ Elev + PPT driest month + PPT seasonality + PPT warmest quarter	499.51	519.54
PA ~ Elev + PPT driest month + PPT seasonality	510.48	526.51
PA ~ (Elev + PPT driest month + PPT seasonality)^2	447.97	476.01
PA ~ Elev + PPT driest month + PPT seasonality + Elev:PPT driest month + PPT driest month: PPT seasonality	446.42	470.46
Phanaeini		
PA ~ Elev + MAT + MAP + PPT wettest month + PPT driest month + PPT warmest quarter + PPT coldest quarter	232.85	248.44
PA ~ Elev + MAT	232.80	244.49
PA ~ Elev + MAT + Elev:MAT	189.25	204.84

Models with the lowest AIC and BIC were selected for further evaluation and final predictions.

TABLE 2 Coefficients and significance statistics of final tribe distribution models using logistic generalized linear regression.

Canthonini

P ~ Elevation + Annual precipitation + Precipitation of coldest quarter + Elevation: Annual precipitation + Annual precipitation: Precipitation of coldest quarter

	Odds estimate	Log odds estimate	Standard error	Z value	Pr (>|z|)
Intercept	2.133088	0.7575708	0.4221209	1.7946772	0.0727052
Elevation	0.997687	−0.0023156	0.0004102	−5.6446864	0.0000000
Annual precipitation.	0.998669	−0.0013321	0.0003237	−4.1147182	0.0000388
Precipitation of coldest quarter	1.009537	0.0094921	0.0014441	6.5728855	0.0000000
Elevation: Annual precipitation	1.000001	0.000001	0.0000002	4.4234679	0.0000097
Annual precipitation: Precipitation of coldest quarter	0.999998	−0.0000016	0.0000003	−4.5809495	0.0000046

Coprini

P ~ Elevation + Precipitation of driest month + Precipitation seasonality + Elevation: precipitation of driest month + Precipitation of driest month: Precipitation seasonality

	Odds estimate	log odds estimate	Standard error	Z value	Pr (>|z|)
Intercept	4.1780556	1.4298460	0.9994721	1.4306012	0.1525445
Elevation	0.9984615	−0.0015397	0.0003580	−4.3015037	0.0000170
Precipitation of driest month	0.9745912	−0.0257371	0.0040670	−6.3282093	0.0000000
Precipitation seasonality	0.9707436	−0.0296929	0.0087657	−3.3873942	0.0007056
Elevation; Precipitation of driest month	1.0000148	0.0000148	0.0000035	4.2638772	0.0000201
Precipitation of driest month: precipitation seasonality	1.0009903	0.0009898	0.0001930	5.1290686	0.0000003

Phanaeini

P ~ Elevation + Mean annual temperature + Elevation: Mean annual temperature

	Odds Estimate	Log Odds Estimate	Standard error	Z value	Pr (>|z|)
Intercept	0.0051192	−5.2747593	1.3899440	−3.7949439	0.0001477
Elevation	1.0017771	0.0017755	0.0005362	3.3110261	0.0009295
Mean annual temperature	1.4615541	0.3795003	0.0662990	5.7240707	0.0000000
Elevation; Mean annual temperature	0.9998195	−0.0001805	0.0000277	−6.5169304	0.0000000

(70% of the data), then predicted tribe presence/absence on the holdout dataset. Variables identified through each pruned classification tree were then used to model tribe distribution using generalized linear models using the package "rpart" (Therneau et al., 2015) in R (R Core Team, 2022). The final models specify the logit (ln(P/(1-P)) of presence probability, P, as a linear combination of the specified predictor variables and interactions between predictors.

We selected elevation, mean annual temperature, annual precipitation, precipitation of the wettest and driest months, precipitation seasonality, and precipitation of the warmest and coldest quarters for inclusion in our models based on a threshold Pearson's correlation of 0.7 (Sedgwick, 2012). Classification tree models predicting tribe presence/absence allowed us to reduce the number of potential predictor variables for further consideration in logistic regression.

Generalized linear models

We began our analysis by exploring potential predictor variables for explaining the distribution of dung beetle tribes across Ecuador. We first plotted univariate histograms of the possible predictor variables (Supplementary Figure S1), the response variable, and tribe presence to understand the underlying distribution of each variable. We then explored a correlation and bivariate scatterplot matrix of all variables to understand the full scope of correlations between the potential predictors. After considering redundancy in several variables and visualizing possible important predictor variables graphically and through the CART model, we decided to explore elevation and all bioclimatic variables, as potential predictor variables in generalized linear models. Because the response variable, tribe presence/absence, is discrete binary count data bounded at zero, we specified a full generalized linear model (GLM) with a binomial distribution and logit-link function for each tribe. We then identified several reduced models predicting tribe presence/absence with predictor variables and determined the statistically significance with an ANOVA – chi-squared test in the entire model. The final models for each tribe were selected by comparing Akaike Information Criterions (AIC) and Bayesian Information Criterions (BIC) (Table 1), as well as their evaluation performance. Using the last models for each tribe (Table 2), we predicted the probability of occurrence across Ecuador based on the climate and elevation raster inputs.

Model diagnostics and validation

To assess whether a binomial GLM with a logit link function was appropriate for characterizing the distribution of different dung beetle tribes, we produced diagnostic plots for the model and performed ANOVA, chi-square analyses to compare its ability to explain variance in the data with the full binomial model. We assessed linearity by plotting the residuals versus the model's fitted values and examining the normal quantile-quantile (Q-Q) plots. The residual versus fitted values plot was used to detect non-linearity, unequal error variances, and outliers. We used Cook's distance and plotted hat values in an index plot to determine if any outliers were exerting undue influence on the model. We examined response, Pearson, and deviance residual plots for each final model to assess for normality. To determine the accuracy of our distribution models, we used a threshold-dependent metric. We took an initial random sample of 70% training data to fit the top distribution models. We then predicted dung beetle tribe presence/absence using the validation set on the training model. We performed this holdout model selection and validation five times to examine consistency in the top model's covariates, parameter estimates, and accuracy, afterwards, we specified the threshold for each validation set around the prevalence of a tribe in the data and converted our predicted probabilities to presence/absence predictions, and produced a contingency table to gauge overall accuracy, false positives, and negatives. We also assessed the error rate in classification using the same threshold. The class agreement command produced the overall accuracy metric and the kappa coefficient, which measures the agreement between predicted and observed data beyond chance agreement between classes. Furthermore, we used receiver operating curves (ROC) based on the overall accuracy to calculate an area-under-curve statistic (AUC) given our specified threshold.

Taxonomic and functional alpha and beta diversity across scales

For our taxonomic approach, within the three tribes, we used the collection data of 100 species spread among 682 observation points throughout Ecuador. Afterwards, we identified 14 functional groups

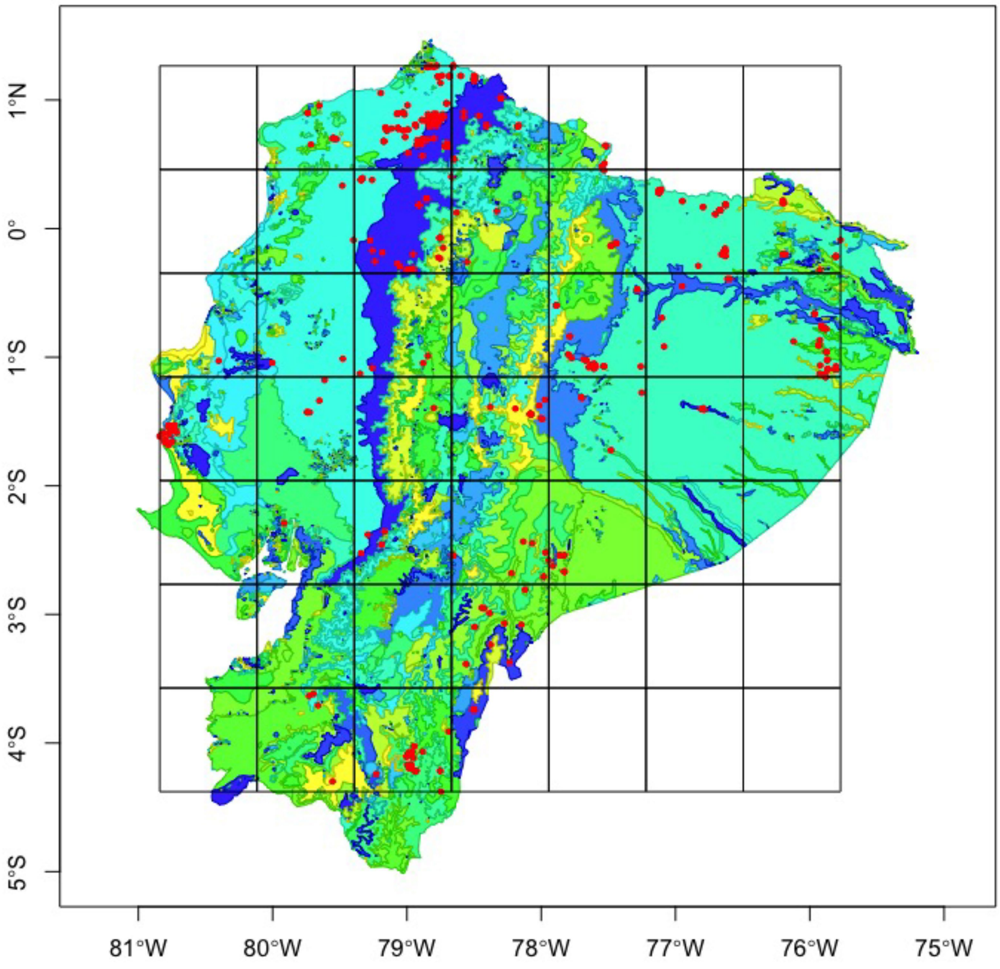

FIGURE 1
Dung beetle occurrence records (red) throughout Ecuador, fitted with a 64-bit grid to calculate taxonomic and functional beta diversity. Base map colors represent vegetation regimes.

TABLE 3 Predictor variables selected in the final distribution model for each tribe.

Tribe	Predictors	Error rate	AUC	Threshold
Canthonini	Elevation Annual precipitation Precipitation of coldest quarter	31.02%	0.73	0.40
Coprini	Elevation Precipitation of driest month Precipitation seasonality	30.88%	0.76	0.40
Phanaeini	Elevation Mean annual temperature	9.28%	0.97	0.31

Average error rate, AUC, and maximum accuracy threshold from five trials of model validation on a holdout data set are also shown.

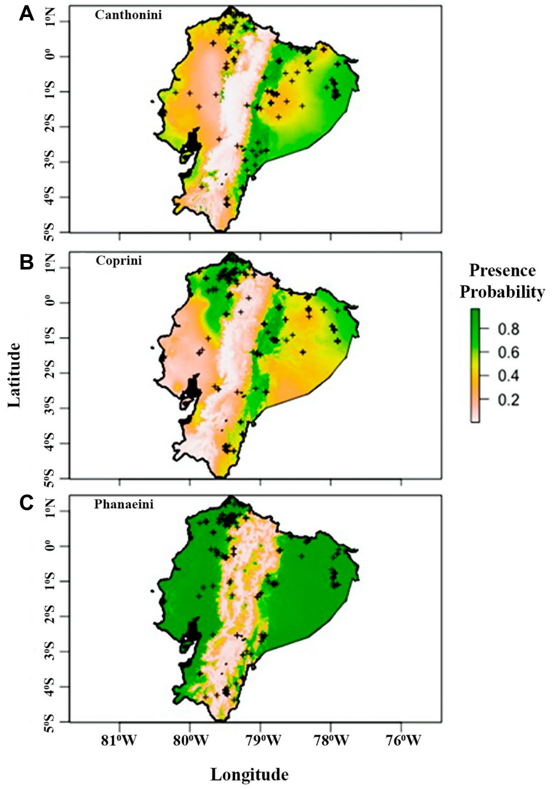

FIGURE 2
Predicted tribe distribution maps from logistic generalized linear models for Canthonini **(A)**, Coprini **(B)**, and Phanaeini **(C)** in Ecuador. Colors represent presence probability. Plus, signs represent presence data points.

(Supplementary Table S2) conceptualized as non-phylogenetic, aggregated units of species sharing an important ecological characteristic and playing an equivalent role in the community (Orfanidis et al., 2011), based on their feeding strategy (coprophagous, necrophagous, generalist), nesting behavior (paracoprid – tunnellers and telecoprid – ball-rollers), and size (big, medium, and small). Using the sf package (Pebesma, 2018), we created 20 different spatial grids, dividing the area of the total spatial extent by (x^2), where x equals two through 21 (Figure 1). The largest grid divided the total area of Ecuador into fourths, each 22,000 km^2, while the smallest grid had 256 cells of area 343.9 km^2. Alpha diversity was calculated as the number of species (taxonomic richness) and the number of functional groups (functional richness) present on each cell; while Beta diversity was calculated for each cell as the total number of species or functional groups present within the entire grid, divided by the species/functional group richness within a given cell, minus one (beta = gamma/richness – 1), following Whittaker (1960) approximation.

To compare the coastal and Amazonian regions, we subsetted the data from these two regions and repeated the above methodology for each using 15 different spatial grids with cell sizes from 5,264 km^2 down to 82.3 km^2. We then compared the coefficients from each linear model. To evaluate whether differences in beta diversity between the two regions was an artifact of differences in species richness between the two regions, we used a null model to compare the observed beta diversity to the expected beta diversity, given richness (Crist et al., 2003; Myers et al., 2013). The null model randomly sampled individuals from the regional species pool to fill each cell within the grid, while keeping the number of individuals sampled per cell equal to that observed and the number of records per species in the regional pool equal to that observed. We then compared the observed beta diversity values to the mean of 1000 iterations of the null model outputs and calculated p-values for each grid as the ratio of iterations with values less than the observed beta diversity value.

Results

Distribution modeling of dung beetle tribes

The probability of presence for each tribe is a function of the predictors specified in Tables 2 and 3, being elevation the most significant predictor variable in all three models. Canthonini presence varied as a function of elevation, annual precipitation, and precipitation of the coldest quarter and based on the tree model, all the precipitation variables worked as important predictor variables, with a 21% error rate predicting on a holdout dataset; its probability decreased as elevation increased, with a much more pronounced negative trend as annual rainfall increased, indicating the importance of the timing of precipitation for this tribe (Figure S5). Coprini presence increased slightly as elevation increased, precipitation of the driest month, and precipitation seasonality, and its classification tree suggested precipitation and seasonality as potentially important variables, with a 24% error rate predicting on a holdout dataset (Figure S6). Finally, Phanaeini presence varied as a function of elevation and

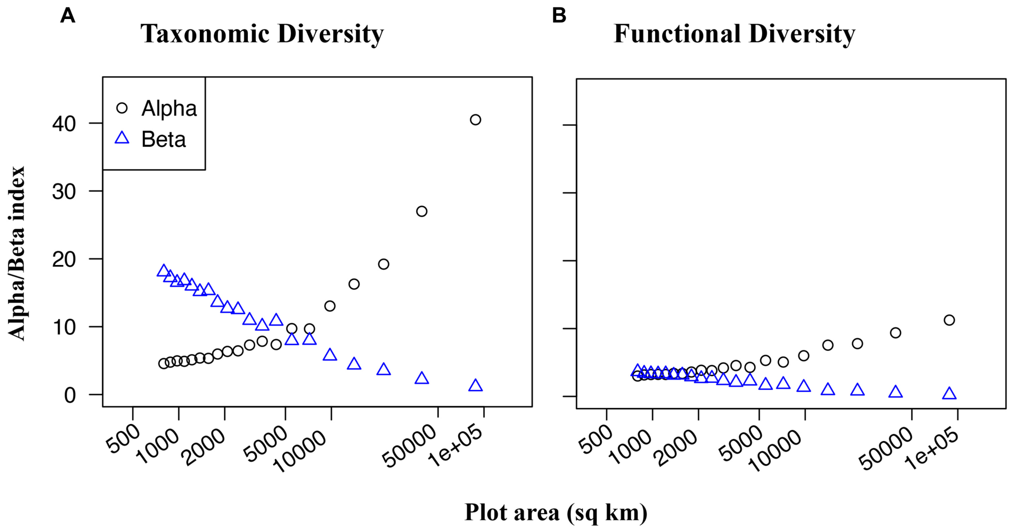

FIGURE 3
Taxonomic **(A)** and functional **(B)** alpha (black circles) and beta (blue triangles) diversity of dung beetles as a function of grain size. Plot area is the size of each grain within a grid, transformed with log base ten for visual examination. 20 grids of decreasing grain size were used, ranging from a 4-bit grid with 22,000 sq km cells, to a 256-bit grid with 344 sq km cells.

mean annual temperature. The probability of Phanaeini presence increased with mean annual temperature but decreased as elevation increased with the classification tree suggesting elevation, mean annual temperature, and precipitation of the wettest month as potentially important variables, with a 5% error rate predicting on a holdout dataset (Figure S7).

The distribution model for the Phanaeini tribe performed significantly better than the final distribution models for Canthonini and Coprini (Table 3). The average error rate from five trials of validating the last models on a holdout dataset was 31.02% for Canthonini, 30.88% for Coprini, and 9.28% for Phanaeini. These error rates are based on average threshold values for each tribe of 0.40 for Canthonini, 0.40 for Coprini, and 0.31 for Phanaeini. The threshold values used were optimized to maximize accuracy in each trial while minimizing false positives and negatives. To evaluate each model with a threshold-independent metric, we used the area under the receiver operating curve (AUC), representing the tradeoff between true positives and false positives. The average AUC for five holdout validation trials were 0.73, 0.76, and 0.97, respectively. Therefore, the Phanaeini distribution model is significantly better at predicting dung beetle presence throughout Ecuador compared to the final Canthonini and Coprini models (Figure 2).

Alpha and beta diversity analyses – Comparing functional and taxonomic diversity

Over the scope of Ecuador, taxonomic beta diversity (species turnover) had an inverse relationship to taxonomic alpha diversity (species richness) (Figure 3A), such that at smaller spatial scales, the rate of species turnover among plots was much higher than the mean species richness of any individual plot. Functional beta diversity (functional turnover) also increased as plot size decreased (Figure 3B), however, unlike with taxonomic turnover, functional turnover was only marginally greater than functional richness at small spatial scales. In other words, even at small spatial scales, there was low variation of functional groups among plots.

Beta diversity analyses – Comparing the coast and Amazonia regions

In this dataset, 72 species of dung beetle from 287 observations were recorded in Amazonia, and 38 species from 291 observations were recorded in the coastal region. Out of the 14 identified functional groups, all 14 were represented in Amazonia and 12 were represented in the coastal region. Taxonomic beta diversity was higher in Amazonia compared to the coast (Figure 4A) while functional beta diversity did not differ between the two regions (Figure 4B). Taxonomic beta diversity levels in Amazonia were in line with what null model analysis predicted based on the region's species richness: the higher levels of taxonomic turnover in Amazonia compared to the coast can be largely attributed to higher species richness in Amazonia (Figure S8A). However, taxonomic beta diversity levels from the coastal region were significantly lower than expected based on the null model in 9 out of the 15 grids and marginally lower in 11 out of 15 grids (Figure S8B). Thus, while some of the divergence in

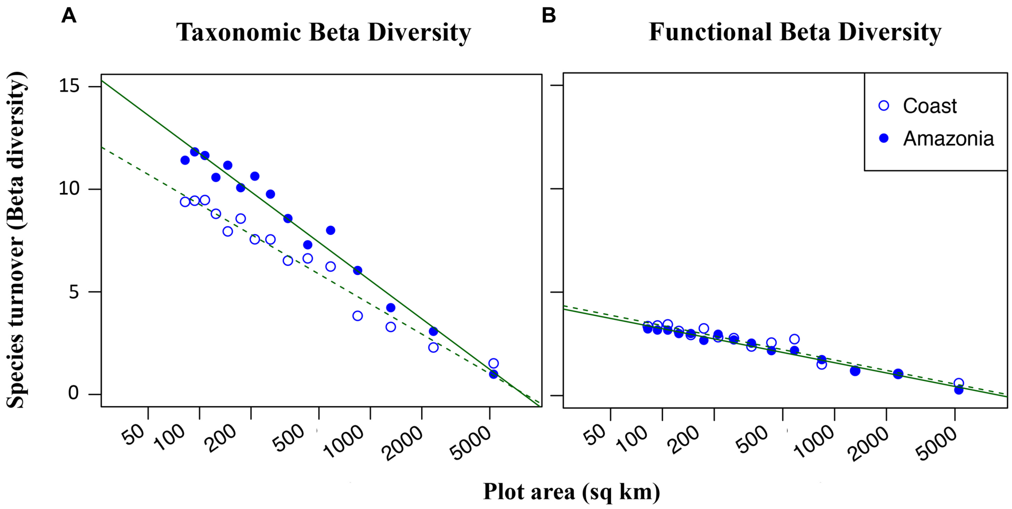

FIGURE 4
Taxonomic **(A)** and functional **(B)** beta diversity as a function of log grain size. At smaller spatial scales, dung beetle beta diversity in Northern Ecuador is higher in the Amazon (closed circles) than in the coastal region (open circles). Functional beta diversity shows equal dependence on grain size in both regions.

taxonomic beta diversity between the two regions is an artifact of differences in species richness in Amazonia versus the coast, the distinction is also due to nonrandomly low taxonomic beta diversity levels in the coastal region. Functional beta diversity did not significantly differ from the null expectation in either region.

Discussion

Distribution modeling of dung beetle tribes

Precipitation and elevation were consistently significant for predicting presence of Canthonini and Coprini, while the temperature was more important for predicting presence of Phanaeini in Ecuador. These climatic distribution patterns of dung beetle taxa reflect historical and current ecological influences, where tribes are correlated to a combination of tropical climate types (Davis et al., 2002). Despite broad limitations to dung beetle diversity associated with annual temperatures below 15°C, and annual rainfall below 250 mm (Halffter, 1991; Espinoza, 2018), taxa distribution models reveal taxa-specific climatic niches, with some taxa exhibiting narrower climatic preferences and consequently more distribution-limited than others. The probability of Canthonini presence decreased with increasing elevation, with a much more pronounced negative trend as annual rainfall increased. Despite these trends, the probability of Canthonini presence increased as the precipitation of the coldest quarter increased, indicating the importance of the timing of precipitation for this tribe. In contrast to Coprini presence increased slightly as elevation augmented, with a stronger positive trend as precipitation of the driest month increased. Furthermore, Coprini presence also increased as precipitation seasonality increased. Phanaeini had a much higher probability of occurrence across much of Ecuador, exhibiting a more generalized climatic niche. The probability of Phanaeini presence increased with mean annual temperature and decreased as elevation increased.

Furthermore, Coprini presence also increased as precipitation seasonality increased. Phanaeini had a much higher probability of occurrence across much of Ecuador, exhibiting a more generalized climatic niche. The probability of Phanaeini presence increased with mean annual temperature and decreased as elevation increased.

Our results suggest that dung beetles were not frequently found in areas above 2000 m, consistent with Halffter (1991) and Espinoza (2018), who emphasizes that dung beetles are well adapted to climatic regions which are warmer and moister than those found at high elevations (Figure 2). Specifically, dung beetles in Ecuador are unlikely to be found in the High Andes, where climatic conditions get colder and have low atmospheric pressure, where only few a species like *Dichotomius cotopaxi*, can tolerate elevations above 2,500 m (Villamarín-Cortez, 2010, 2013; Carvajal et al., 2011).

All tribes analyzed are well distributed throughout the Neotropics and are expected to be found in areas where environmental conditions are favorable to their survival, especially the Coast and Amazonia, consistent with our distribution predictions. These regions have an appropriate environment for dung beetles to accomplish their life cycle. For example, the Coast has the most fertile and productive land, along with a tropical climate and a mean temperature of

25°C (77°F). Amazonia, in contrast, has less productive soil but is comprised mainly of rainforest, with a mean temperature of 23–25°C. Despite known temperature limitations, tribes were most strongly correlated to both rainfall (Walter and Lieth, 1964; Noriega et al., 2015) and elevation (Espinoza, 2018), which may reflect past Cenozoic dispersal patterns into northern regions when their climates were warmer (Laporte and Zihlman, 1983; Parrish, 1987; Carvajal et al., 2011), these different climate conditions have helped dung beetles to evolve and survive since the megafauna extinction and Pleistocene climate oscillations (Maldaner et al., 2021). Nevertheless, these regions and ecosystems have changed drastically, due to the expansion of the agricultural border, such activities reflect deep modifications in dung beetle assemblage composition, mainly because they are a very sensitive group to even low-intensity habitat modification (Bicknell et al., 2014) While our results suggest differences in climatic niche breadth for the three taxa, it is important to recognize the limitations of the distribution models presented here, specifically, the lack of true absence data and the importance of species interactions and finer scale resource limitations in moderating habitat use and distributions. However, this broad scale understanding of taxa distribution and climatic preferences aids our understanding of potential climate change impacts and helps identify critical habitat for dung beetle diversity from Ecuador.

Beta diversity patterns

Taxonomic beta diversity (species turnover) was more sensitive to spatial scale than functional beta diversity (functional group turnover) in assemblages of dung beetles throughout Ecuador (Figure 3). When plot size was decreased, species turnover increased at a greater rate compared to functional group turnover. In other words, plots were more likely to contain distinct species of beetle, but not necessarily distinct functional groups. This pattern signifies that a few key functional groups are present in most habitats, but that these functional roles are often filled by unique species. The presence of many functionally redundant species suggests that dispersal limitation may structure dung beetle communities in Ecuador. When species are dispersal limited, communities often become spatially heterogeneous through ecological or evolutionary drift (Baur, 2014), which creates high taxonomic beta diversity. However, it is also possible that the functional groups that we have delineated, which are based on size, feeding strategy, and nesting behavior, do not capture critical traits that distinguish a species' ability to survive in a particular habitat or community. Additionally, while this analysis considered an array of spatial scales, all were above 80 km^2. Taxonomic and functional beta diversities may perform differently at smaller scales, where dispersal is likely to be less limiting.

According to our findings, taxonomic and functional beta diversity was higher in the Amazon basin compared to the coastal region. This may be due to the higher rate of dung production in Amazonia, which is known to influence dung beetles' abundance and diversity (Campos and Hernández, 2013, da Silva and Hernandez, 2014, Silva and Hernández, 2015, Silva and Hernández, 2016). The physical structure of the forest floor, which is influenced by leaf litter, can affect the nesting activities of certain dung beetles' guilds such as rollers (Nichols et al., 2008). Roller dung beetles roll food resources several meters away from their source until they find an adequate place to bury them. This behavior helps them escape high competition on ephemeral resources such as dung and carrion. In contrast, we see lower levels of species heterogeneity in the Coast. We expected the drier climate in this region to reduce the diversity of dung beetle nesting behaviors found in Amazonia. However, surprisingly, the two regions contained a similar number of functional groups (12 in the coast and 14 in Amazonia) and, furthermore, functional beta diversity responded to spatial scale equally in both regions (Figure 4B). This suggests that ecological drift and dispersal limitation, affect taxonomic diversity more than functional diversity, may play large roles in maintaining high species richness in the Amazonian region. While deterministic factors such as niche partitioning certainly must also be at play, the similarity of functional beta diversity between the coast and Amazonia suggests that stochastic processes are more responsible for the maintenance of species diversity in the Amazon.

In the context of threats due to land use, our results demonstrate the necessity of conserving landscapes across a wide variety of environmental gradients to respond to beetle diversity. Dung beetle communities can be sensitive to habitat change and it is common to see the reduction in diversity and compositional changes in degraded habitats (Nichols et al., 2007; Solar et al., 2016). Our results suggest that habitat changes primarily drive these responses to the microclimate and vegetation composition and structure. The high levels of taxonomic beta diversity at small spatial scales suggests that the amazon maintains a high species richness by having higher species turnover, especially because vegetation is well preserved, maintaining good soil conditions, augmenting successful breeding and manure burial (Maldonado et al., 2019), which are essential for dung beetle survival.

Our results provide an essential framework for evaluating potential dung beetle habitat and diversity at different scales. Overall, our results are consistent with the knowledge of dung beetle biological and ecological requirements, and provides a country-wide analysis of Canthonini, Coprini, and Phanaeini dung beetle tribes distribution and diversity. Therefore, by identifying dung beetles' diversity, combined with considerations of habitat fragmentation, human land-use alteration, and climate change, will be an important next step to inform better and prioritize dung beetle conservation efforts in other countries.

Data availability statement

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

Author contributions

SV-C: study concept and design. SV-C, LH, SC, and JM: analysis, interpretation of data, and statistical analysis. SV-C, LH, SC, JM, and JN: drafting of the manuscript. All authors contributed to the article and approved the submitted version.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

Supplementary material

The Supplementary material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2022.1008477/full#supplementary-material

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Effects of dung beetle activity on tropical forest plants

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Dung beetles are recognized as providers of important ecosystem functions, most of which are derived from the removal of vertebrate dung from the soil surface. These insects occur in nearly all terrestrial biomes but are most diverse in the humid tropics. Several of the ecological functions attributed to dung beetles are related to their direct and indirect interactions with plants. Among these functions, the secondary dispersal of seeds defecated by mammals has received the most attention in tropical forests. Nonetheless, while several aspects of secondary seed dispersal by dung beetles are relatively well understood, others remain understudied or have not been addressed at all. Thus, a broad generalization about the effects of secondary seed dispersal by dung beetles on plant fitness remains somewhat elusive. Furthermore, other effects of dung beetle activity on tropical plants have received very little attention. A few studies have shown that through their behaviors of dung burial and soil-excavation, dung beetles can shape seed bank structure and dynamics. Also, though numerous greenhouse studies and field experiments in agricultural lands and temperate grasslands have shown that dung beetle activity increases plant nutrient uptake and yield, it is uncertain whether such effects are common in tropical forests. Here, we review and synthesize our current knowledge on how dung beetles affect tropical forest plants by dispersing defecated seeds, shaping the structure and dynamics of seed banks, and influencing the performance of understory seedlings. We focus on the Neotropics, where most studies on the effects of dung beetles on tropical forest plants have been carried out, but we also show results from other regions and biomes, to present a more general picture of these beetle-plant interactions. Throughout the review we emphasize aspects that need more research to allow generalizations and point out those questions that remain unanswered. We hope that this review will stimulate more research about the fascinating interactions between dung beetles and plants in tropical ecosystems.

KEYWORDS

bioturbation, ecological functions, secondary seed dispersal, seed bank, seedlings, Scarabaeinae, soil conditioning

Introduction

Dung beetles are conspicuous insects found in terrestrial ecosystems of all continents, except Antarctica (Hanski and Cambefort, 1991). Adults and larval beetles feed on animal feces, preferring the dung of mammals. Through their feeding and nesting behaviors, most dung beetle species remove feces from the surface and incorporate it into the soil. The ecological consequences of this activity are manyfold, from soil conditioning and increased plant yield, to livestock parasite control and secondary seed dispersal, among others (Nichols et al., 2008; Scholtz et al., 2009). Dung beetle communities reach their highest abundance and diversity in tropical forests and savannas, where the mammal faunas that provide their main food resource also display their highest richness and biomass (Hanski and Cambefort, 1991). Because several of the ecological functions attributed to dung beetles can affect plants, it is believed that these insects can play an important role in structuring tropical plant communities (Andresen and Feer, 2005). However, except for the secondary dispersal of seeds defecated by mammals, most studies quantifying the effects of dung beetle activity on plants have been carried out in productive systems and/or temperate regions and have mostly focused on aspects related to soil conditioning (Nichols et al., 2008; Scholtz et al., 2009). The lack of empirical evidence often leads to the assumption that effects of dung beetles measured in other study systems (e.g., greenhouse experiment on temperate grasses) can be extrapolated to natural conditions in tropical forests. However, such an assumption is not justified because the effects of dung beetle activity on plants are context dependent (Slade et al., 2011; Griffiths et al., 2016; Urrea-Galeano et al., 2021).

Dung beetle functions performed at any given site depend on the composition of the local dung beetle community, which varies strongly among ecosystems, regions, and continents (Hanski and Cambefort, 1991), as well as the type and degree of habitat disturbance (Fuzessy et al., 2021a; López-Bedoya et al., 2022). Most tropical dung beetle species belong to the subfamily Scarabaeinae (often referred to as the 'true dung beetles'), although other dung-feeding beetle taxa (Aphodiinae, Geotrupidae) are important in other bioregions (Scholtz et al., 2009). Furthermore, dung beetle species vary in their nesting, feeding, and dung-relocating behaviors (Halffter and Edmonds, 1982), which also affects their functional impact in ecosystems. Though definitions can vary according to authors (Tonelli, 2021), three general behavioral groups are distinguished: (i) dwellers (including both non-nesting species as well as endocoprid nesters) use the dung directly at the source; (ii) rollers relocate dung portions by rolling them away from the source and then burying them in underground tunnels and chambers; and (iii) tunnellers or burrowers relocate dung portions underneath or very close to the dung source, also into underground tunnels and chambers. Most tropical dung beetles are rollers and tunnellers.

Through the burial of dung in underground tunnels, dung beetles can have direct or indirect interactions with plants. Direct interactions occur through the fortuitous manipulation of seeds that are imbedded in dung or in the soil. On the other hand, indirect interactions between beetles and plants, are those driven by the changes that beetle activity can cause in the biological, chemical and/or physical properties of the soil. In some rare cases dung beetles can also have effects that are not a consequence of their dung-relocation behavior, including the pollination of plant species with decay-scented flowers (Nichols et al., 2008), and the use of acorns as food/nesting resource (i.e., seed predation or seed dispersal when the embryo is not killed; Pérez-Ramos et al., 2007, 2013). In this review, we focus only on the effects that are derived from the dung-relocation activity of dung beetles (Figure 1; Table 1), because they are the most widespread. First, we review the secondary dispersal of seeds imbedded in dung (Secondary seed dispersal), which is the ecological function of dung beetles that has received the most attention in tropical forests, particularly in the Neotropics. Then, we present the findings of those few studies that have addressed the effects that dung beetles can have on the structure and dynamics of tropical soil seed banks (Seed banks). Finally, we evaluate our knowledge about the indirect effects of dung beetle activity on plant nutrient uptake and performance in tropical forests (Plant performance). The aims of this review are to present a concise synthesis of our understanding about these three interactions between dung beetles and tropical forest plants, to point out research gaps, to discuss some methodological aspects, and to encourage researchers to critically question and assess whether the functions of dung beetles can be extrapolated among different study systems.

Secondary seed dispersal

Secondary seed dispersal by dung beetles occurs when they move seeds that have been defecated by a fruit-eating vertebrate (i.e., the primary disperser). Beetles are attracted to the defecations and when they relocate portions of it, seeds present in the dung are incidentally relocated as well. From the beetles' perspective, seeds are useless 'contaminants'; thus, they may exclude seeds prior or during dung-relocation. Seeds dispersed by beetles may be buried by them (vertical dispersal) and may be moved some horizontal distance away from the site of deposition (horizontal dispersal). One or both movements can occur and can have consequences for seed fate. Secondary seed dispersal by dung beetles was initially reported in a greenhouse experiment, in which burial of seed-containing cattle dung by dung beetles promoted seedling establishment of a temperate prairie grass (Wicklow et al., 1984). A few years later, the first field study quantifying some aspects of secondary seed dispersal by dung beetles in a tropical forest was published (Estrada and Coates-Estrada, 1986, 1991), and seven years elapsed before the next study (Shepherd and Chapman, 1998). Since then, the publication stream has been steady, though modest, yielding a total of 71 articles (not including reviews) worldwide between 1984 and June 2022, which assess some aspect of secondary seed dispersal by dung beetles, 83% of them in tropical biomes (Figure 2).

Why did secondary seed dispersal by dung beetles catch the interest of tropical ecologists in the 90s? The following lines of

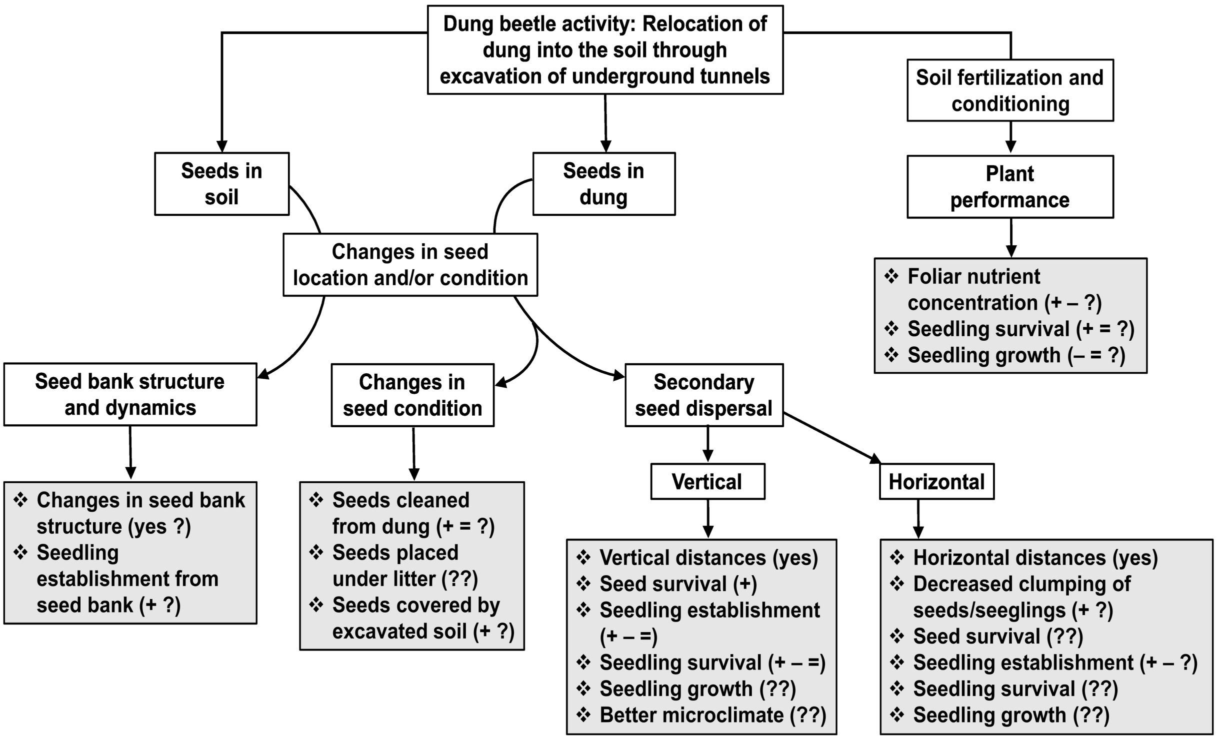

FIGURE 1
Flowchart showing the consequences that dung beetle activity can have on plants that are reviewed in this article (Secondary seed dispersal; Seed banks; and Plant performance). The activity of dung beetles that we focus on, is the relocation of animal feces (mostly mammal dung) from the soil surface into deeper soil layers, which in turn occurs through the excavation of soil to build underground tunnels and chambers for feeding and nesting. The consequences for plants result from a direct interaction between dung beetles and seeds (seeds in dung and seeds in soil), and from an indirect interaction between beetles and plants, which is mediated through soil fertilization and conditioning. Grey boxes show specific responses that have been measured (those followed by "yes", "+", "–", and/or "="), or have been suggested to occur. Signs indicate positive (+), negative (–), and no effect (=) of dung beetles reported for each of the responses; question marks indicate that a response has been little studied (?), or not at all (??). Studies that have assessed one or more of these responses are shown in Table 1. For secondary seed dispersal, information for specific plant species can be found in Supplementary Table S1.

ecological evidence had to align for this to occur: (i) that the great majority of tropical woody plants depend on frugivorous birds and mammals for primary seed dispersal (Howe and Smallwood, 1982); (ii) that the effectiveness of a primary disperser depends not only on the quantity of seeds dispersed, but also on the quality of dispersal, which is related to how seeds are handled and deposited (Schupp, 1993); (iii) that it is necessary to assess post-dispersal seed fate to determine seed dispersal quality and have a better understanding of the seed dispersal process (Chapman, 1989); and (iv) that the dung surrounding seeds dispersed by mammals can affect post-dispersal seed fate by attracting rodent seed predators (Janzen, 1982) and dung beetles (Estrada and Coates-Estrada, 1986). Thus, it was realized that dung beetles processing the feces of mammalian frugivores were likely to affect the post-dispersal fate of defecated seeds, and therefore seed dispersal effectiveness. Indeed, the mammal-seed-beetle interaction was defined by Vander Wall and Longland (2004) as a 'diplochory', i.e., a system in which the primary and secondary dispersal vectors are different (i.e., mammal and dung beetle, respectively), and often confer different advantages to the plant. According to these authors, while the mammal allows the seed to escape an area of low survival probability near the parent plant, the dung beetles move the seeds deterministically to microsites that favor seed fate (i.e., respectively 'Escape Hypothesis' and 'Directed Dispersal Hypothesis' *sensu* Howe and Smallwood, 1982).

Almost two decades ago, a first review on secondary seed dispersal by dung beetles synthesized our initial understanding of this interaction and pointed out many research gaps (Andresen and Feer, 2005). A few years later, two publications that reviewed the ecological functions of dung beetles, also included accounts on secondary seed dispersal (Nichols et al., 2008; Scholtz et al., 2009). Since then, many more studies have assessed different aspects of secondary seed dispersal by dung beetles. In the next subsections we try to summarize old and new insights about this plant–animal interaction. First, we review the factors that determine whether and how a seed is secondarily dispersed by dung beetles. Second, we present an overview of the consequences of secondary seed dispersal by beetles for plants and discuss to what extent they can be generalized. Third, we describe how secondary seed dispersal is currently often included in sampling protocols of applied biodiversity conservation research that uses dung beetles as a focal taxon. Throughout the text, we point out how methodological choices may affect the results we obtain when quantifying secondary seed dispersal by dung beetles.

TABLE 1 List of publications (excluding reviews) that include information on the effects of dung beetle activity on plants in three realms: Neotropical, Paleotropical, and Extratropical.

Topic	Neotropical	Paleotropical	Extratropical
(A) SSD: predictors			
Seed size	1,2,3,4,8,9,11[b],12,13,18,21,23[b],24,25[b],29,31,32,34,35,36[b],37,41[b],43,44,46,48[b],49[b],56,76,79,86	52,57,85,89[b],90[b]	72,73,75,88
Other seed traits	12,18,44	--	--
Seed density	10,16,18,22,33	--	--
Beetle traits/species	1,2,3,4,8,9,24,25,44,46,79	--	80[a],82[a],87
Beetle community attributes	7,11,23,25[b],28,29,34,36, 41[b],46,47[b],49[b],91[b]	81[b],85	66,72,73,75
Dung amount	2,5,9,10,13,16,18,25[b],33	--	--
Dung type	15,16,17,18,21,32,33,86	--	66,72
Dung removal	7[b],23[b],24,34,36[b],41[b],48[b], 49[b]	55,81[b],90[b]	73,80[a],92
Defecation pattern	10,14,15,17,20,24,38,43	55	77[a],92
Time of day/season/year	6,9,16,18,33,42[b]	53	73,75,88,92
Habitat type/environment	28,32,34,47[b],79	53,55,57	66,69,72,73
Habitat disturbance	7[b],11[b],18,19[b],21,23[b],25[b], 33,36[b],38,41[b],42[b],47[b], 48[b],49[b],91[b]	81[b],89[b],90[b]	69,88
(B) SSD: consequences			
Seed survival	1,2,3,5,6,7[b],13,17,21,27,32,33,38,76,86	52,53,54	69,87
Seed/seedling aggregation	22,40	--	--
Seedling establishment	1,3,5,6,7[b],11[b],13,21,22,27, 29,33,40,47[b],76,86[a]	52,53,54,55	66,67[a],69,80[a],87[a],92
Seedling survival	7[b],27,29,33	53	--
(C) Seed banks			
Structure	24	--	--
Movement of seeds	26,36[b],39	--	--
Seedling establishment	26,35,39	--	--
(D) Plant performance			
Chemical composition	30,45,50[ac]	59[ac]	58[ac],63[ac],64[ac],68[ac],70[c], 71,83[ac],84[c]
Survival	30,45	--	68[a]
Growth/allocation	30,45,50[ac],51[ac]	59[ac],60	58[ac],61,62,63[ac],64[ac],65, 68[ac],70[ac],71,74[c],78,83[ac],84[c]

Publications are organized into four main topics, according to the information that readers can find in them: **(A)** predictor variables affecting secondary dispersal of defecated seeds (SSD) by dung beetles; **(B)** consequences for plant fitness of secondary seed dispersal by dung beetles, **(C)** effects of dung beetles on soil seed banks; **(D)** effects of dung beetles on plant performance. Each topic has several sub-topics that correspond to specific variables included in the studies. Two dashes (--) indicate lack of published studies for a sub-topic. [a] Data obtained under highly controlled conditions (e.g., greenhouse). [b] Studies using dung beetles as a focal taxon in applied biodiversity conservation research. [c] Data for plants of productive interest (e.g., crops, livestock pastures). This table does not include studies on pollination, dispersal of seeds that mimic the odor of dung, or dispersal of seeds that are used as food; however, these studies are mentioned in the text.

1 Estrada and Coates-Estrada (1991); 2 Andresen (1999); 3 Feer (1999); 4 Vulinec (2000); 5 Andresen (2001); 6 Feer et al. (2001); 7 Hingrat and Feer (2002); 8 Vulinec (2002); 9 Andresen (2002a); 10 Andresen (2002b); 11 Andresen (2003); 12 Vulinec et al. (2003); 13 Andresen and Levey (2004); 14 Wehncke and Dalling (2005); 15 Ponce-Santizo et al. (2006); 16 Culot et al. (2009); 17 Santos-Heredia et al. (2010); 18 Culot et al. (2011); 19 Giraldo et al. (2011); 20 Muñoz-Lazo et al. (2011); 21 Santos-Heredia et al. (2011); 22 Lawson et al. (2012); 23 Braga et al. (2013); 24 Feer et al. (2013); 25 Nichols et al. (2013); 26 Santos-Heredia and Andresen (2014); 27 Culot et al. (2015); 28 Griffiths et al. (2015); 29 Griffiths et al. (2016); 30 Santos-Heredia et al. (2016); 31 Braga et al. (2017); 32 Lugon et al. (2017); 33 Culot et al. (2018); 34 Nunes et al. (2018); 35 Ocampo-Castillo and Andresen (2018); 36 Santos-Heredia et al. (2018); 37 Genes et al. (2018); 38 Zárate et al. (2019); 39 Urrea-Galeano et al. (2019b); 40 Urrea-Galeano et al. (2019a); 41 Carvalho et al. (2020); 42 França et al. (2020); 43 Fuzessy et al. (2021b); 44 Pedersen and Blüthgen (2022); 45 Urrea-Galeano et al. (2021); 46 Morales-Alba et al. (2022); 47 Almeida et al. (2021); 48 Oliveira et al. (2021); 49 Arias-Álvarez et al. (2022); 50 Miranda et al. (1998); 51 Barragán et al. (2022); 52 Shepherd and Chapman (1998); 53 Balcomb and Chapman (2003); 54 Beaune et al. (2012); 55 Petre et al. (2015); 56 Stanbrook et al. (2017); 57 Kunz and Krell (2011); 58 Bang et al. (2005); 59 Badenhorst et al. (2018); 60 Howison et al. (2016); 61 Wu et al. (2015); 62 Wu et al. (2014); 63 Kaleri et al. (2020); 64 Kaleri et al. (2021); 65 Xie et al. (2021); 66 D'hondt et al. (2008); 67 Wicklow et al. (1984); 68 Macqueen and Beirne (1975); 69 Leiva and Sobrino-Mengual (2022); 70 Slade et al. (2017); 71 Nervo et al. (2017); 72 Milotić et al. (2017); 73 Milotić et al. (2019); 74 Slade and Roslin (2016); 75 Ardali et al. (2016); 76 Estrada and Coates-Estrada (1986); 77 Verdú et al. (2009); 78 Borghesio et al. (1999); 79 Niero et al. (2022); 80 deCastro-Arrazola et al. (2020); 81 Derhé et al. (2016); 82 Manns et al. (2020); 83 Bornemissza and Williams (1970); 84 Johnson et al. (2016); 85 Slade et al. (2007); 86 Landim et al. (2022); 87 Koike et al. (2012); 88 Enari and Sakamaki-Enari (2014); 89 Hosaka et al. (2014); 90 Slade et al. (2011); 91 Gómez-Cifuentes et al. (2020); 92 Ishikawa (2011).

Factors influencing secondary seed dispersal by dung beetles

There is tremendous variation in the patterns of secondary seed dispersal by dung beetles: (i) all or none of the seeds in a defecation may be relocated by dung beetles, with all the possibilities in between (Andresen and Feer, 2005); (ii) most seeds buried by beetles are found at depths ≤ 10 cm, but some may be buried as deeply as 40 cm (Griffiths et al., 2015); (iii) most seeds are moved short horizontal distances (≤ 50 cm), but some can be moved a few meters in tropical forests (e.g., Estrada and Coates-Estrada, 1991) and up to 20 m in African savannas (Kunz and Krell, 2011). Also, while some of the seeds dispersed vertically remain inside the dung portions buried by beetles, others

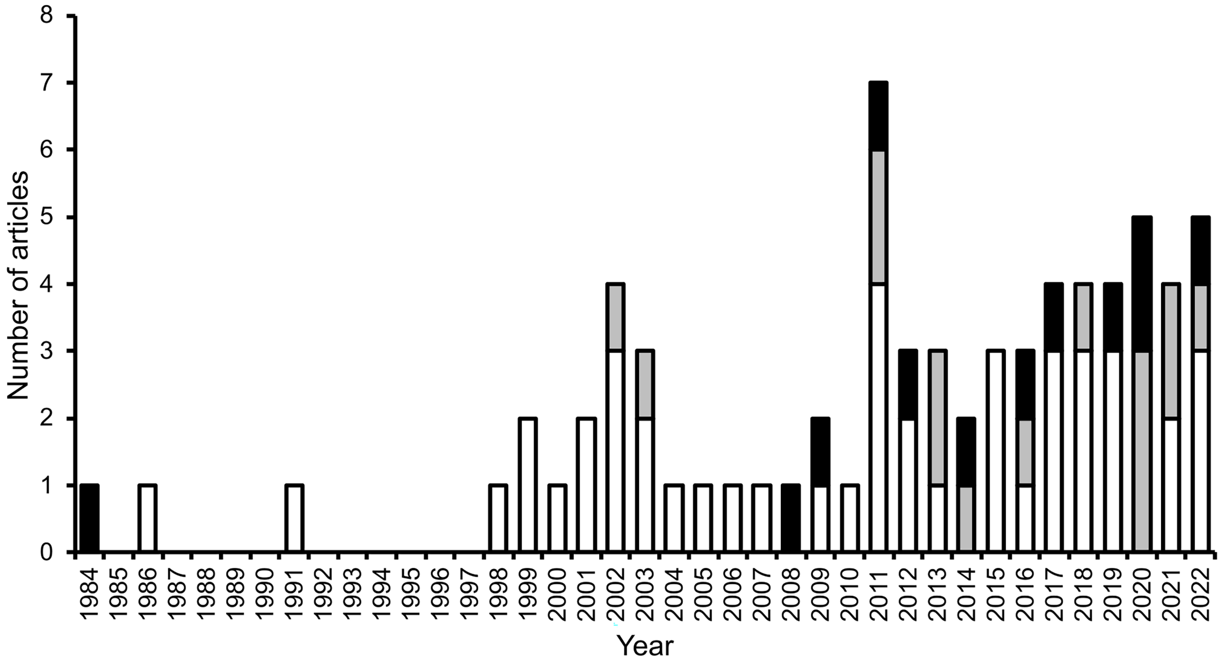

FIGURE 2
Number of scientific articles (excluding reviews) published per year, which include information on some aspect related to the secondary dispersal by dung beetles of seeds embedded in the feces of vertebrates (mostly mammal dung), in tropical (white and grey bars) and extratropical biomes (black bars). Grey bars represent studies that use dung beetles as a focal taxon in applied biodiversity conservation research (all carried out in the tropics; see Biodiversity studies using dung beetles as a focal taxon).

(particularly larger seeds) are excluded from the dung portions at some point during burial (Andresen and Feer, 2005; Stanbrook et al., 2017).

Many factors can influence if and how a defecated seed is secondarily dispersed by beetles. Some of these have been assessed often, while others only a few times (Table 1A). It is important to mention that all studies quantify the vertical dispersal of seeds (i.e., seed burial), but fewer quantify horizontal dispersal. Also, we want to point out that in experiments that only aim to measure the probability and distances of seed movement without determining the subsequent fate of those seeds (i.e., whether they die, germinate, or establish as seedlings), it is very common to use seed mimics (Andresen, 2002a). Seed mimics are usually plastic beads, though other types of mimics can also be used. Dung beetles show the same behavior towards all dung 'contaminants', be they real or artificial seeds. Using seed mimics has many methodological advantages for assessing secondary seed dispersal by dung beetles: they are not removed by granivorous animals; their characteristics, such as size and shape, can be controlled; large numbers can be deployed; they can be reused etc. However, since measuring the fate of seeds dispersed by beetles is necessary to determine if secondary seed dispersal has a positive effect on plant fitness or not (see next section), the usefulness of seed mimics is limited.

Two of the factors that most consistently affect secondary seed dispersal by dung beetles are seed size and beetle size. The relationships are driven by the facts that seeds are dung contaminants from the beetle's perspective and that larger beetles relocate larger portions of dung. Thus, secondary seed dispersal by dung beetles is negatively related to seed size, and positively related to beetle size. In other words: smaller seeds are relocated more often, more deeply, and to larger horizontal distances, than larger seeds, and seeds have a higher chance of being secondarily dispersed when handled by larger beetles. However, some exceptions occur, as not all studies have found an effect of seed size (e.g., no effect of seed size on burial probability: Culot et al., 2011; no effect of seed size on all secondary seed dispersal variables: Hosaka et al., 2014; no effect of seed size on burial depth: Andresen and Levey, 2004). Exceptions are probably due to methodological aspects, such as the range of seed sizes used in studies, relative to the size distribution of the beetles at the study site. One study determined that the maximum seed size that is dispersed by beetles approximates the beetle's body length (Pedersen and Blüthgen, 2022). So, for example, if in a study all seed sizes used are smaller or larger than the largest beetles, an effect of seed size on secondary seed dispersal might be more difficult to detect or non-existent. What is important, however, is that researchers choose seed sizes that are realistic (e.g., dung beetles are likely to encounter them in vertebrate's feces in their study site) and that allow them to answer their research questions. Also, one must consider that even for seeds of the same size variability in dispersal probabilities and distances can be very high, and thus large sample sizes are necessary to statistically confirm biological trends.

Other seed characteristics, aside from seed size, may also affect secondary seed dispersal, but evidence is scant. For example, one study found that spherical seeds are more likely to be buried by beetles than elongated ones (Culot et al., 2011), but two other studies found no effect of seed shape (Vulinec et al., 2003; Pedersen and Blüthgen, 2022). Additionally, one study found that large pubescent seeds are more likely to be incorporated into the dung portions relocated by beetles than large seeds that are smooth (Pedersen and Blüthgen, 2022). The latter relationship is explained by the fact that dung is more likely to stay attached on the surface of pubescent seeds. Indeed, the authors found that very large pubescent seeds with a thin layer of feces on their surface are seemingly mistaken by dung beetles to be piles of dung and buried as such. Such 'secondary seed dispersal by mistake' had also previously been reported in African savannas (Kunz and Krell, 2011). But the 'ultimate deception' occurs in at least two plant species of the South African fynbos, which have dung-smelling seeds that emit volatiles found in herbivore feces (Midgley et al., 2015, 2021). These seeds, without having been defecated by any frugivore, attract dung beetles that roll and bury them, to later abandon them when the deception is discovered. For these seeds, dung beetles are acting as primary dispersers of fallen seeds (*sensu* Vander Wall et al., 2005), rather than secondary seed dispersers. We do not yet know if secondary seed dispersal by mistake and/or primary seed dispersal through fecal mimicry are common in certain ecosystems and/or plant taxa.

As with seed traits, other dung beetle traits aside from size can also influence secondary seed dispersal. One trait that has received relatively more attention is the nesting and dung-relocation behavior of beetles (see Introduction). In general, it is considered that dwellers do not play a role in secondary seed dispersal of defecated seeds, that tunnellers bury more seeds than rollers, and that rollers are more likely to move seeds to greater horizontal distances than tunnellers (Andresen and Feer, 2005). It is also argued that rollers are more selective than tunnellers of similar size, i.e., they tend to exclude larger seeds from the dung portion they relocate more often than tunnellers (Feer et al., 2013). While these broad patterns are likely accurate, we are probably still missing much detailed knowledge, considering that beetle nesting and dung-relocation behaviors can vary tremendously among species within each of the three general behavioral categories (Halffter and Edmonds, 1982; Hanski and Cambefort, 1991). For example, beetles of the Neotropical genus *Eurysternus*, which technically belong to the rollers, are sometimes considered functional dwellers (e.g., Feer et al., 2013; Griffiths et al., 2016). The truth is, that beetles in this genus, which can be very abundant, process dung very differently from rollers and dwellers, as they relocate dung balls just underneath the dung source (Halffter and Edmonds, 1982). Thus, these beetles, which have been classified as marginally or not at all involved in secondary seed dispersal (Vulinec, 2000), might actually have a positive effect on seed fate by hiding them from predators at shallow depths that are optimal for germination and seedling establishment (e.g., Griffiths et al., 2016; see next section). Also, many species of tunnellers push fragments of dung, showing a behavior that, in terms of secondary seed dispersal, has some characteristics of tunnellers (they are less selective, excluding fewer seeds) and some of rollers (they move smaller portions of dung but to larger horizontal distances; Culot et al., 2011). Finally, while several studies have assessed the secondary seed dispersal capacities of particular beetle species (Estrada and Coates-Estrada, 1991; Vulinec, 2000; Vulinec, 2002; Andresen, 2002a; Vulinec et al., 2003; Koike et al., 2012; Feer et al., 2013; deCastro-Arrazola et al., 2020; Manns et al., 2020; Niero et al., 2022), the number of species compared is usually low (1–10) and experimental manipulations probably alter beetle behavior (i.e., beetles are placed in relatively narrow cylinders manually filled with soil). Thus, this is an area of many research opportunities.

In addition to beetle and seed traits, dung amount, dung type, seed density, and the spatial defecation pattern can also affect secondary seed dispersal by dung beetles. These are interrelated factors, as they all depend on the characteristic of each species of frugivorous vertebrate (e.g., size, behavior, diet). With the exception of one study, which assessed secondary seed dispersal for seeds defecated by a bird species (guan; Landim et al., 2022), all others have focused on seeds in mammalian dung, particularly that of primates. Consistently, studies comparing different amounts of dung while controlling for the other factors have found that seeds surrounded by more feces have a higher probability of secondary seed dispersal and are often buried more deeply. On the other hand, two studies comparing dung types while controlling for the other factors found differences in secondary seed dispersal (Ponce-Santizo et al., 2006; Santos-Heredia et al., 2011), while one did not (Culot et al., 2009). Yet, another study found an effect of dung type in one experiment, but not in another, which was attributed to seasonal differences in the frugivores' diets, which in turn affected dung texture (Santos-Heredia et al., 2010). Studies comparing the spatial distribution of dung (clumped vs. scattered), while controlling dung type and amount, have either found no effect on secondary seed dispersal (Andresen, 2002b; Ponce-Santizo et al., 2006) or have found that seeds in clumped defecations are buried more often and more deeply (Santos-Heredia et al., 2010). Some studies have used an integrative approach for comparing the secondary dispersal of seeds defecated by different frugivores, in which all characteristics associated with the defecation pattern of each species are mimicked (Lugon et al., 2017; Landim et al., 2022) or the secondary dispersal is measured *in situ* where seeds are defecated, with very little manipulation (Culot et al., 2009, 2018). These studies have found differences in secondary seed dispersal among the frugivore species being compared. These differences were strongly driven by the effect of dung amount, but also by dung texture (Lugon et al., 2017), and the number of seeds in a dung pile (Culot et al., 2009, 2018).

The deposition of dung may not only be aggregated in space, but also in time. This occurs when mammals defecate in the same sites (often sites used for resting) recurrently over time, creating a 'latrine effect'. A latrine effect occurs when, due to the recurrent defecations, certain biotic and/or abiotic characteristics of the habitat (e.g., density of seedlings, soil nutrients) differ between latrines and non-latrine sites (Whitworth et al., 2019). Only two studies have evaluated secondary seed dispersal by dung beetles in latrines, finding that seed burial by beetles was higher in latrines than non-latrines (Fuzessy et al., 2021b) and higher in latrines used more frequently vs. less frequently (Feer et al., 2013). This is an area of interest for future research, given that the habitat heterogeneity generated by the latrine behavior of certain mammals may be accentuated by the differential activity of dung beetles (see also Seed banks).

Other environmental factors that can either influence the composition of the dung beetle assemblage attracted to a seed-containing defecation (e.g., season of the year, time of day, vegetation characteristics) and/or dung beetle behavior (e.g., soil type, soil compaction, soil water content) can also affect secondary seed dispersal but have been explored very little (Table 1A), or not at all. On the other hand, the effects of habitat disturbance and dung beetle community attributes (e.g., species richness) are increasingly being related to secondary seed dispersal due to the tremendous popularity of dung beetles as a focal taxon in biodiversity studies. We will come back to this topic below (see Biodiversity studies using dung beetles as a focal taxon).

The consequences of secondary seed dispersal by dung beetles

The immediate consequences for seeds embedded in the dung that is processed by dung beetles are potential changes in their location and condition. However, what is relevant to know are the long-term consequences of those changes. Unfortunately, we know much less about these long-term consequences than we know about the immediate ones, given that relatively few studies on secondary seed dispersal by dung beetles have followed seed fate until seedling establishment and even fewer assess seedling survival (Table 1B; Supplementary Table S1).

In terms of location, as already explained, dung beetles may bury seeds and/or they may move them horizontally away from the original site of deposition. The best studied consequences of secondary dispersal on seed fate are those related to seed burial (Supplementary Table S1). There is a strong consensus in the literature that seed burial by dung beetles increases seed survival by lowering the probability of seed predation. However, researchers also agree that seeds buried too deeply may suffer negative effects because seedling establishment is hindered. While the first effect (lower seed predation) can be generalized to most plant species, the second cannot, since the range of depths from which a seed can emerge as seedling varies strongly among plant species and biomes (Gallagher, 2014). To some extent, the negative effect of seed burial is likely related to seed size, with larger seeds suffering less from non-emergence of seedlings than smaller seeds, in general. However, even for large tropical seeds, there is high variability regarding this negative effect, but with no clear relationship to seed size (Andresen and Levey, 2004; Culot et al., 2015, 2018). Thus, other seed/seedling functional traits (e.g., type of germination, type of cotyledons) are likely important too in determining whether a seed buried by dung beetles will be able to emerge as seedling, or not (Andresen and Feer, 2005). Additionally, the challenge of following the long-term fate of small seeds (< 3 mm), pointed out long ago (Andresen and Feer, 2005), has not yet been completely solved. Also, we know little about the specific mechanisms that hinder seedling establishment from a seed buried by dung beetles. In some cases, buried seeds seem to germinate well but the elongating seedling is unable to emerge (e.g., Andresen and Levey, 2004), in other cases germination itself may be hindered, or buried seeds may suffer higher rates of mortality due to pathogen attack or other causes (Lugon et al., 2017). Unfortunately, most studies on seed burial by dung beetles are not designed to determine which mechanism is responsible, since germination is quantified indirectly by assessing seedling establishment (Supplementary Table S1). Overall, the species-dependent variation in seedling establishment from seeds buried by dung beetles strongly limits our ability to generalize whether secondary seed dispersal by these insects has mostly a net positive effect on plant fitness, or not.

Seed burial can also affect seed fate through other mechanisms. Since the first studies on secondary seed dispersal by dung beetles, it was argued that seeds buried by dung beetles might encounter microclimatic conditions (e.g., temperature, moisture) that could favor their survival and/or germination (Wicklow et al., 1984; Andresen and Feer, 2005; Nichols et al., 2008). While the effects of the microclimate on the germination of buried seeds has been studied (Gallagher, 2014), they have not been assessed for seeds buried by dung beetles. In tropical forests, encountering better microclimatic conditions when buried could be of particular importance for plant species whose seeds' viability quickly decreases when they lose moisture. This potential effect of seed burial by dung beetles may also be more relevant in tropical dry forests or secondary forests (e.g., Culot et al., 2018), where conditions on the soil surface can be harsh (high temperature, low moisture). Similarly, in soils that are highly compacted (e.g., grasslands used by large domestic or wild herbivores), seed burial by dung beetles may be crucial for seed germination and seedling establishment. Future studies will need to test whether this often-cited advantage of secondary seed dispersal by dung beetles occurs or not.

Another positive aspect of secondary seed dispersal by dung beetles that was proposed early on, but for which we also lack empirical evidence, is increased plant fitness due to the reduction of density-dependent processes, such as predation and/or competition (Andresen and Feer, 2005; Nichols et al., 2008). Mammal defecations can often contain large numbers of seeds; thus, it has been argued that redistribution of those seeds through dung beetle activity would diminish the degree of clumping and consequently improve seed survival, seedling establishment, and, eventually, seedling performance. While many studies on secondary seed dispersal by dung beetles report horizontal movement of seeds, the effects on seed fate have not been assessed.

Two studies have experimentally proven that dung beetle activity indeed decreases the spatial aggregation of seeds deposited in dung and of the seedlings that establish from them (Lawson et al., 2012; Urrea-Galeano et al., 2019a). However, of the four plant species tested (two in each study; Supplementary Table S1), only one showed a higher probability of seedling establishment in plots with dung beetle activity (Lawson et al., 2012), while for the other three species the effect was negative. The challenge in these types of studies is to design experiments that allow us to disentangle the different effects of secondary seed dispersal by dung beetles on seed fate and seedling establishment, which occur simultaneously in the field, and some of which may only be detectable after longer periods of time (Lawson et al., 2012; Urrea-Galeano et al., 2019a). So, for example, in the studies mentioned above, the negative effect of dung beetle activity on seedling establishment might have been caused by seed burial, and not by the horizontal dispersal of the seeds. Alternatively, diminished spatial aggregation due to horizontal dispersal might have positive effects on seedling survival or growth that are only detectable in the long term.

Aside from the vertical and horizontal movement of seeds by dung beetles, other more subtle changes in seed location and/or condition could also affect seed fate (Braga et al., 2017). For example, seeds are often moved by beetles from an exposed location on the soil, to a location under the leaf litter (e.g., Zárate et al., 2019), particularly when moved by rollers. In other cases, although seeds are not buried by beetles, they nonetheless end up covered by the soil that beetles excavate when building underground tunnels and chambers for dung burial (Braga et al., 2017). It is possible that seeds in these conditions might experience the positive effect of reduced seed predation and/or improved microclimate, while avoiding the negative effect of being buried too deeply to establish as seedlings, but we lack the information to confirm this. However, a recent study in a Mediterranean savanna used for cattle grazing, showed that seedling establishment was much higher for acorns falling on cattle dung than for acorns falling on the ground, due to the covering of acorns with soil excavated by dung beetles (Leiva and Sobrino-Mengual, 2022). Though this phenomenon is not secondary seed dispersal *sensu stricto*, given that the acorns where not defecated by cattle but rather fell from the parental crown on top of a dung pad, the result is the same as described by Braga et al. (2017) for defecated seeds, and may be considered as 'passive seed burial' by dung beetles (Leiva and Sobrino-Mengual, 2022).

Another important change in seed condition that is a consequence of dung beetle activity, though not necessarily associated to secondary seed dispersal, is the 'cleaning' of seeds. After dung removal by beetles, seeds that are not buried by them remain on the soil surface, often in the same location of original deposition, but without dung. We know very little about the positive and negative effects that the dung surrounding seeds can have on seeds and seedlings (Traveset et al., 2007) and consequently we do not know the effects of seed cleaning. The little information we have for tropical forests, shows that seeds embedded in dung may suffer higher mortality due to seed predators (Janzen, 1982) and seed pathogens (Jones, 1994). Nonetheless, for seeds defecated by certain mammal species, the feces may have a protective effect. This possibly occurs in the case of seeds dispersed by tapirs, as studies have suggested that the dung of this mammal, which disintegrates slowly, may protect seeds against desiccation, vertebrate predation, and invertebrate parasitism (Rios and Pacheco, 2006; Lugon et al., 2017). Even seeds that are buried by dung beetles may or may not be embedded in dung, as beetles re-process the dung portions during burial, often removing seeds, which then remain in the tunnels but not imbedded in dung (Stanbrook et al., 2017). Buried seeds that are embedded in dung have been reported to suffer higher seed predation when compared to buried seeds not surrounded by dung (Andresen, 1999). On the other hand, seeds buried with the dung may encounter a boost of nutrients upon germinating, which might enhance seedling establishment and/or survival (Traveset et al., 2007). To our knowledge, only two studies have assessed the latter effects of secondary seed dispersal by dung beetles, finding a negative effect of the dung on germination (Fuzessy et al., 2021b) and no effect on seedling establishment (Griffiths et al., 2016; Fuzessy et al., 2021b). Again, this is a topic that needs to be investigated further.

Biodiversity studies using dung beetles as a focal taxon

Since dung beetles were proposed as an ideal animal group for analyzing and monitoring biodiversity in modified tropical landscapes 30 years ago (Halffter and Favila, 1993), they have become tremendously popular as a focal taxon in these types of studies (Nichols and Gardner, 2011; Fuzessy et al., 2021a; López-Bedoya et al., 2022). More recently, many of these studies have started quantifying ecological functions of dung beetles, in addition to community attributes, and assessing the relationships between both types of variables. While dung removal is the most frequently measured function (Raine and Slade, 2019), secondary seed dispersal is now often included in sampling protocols too (Figure 2; Table 1). In addition to being used as a focal taxon in applied biodiversity conservation research, beetles are also used as a model taxon in studies that focus on understanding the relationship between biodiversity and ecosystem functioning (i.e., BEF studies). In these two types of biodiversity studies, researchers often use seed mimics instead of real seeds, which allows for a quick and easy quantification of secondary seed dispersal in experimental mesocosms (e.g., Braga et al., 2013). The caveat, however, is that it is taken as a fact that secondary seed dispersal is an ecological function that has positive effects on plant regeneration, which, as we have seen, is not something that we can yet generalize. We are not arguing that biodiversity studies using dung beetles as a focal taxon should stop measuring secondary seed dispersal, we are merely asking researchers to be prudent with their justifications and interpretations. Better still, researchers could use real seeds rather than (or in addition to) seed mimics to assess the true effect of secondary seed dispersal on plant regeneration in their study systems (e.g., Andresen, 2003; Griffiths et al., 2016).

We have learned interesting lessons from biodiversity studies using dung beetles as a focal taxon. First, secondary seed dispersal is often correlated to one or more attributes of the dung beetle community (e.g., species richness, abundance, biomass, functional diversity, community weighted means of functional traits, etc.). However, which community attribute has the strongest relationship with secondary seed dispersal is still a matter of contention, and most likely context-specific (Nichols et al., 2013; Griffiths et al., 2015; Derhé et al., 2016). Second, while secondary seed dispersal is a consequence of dung removal, these two functions are not always positively correlated (e.g., Carvalho et al., 2020). Thus, inferences about secondary seed dispersal should not be reached based on dung removal rates. Third, methodological choices may in part be responsible for discrepancies among studies (Raine et al., 2020). For example, it is common that, in the same study, different amounts or types of dung are used to measure secondary seed dispersal and to sample the dung beetle community, which can create spurious relationships (Nichols et al., 2013). Furthermore, the dung in pitfall traps remains attractive during a long period of time (24 h or more), whereas dung piles in secondary seed dispersal experiments are usually buried within few hours. Consequently, the dung beetle assemblage captured in a pitfall trap, is probably not very representative of the assemblage responsible for processing a dung pile. This problem can be avoided by using modified pitfall traps, in which beetles are allowed to bury the dung inside the trap (Culot et al., 2011), or by using an experimental setup that captures the individual beetles responsible for processing the dung and relocating the seeds (Griffiths et al., 2015, 2016). The latter method is labor-intensive but yields very precise data for relating community metrics and functions.

Finally, we want to draw attention to the way secondary seed dispersal is measured in many biodiversity studies, which does not yield an estimate that is independent of dung removal; this, in our opinion, is inadequate. Studies usually deploy large piles of dung (e.g., 100–200 g) that contain a known number (or weight) of plastic beads used as seed mimics. Generally, not all dung has been removed by beetles by the time secondary seed dispersal is measured (usually after 24–48 h). The remaining dung is then collected, the beads still imbedded in it are counted, and by subtraction, all the beads not found in the dung are considered as having been dispersed by beetles. Sometimes, only beads that are not on the soil surface are considered as dispersed by beetles, but the percentages of secondary seed dispersal are still calculated with respect to the total number of beads originally placed in the dung pile (e.g., Gómez-Cifuentes et al., 2020), thus yielding an estimate that is dependent on dung removal. We argue that to have a measure of secondary seed dispersal that is independent of dung removal, secondary seed dispersal should only be quantified for the portion of dung that was buried by beetles. For example, if a pile of 100 g containing 100 seed mimics was used in an experiment, and after 48 h 70 g of dung remained on the soil surface containing 60 seeds, then secondary seed dispersal should be assessed for the 40 seeds that were in the 30 g of dung that were buried by beetles. Then, for those 40 seeds, one should determine which ones were moved by beetles (horizontally and/or vertically), and only those should constitute the quantity of seeds dispersed.

Seed banks

As seen in the previous section, dung beetles can affect the fate of seeds through secondary seed dispersal and through other less studied mechanisms. For example, as already mentioned, seeds can be cleaned of dung (Braga et al., 2017), covered by excavated soil (i.e., passive burial; Braga et al., 2017; Leiva and Sobrino-Mengual, 2022), and in some cases eaten by dung beetles (Pérez-Ramos et al., 2007, 2013). However, in addition to their effect on the fate of individual seeds, dung beetles can have community-wide effects by shaping seed banks.

Seed banks play important roles in driving plant-community composition and dynamics (Gallagher, 2014). The characteristics of soil seed banks vary tremendously among ecosystems. While persistent soil seed banks are common in temperate biomes due to long dormancies of many seed species, seed banks in tropical forests tend to be transient, as few plant species have prolonged dormancy (Garwood, 1989). Thus, the effects that dung beetles may have on plant communities through their interactions with seed banks will also differ among ecosystems and regions. However, we know next to nothing about how dung beetle activity drives seed bank structure and dynamics, either in tropical forests or in any other biome, although their potential influence had been suggested more than once (D'hondt et al., 2008; Pouvelle et al., 2009; Koike et al., 2012).

Dung beetles could influence seed bank structure and/or dynamics through at least four potential mechanisms: (1) through the burial of seeds (either vertical secondary dispersal or passive burial) they incorporate seeds into the underground layers of the seed bank (Feer et al., 2013); (2) through their soil-excavation behavior, they move seeds that are buried in the soil, both upwards and downwards, which may promote or hinder germination (Urrea-Galeano et al., 2019b); (3) through their activity in the dung-soil interface they create irregularities in the soil surface that may facilitate the incorporation of small seeds into the soil, either through gravity or hygroscopic self-burying mechanisms (e.g., Verdú et al., 2009); and (4) through soil bioturbation and dung burial, they may create conditions that stimulate the germination of buried seeds (Urrea-Galeano et al., 2019b).

The little we know about the effects of dung beetles on soil seed banks comes from four studies (five publications) carried out in the Neotropics (Table 1C). First, a study in French Guiana described seed bank variability in monkey latrines (i.e., sites in the understory where monkeys defecate recurrently) associated to dung beetle activity (Feer et al., 2013). Researchers found that the abundance and species richness of small seeds buried in the soil were higher in latrines vs. non-latrine sites, and higher in latrines used by monkeys more frequently than those used less frequently. While the monkeys were responsible for the higher numbers of seeds reaching the soil surface, the authors argue that it was mostly due to dung beetle activity that those seeds were buried, and thus the structure of the seed bank shaped. Through a field experiment, the authors also found that seed burial activity by beetles was higher in frequently-used latrines than in those used less frequently. Though not focused on seed banks, a study in Brazil and a study in Spain found a similar pattern, with more seeds buried actively by beetles in monkey latrines (Fuzessy et al., 2021b), and more seeds buried passively after dung beetle activity in rabbit latrines (Verdú et al., 2009), than in non-latrine sites. Overall, it seems that dung beetle activity plays an important role in shaping the seed banks in mammal latrines, but more studies are needed.

Second, the other three studies, carried out in different tropical forests in Mexico, have shown that dung beetle activity enhances the establishment of seedlings originating from the natural seed bank (Santos-Heredia and Andresen, 2014; Ocampo-Castillo and Andresen, 2018; Urrea-Galeano et al., 2019b). In these studies, mammal dung was placed on the forest floor inside small circular plots (~ 30 cm diameter) where dung beetles could enter but were forced (by a small perimeter fence) to bury all dung within the plot. Control plots had no dung added to them, and seed rain was excluded from all plots. After several months, the number of seedlings establishing in plots with access to dung beetles was statistically higher than in control plots, in the three studies. While various mechanisms could be responsible for enhancing seedling establishment from the seed bank after dung beetle activity, the spatial re-distribution of buried seeds seems to be one of them, particularly the upward movement of buried seeds to more superficial layers or even to the surface (i.e., seed exhumation; Santos-Heredia and Andresen, 2014; Santos-Heredia et al., 2018). To test this mechanism, in one of these studies, seeds of two plant species were buried at known depths (3–10 cm) in experimental cylinders, a dung pile was placed on the soil surface and beetles were allowed to bury the dung (Urrea-Galeano et al., 2019b). In these cylinders, compared to the two controls (no dung added, and dung added but beetles excluded), seedling establishment was higher. Overall, there seems to be enough evidence to suggest that dung beetle activity affects tropical seed bank dynamics by promoting the germination of buried seeds, but again, more studies are needed to assess the generality of this effect and to determine the specific mechanisms driving it.

Plant performance

When dung beetles bury feces, they fertilize and bioturbate the soil. These actions modify the chemical, biological and physical properties of the soil (e.g., higher availability of nutrients, increased aeration and permeability, enhanced microbial activity, etc.), which in turn may improve plant nutrient uptake and plant productivity (see references in Nichols et al., 2008 and in Scholtz et al., 2009). Evidence for these effects comes from greenhouse studies and controlled field experiments with crops and/or temperate grasslands (Table 1D). In tropical forests, it has generally been assumed that similar positive effects on plants must also occur, but until recently no study had tested this assumption.

In a study in Brazil, researchers found that for one plant species, seedlings established from seeds buried by dung beetles survived better in plots where dung beetles had buried dung, compared to plots where dung was added but beetles were excluded (Griffiths et al., 2016). That same year, a study in Mexico found that seedlings of one plant species established in the forest understory had higher phosphorous concentrations in their leaves in plots where beetles buried small dung piles placed at their base, compared to seedlings in plots with no dung, and in plots with dung added but beetles excluded (Santos-Heredia et al., 2016). These studies gave us the first data suggesting that dung beetle activity might change the soil environment in a way that favors nutrient uptake and survival of seedlings established in the tropical forest understory. To gather more evidence, a third study in a different Mexican rainforest assessed the effects of dung beetle activity for the seedlings of six plant species, measuring foliar nutrients, growth, and survival (Urrea-Galeano et al., 2021). However, contrary to the previous results, no positive effect of dung beetle activity was detected for any of the variables in any of the seedling species. Furthermore, a negative effect of dung beetle activity was found for seedling growth. So, back to ground zero.

Whether dung beetle activity, through soil fertilization and/or bioturbation, has positive effects on the performance of tropical forest plants remains an unanswered question. At this point, to guide future studies, we can only summarize some recommendations that have been previously voiced by us or others (Nichols et al., 2008; Griffiths et al., 2016; Santos-Heredia et al., 2016; Urrea-Galeano et al., 2021): (i) to avoid extrapolating into natural conditions of tropical forests, results obtained in other study systems and regions; (ii) to carry out field experiments in tropical forest that would allow us to distinguish the effects that dung beetle activity has through fertilization vs. bioturbation on plant performance; (iii) to empirically measure the changes that feces burial by beetles causes in the tropical forest soil (i.e., physical, chemical, and biological changes) to better understand the mechanisms driving plant responses; (iv) to measure other responses in plants, such as herbivory and pathogen attack, since these plant antagonists are known to prefer plants with higher nutrient content; (v) to replicate these studies in forests that vary in soil characteristics (e.g., soil fertility, soil compaction, texture), and with plant species that differ in their functional traits (e.g., seed reserves, shade tolerance). There is much work to be done here.

Conclusion

To conclude, we want to emphasize two interrelated take-home messages. First, dung beetles are very abundant in tropical forests, and the large amounts of dung produced by forest mammals are buried by them within hours (Hanski and Cambefort, 1991). Thus, the impact that dung beetles can have on plants, through their direct and indirect interactions with seeds, seedlings, and even mature individuals, is potentially large. It has been suggested that, given the patchy distribution of mammal feces, dung beetles probably contribute to creating spatial heterogeneity in soil conditions and plant regeneration niches, and may even facilitate the co-existence of plant species (Nichols et al., 2008; Griffiths et al., 2016; Urrea-Galeano et al., 2019b). However, we still lack the necessary information that would allow us to estimate the true ecological impact of dung beetle interactions with tropical forest plants. Second, dung beetles have become a tremendously popular focal taxon in biodiversity studies that assess the effects of anthropogenic disturbances in tropical forests. The use of dung beetles is often justified by the ecological functions attributed to them, including their potentially positive effects on plants. These ecological functions can be services of huge economic impact in agricultural systems (e.g., Lopez-Collado et al., 2017), and so, much of what we know about dung beetle functions comes from such systems. However, except for secondary seed dispersal, we have neglected to accurately quantify the ecological consequences that dung beetle activity has in tropical forests. It is important to fill these gaps because we know that dung beetle communities vary tremendously among ecosystems, regions, and continents (Hanski and Cambefort, 1991), and that so do the ecological impacts of their activity (e.g., Milotić et al., 2017, 2019). Thus, as previously stressed, extrapolating results among regions and study systems is problematic and should be avoided (Slade et al., 2011; Koike et al., 2012; Griffiths et al., 2016; Urrea-Galeano et al., 2021). We finish with an invitation for young researchers to tackle the many questions that remain unanswered in the fascinating network of interactions between mammal dung, dung beetles, soil, and plants.

Author contributions

EA wrote the manuscript with feedback from LAUG. LAUG reviewed the literature and produced Figure 2, Table 1, and Supplementary Table S1, with feedback from EA. EA and LAUG produced Figure 1. All authors contributed to the article and approved the submitted version.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

Supplementary material

The Supplementary material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2022.979676/full#supplementary-material

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Evolutionary history and diversity in the ball roller beetle *Canthon cyanellus*

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To understand the evolutionary history of species, it is necessary to know the mechanisms for reproductive isolation, divergence-time between populations, and the relative action of the evolutionary forces (e.g., mutation, genetic drift, gene flow) within and between populations of the same, or closely related species. Although *Canthon* is one of the more diverse genera of neotropical beetles, insufficient research has been done to comprehend the divergent patterns that explain its speciation process. The absence of diagnostic morphological characters and the wide geographic variation of qualitative traits in Scarabaeinae obscures species delimitation, genealogical limits between populations, and its taxonomy. *Canthon cyanellus* is one of the best-known species in ecological and evolutionary aspects. It is a widely distributed species in the tropical forests of America. Also, the current deforestation has facilitated its incursion into open areas. Individuals from different populations have similar morphological characters but show wide variation in body color throughout their distribution, which makes it difficult to delimit the subspecies that comprise it. Recently, studies have been carried out to elucidate the pre-and postzygotic isolation mechanisms between populations and the historical biogeographical processes favoring cladogenesis events during the Pleistocene. Morphological variation of the male genitalia does not correspond to the phylogeographic structure. However, the morphological differences in one of the pieces of the endophallic sclerites have allowed a preliminary delimitation of some genetically differentiated clades. Finally, we consider that the joint analysis of traditional morphological taxonomy and phylogeography is important to understand the speciation process in the *C. cyanellus* complex.

KEYWORDS

aedeagus, allopatric populations, color polymorphism, genetic structure, incipient speciation, Mexican Transition Zone, reproductive barriers, taxonomic status

1. Introduction

Biological evolution is a complex hierarchically structured process encompassing microevolution, speciation, and evolution above the species level (Gould, 2002). Thus, to understand the evolutionary history and the mechanisms involved in the formation of new species is necessary to know the historical biogeographical processes (e.g., the geographical separation between regions), which modify the distribution and population densities of the species (Mayr, 1963; Endler, 1977). Likewise, it is important to know the pre-and post-zygotic reproductive isolation mechanisms (Dobzhansky, 1970; Coyne and Orr, 1998), which are the first step toward the formation of new species.

With this knowledge, it is possible to test different biogeographic scenarios and establish their relationship with the patterns of genetic differentiation among populations and among species (Hewitt, 1996; Irwin, 2002). Reproductive isolation mechanisms are intensified when genetic drift, recurrent point mutation, and inbreeding affect populations with small effective sizes (Wright, 1982). In this regard, some studies have compared divergent patterns of characters (e.g., morphological, genetic, ecological, behavioral, niche, etc.) between populations of the same species, or between populations of phylogenetically close species founded evidence of genetic structure between populations, mechanisms of reproductive isolation, and morphological differences (e.g., in the grasshopper *Chorthippus parallelus*: Tregenza et al., 2000; in the bumblebees *Bombus ephippiatus* and *Bombus wilmattae*: Duennes et al., 2012, 2017; in the cicada *Subpsaltria yangi*: Liu et al., 2019).

Within the order Coleoptera, the coprophagous beetles Scarabaeinae Latreille, 1802 are very diverse (*ca.* 6,700 species; Bánki et al., 2022). Their widespread distribution, behavioral complexity, and diverse morphology make them a good model for studying the evolutionary processes that have given raise to them (Mullen and Shaw, 2014). Different analysis and phylogenetic approaches have brought advances in the systematics of Scarabaeinae dung beetles (Monaghan et al., 2007; Tarasov and Génier, 2015; Gunter et al., 2016; Tarasov and Dimitrov, 2016). Phylogenetic studies for taxonomic levels below subfamily are recent (Nolasco-Soto et al., 2017, 2020; Hensen et al., 2018, 2020, 2021; Maldaner et al., 2019; Pardo-Diaz et al., 2019; Mello et al., 2021; Moctezuma et al., 2021; Halffter et al., 2022). Those studies have explored different data sets (e.g., molecular, morphometric, behavioral, ecological).

The Scarabaeinae Deltochilini Lacordaire, 1856 is one of the oldest tribes along with the Dichotomiini (Davis et al., 2002). *Canthon* Hoffmanssegg, 1817 is the most specious lineage of neotropical Deltochilini (Halffter and Martínez, 1977). The phylogenetic relationships established within *Canthon* and close related genera from morphological characters indicate that it is a polyphyletic group (Medina et al., 2003). These data led to the creation of putative subgenera; however, it is difficult to set clear boundaries between species and subspecies due to the absence of diagnostic morphological characters (Cupello and Vaz-de-Mello, 2018; Vieira et al., 2019; Nunes et al., 2020; Vaz-de-Mello et al., 2020). In addition, many Scarabaeinae species exhibit intraspecific geographic variation in body color (e.g., *Silvicanthon obscurus* Schmidt, 1920, *Phanaeus tridens* Castelnau, 1840, and *Canthon quinquemaculatus* Castelnau, 1840). Therefore, some authors have designated subspecies based on the patterns of coloration in some species (e.g., *Canthon rutilans* Harold, 1868; *Canthon latipes* Blanchard, 1845; *Phanaeus pyrois* Bates, 1887; Arnaud, 2002, Medina et al., 2003).

Canthon cyanellus LeConte, 1859 is a necrophagous roller beetle from the Neotropics (Favila, 2001), which provides valuable ecosystem services similar to other Scarabaeinae (e.g., nutrient recycling, fly control, carrion removal, secondary seed dispersal, soil aeration; Nichols et al., 2008). It is a well-studied species in ecological and evolutionary aspects related to reproductive behavior (Favila, 2001; Favila et al., 2005; Chamorro-Florescano and Favila, 2008, 2009, 2016; Chamorro-Florescano et al., 2011, 2017), larval development (Hernández-Martínez and Martínez, 2003; Martínez, 2005), chemical communication (Bellés and Favila, 1983; Ortiz-Domínguez et al., 2006a,b; Cortez et al., 2012, 2015; Favila et al., 2012), population genetics and phylogeography (Ortiz-Domínguez et al., 2010; Nolasco-Soto et al., 2017; Arce-Valdés et al., 2021), among others. Traditionally, the taxonomy of *C. cyanellus* was based in non-informative morphological characters like variations in body color (Halffter, 1961). This has created uncertainty about genealogical limits among populations, which has led some authors not to recognize several of the subspecies (i.e., *Canthon cyanellus cyanellus* LeConte, 1859; *C. c. sallei* Harold, 1863, and *C. c. violetae* Halffter, 1961; Solís and Kohlmann, 2002, 2012).

Here, we will discuss the historical (e.g., cladogenesis, genetic structure) and contemporary processes (e.g., sexual recognition) that explain the evolutionary history and diversity of the *C. cyanellus* complex in its distribution range. This will allow a better understanding of the historical processes and mechanisms that have contributed to the formation of new species.

2. Evolutionary history of *Canthon*

The Scarabaeinae are of Gondwanan origin (Gunter et al., 2018). Depending on the author 12 (Smith, 2006) or 11 (Bouchard et al., 2011) tribal names have been proposed. Currently, the tribe Deltochilini encompasses over 100 genera, but according to Tarasov and Dimitrov (2016) it should comprise only 22 genera. *Canthon* belongs to the rolling beetle's group, characterized by long middle and hind legs and a head without any tubercles, keels, or horns (Halffter, 1961). Nearly 180 species are included within this genus (Bánki et al., 2022). Recently, Cupello and Vaz-de-Mello (2018) based on a taxonomic review for '*Canthon sensu* lato' concluded that at least 22 species should be considered *incertae sedis* as they do not belong to any of the subgenera currently recognized.

Although *Canthon* is mainly Neotropical, several species have Nearctic distribution (Kohlmann and Halffter, 1990). It is found from southern Canada to Argentina occupying a great diversity of ecosystems in an extremely rugged topography (Medina et al., 2003). It is absent in Chile and on the United States Pacific coast

(Halffter, 1961). The hypothesis about the origin of *Canthon* indicates that the great richness of species that occurs in the north of South America, associated with its absence in Chile and the Patagonian region, suggests a possible center of origin in the Arquibrasil massif (Halffter, 1962). However, there is no hard data that corroborates this hypothesis.

Since 1963, Halffter has made a series of contributions to the biogeography of the Mexican entomofauna, mainly from the beetles Scarabaeidae, which propose hypotheses about its evolutionary history. These contributions suggest the existence of the biogeographic zone known as the Mexican Transition Zone (MTZ), which was invaded by different lineages (i.e., cenocrons) that evolved in the Nearctic and Neotropic zones (Morrone, 2015; Halffter, 2017; Halffter and Morrone, 2017; Morrone, 2020). Apparently, *Canthon* colonized the neotropical part of the MTZ during different migratory events that occurred from South to North America One migratory movement occurred before or during the Miocene, which included lineages that diversified widely in the Mexican Altiplano and the north of USA (e.g., *Canthon obliquus* Horn, 1894; *humectus* Say, 1932 and *pilularius* Linnaeus, 1758 species groups; Halffter, 1964; Kohlmann and Halffter, 1990; Halffter et al., 2022). A second ongoing migratory movement started after the reconstitution of the Isthmus of Panama (e.g., *Canthon viridis* Palisot de Beauvois, 1805, *C. cyanellus* and *Canthon indigaceus* LeConte, 1866; Halffter, 2017; Halffter and Morrone, 2017; Nolasco-Soto et al., 2017). Also, a current migratory movement associated with the expansion of rainforests in the last 10,000 years (e.g., *Canthon subhyalinus* Harold, 1867; *Canthon euryscelis* Bates, 1887, *Canthon angustatus* Harold, 1867) (Kohlmann and Halffter, 1990; Halffter and Morrone, 2017).

2.1. *Canthon cyanellus*

The mating of *Canthon cyanellus* takes place during the rainy season. This species uses small vertebrate carcasses to feed and reproduce (Halffter et al., 1983; Favila and Díaz, 1996). Sexual recognition occurs in the food source through cuticular compounds (Ortiz-Domínguez et al., 2006b). Sexually mature pairs cooperate in building and rolling a food ball; then, both cooperate in nest construction. At a distance of 2 to 3 m from the carcasses, the male buries the ball on which the female is mounted. On the nest, the pair copulates, and the female makes 2–6 brood balls (Favila and Díaz, 1996). One fertilized egg is laid in each brood ball; the larval development takes place in the ball until the adult hatches nearly 25 days later (Favila, 1993). The male remains in the nest with the female protecting the brood balls with chemical compounds that prevent the development of fungi and bacteria (Cortez and Favila, 2007). During his stay, the male also prevents the female from copulating with other males (Favila et al., 2005).

Canthon cyanellus has a wide distribution in the Neotropics (Figure 1): Mexico, Guatemala, Honduras, Nicaragua, Costa Rica, Panama, Trinidad, Colombia, Venezuela, Brasil, Ecuador, and Peru (Solís and Kohlmann, 2002). At its northern limit distribution, it reaches the Nearctic region to the eastern side of the United States in Texas (Halffter, 1961). Different subspecies are recognized according to the variation in body coloration (Robinson, 1948). Halffter (1961), following the ideas of Robinson (1948), places the different color morphs in a single species (i.e., *C. cyanellus*), but recognizes three subspecies: (1) *Canthon cyanellus cyanellus* LeConte, 1859 (Figure 2A) with monochromatic green or blue color; this is distributed from Texas and part of the tropical region in Mexico; it is considered synonymous with *Canthon speciosus* Harold, 1868 and *Canthon spinosus* Harold, 1863 (Howden, 1966); (2) *Canthon cyanellus violetae* Halffter, 1961 (Figure 2B) with the elytra dark metallic green, the pronotum, and pygidium disc, except lateral–posterior margins, are orange-reddish; it is found in southwestern Mexico. Howden (1966) suggests that *C. c. violetae* may be synonymous with *C. c. sallei* given the great similarity with individuals from Nicaragua, the type locality of *C. c. sallei*; and (3) *Canthon cyanellus sallei* Harold, 1863 (Figure 2C) has the dorsal surface largely reddish brown; its distribution ranges from Guatemala to Peru (Blackwelder, 1944). This is considered a synonym with *C. sallei triangulatus* Schmidt, 1920 and *C. sallei gutticollis* Schmidt, 1920 (Howden, 1966).

Canthon cyanellus is part of the entomofauna that was established in the MTZ during the Plio-Pleistocene, following a dispersion path from South America to southern and southeastern Mexico through the Gulf slope of Mexico and the Pacific Ocean (Kohlmann and Halffter, 1990; Morrone, 2015; Halffter and Morrone, 2017). This distribution corresponds to a Typical Neotropical pattern (*sensu* Halffter, 1962) that is associated with tropical dry forests, cloud forests, and tropical forests with an altitudinal distribution from 0 to 2,000 m (Halffter and Morrone, 2017).

Nolasco-Soto et al. (2017, 2020) concluded that at the MTZ *C. cyanellus* has gone throughout at least seven cladogenetic events (i.e., GF, ChaCal, Ixt, SEM, NGM, Hua, SPS + SGM; Table 1 and Figure 3) during the Pleistocene (Figure 4). The ancestor of *C. cyanellus* gets in the MTZ during the Plio-Pleistocene when the main mountain systems had already formed. The most likely ancestral area for *C. cyanellus* in Mexico was on the Pacific slope, later the ancestor could follow an invasion route through the foothills of the Trans Mexican Volcanic Belt and then to northern and southern Gulf of Mexico (Nolasco-Soto et al., 2017). Subsequently, cladogenesis might have occurred in a north–south spatial sequence, initially separating the Chamela populations in Jalisco (Cha clade) and Goméz-Farías (GF clade) in the Sierra Madre Oriental from the rest of the southern populations (Nolasco-Soto et al., 2017). The GF population could be a relict at "El Cielo" Biosphere Reserve in Tamaulipas (Nunes, 2019). The next cladogenetic event is dated at *ca.* 1.43 Myr splitting the northern Gulf of Mexico populations (NGM clade), and the populations in southern Mexico. The Huatulco populations (Hua clade) split from the remaining southern ones (SGM + SPS clades) around 1.26 Myr. One more cladogenetic event

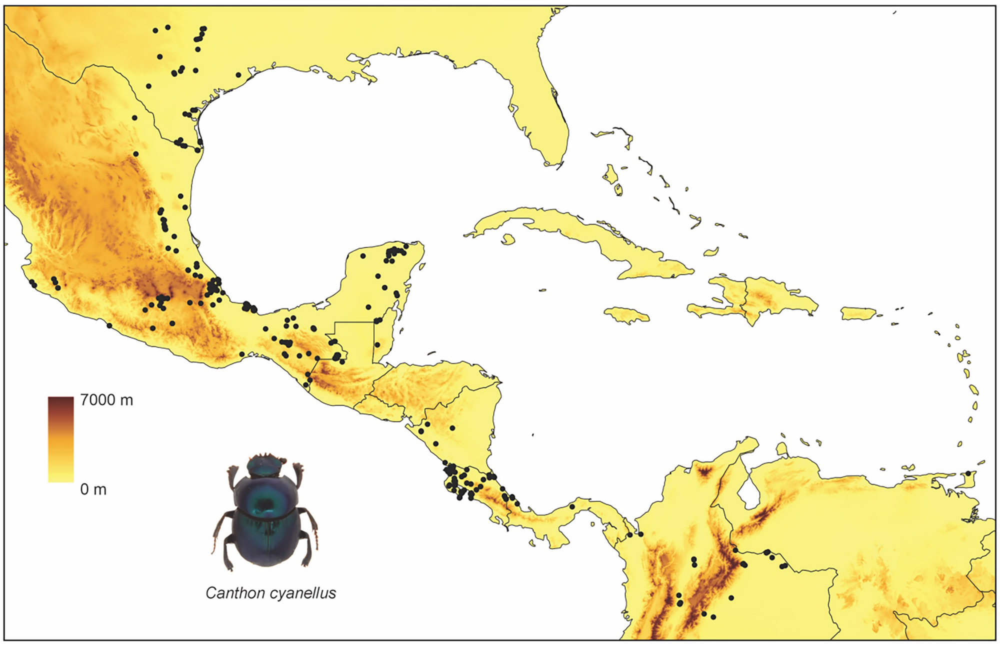

FIGURE 1
Distribution of *Canthon cyanellus*. This is how GBIF suggests citing records from different datasets: https://www.gbif.org/ occurrence download, Global Biodiversity Information Facility (2020).

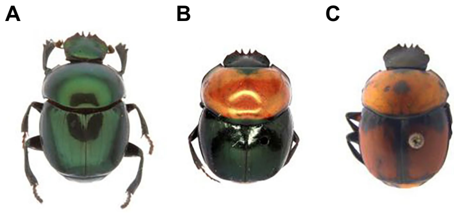

FIGURE 2
Canthon cyanellus subspecies *sensu* Halffter (1961). **(A)** *C. c. cyanellus*; **(B)** *C. c. violetae*, and **(C)** *C. c. sallei*.

that occurred at *ca*. 0.97 Myr separated the Chamela and GF clades. Finally, the estimated divergence time between the SGM and SPS clades occurred at *ca*. 0.91 Myr.

Those Cladogenetic events could be related to the contraction and expansion of tropical forests associated with glacial and interglacial cycles during the Pleistocene. A cladogenetic event that separated the NGM and SGM clades might be associated with the geological activity that occurred *ca*. 1.5 Myr east of the Trans Mexican Volcanic Belt in the state of Veracruz (Ferrari et al., 2005). Similarly, Ornelas et al. (2013) concluded that several cloud forest taxa distributed in Mexico diverge during the Pleistocene. These divergences suggest that the genetic differentiation of those species can be explained by the dynamics of the forests influenced by the climatic fluctuations of the Quaternary. On the other hand, the Isthmus of Tehuantepec may represent a biological corridor for *C. cyanellus* similarly as what has been observed for other taxa (e.g., fruit flies *Anastrepha*: Antonio-Hernández et al., 2018; *Sturnira hondurensis* bats: Torres-Morales, 2019).

The demographic history of the *C. cyanellus* populations in the MTZ indicates that they remained in stasis during most of the Pleistocene (Nolasco-Soto et al., 2017). Postglacial demographic expansions began *ca*. 180,000–20,000 years and continue to the present (Figure 4). Currently, these expansions can be associated with landscape changes due to tropical deforestation and intensive farming, favoring their incursion into open areas such as grasslands (Arellano et al., 2008; Salomão et al., 2018).

3. Incipient speciation

3.1. Reproductive barriers

During the speciation process, prezygotic (e.g., ecological, behavioral, reproductive seasonality, gametic incompatibility) or postzygotic (e.g., sterility or hybrid unviability) barriers are formed which restrict gene flow between populations, which leads to their differentiation (Tregenza et al., 2000; Sánchez-Guillén et al., 2012). During the divergence process between sister species, it is possible to evaluate the selection forces that act on the reproductive barriers because they are acquired during this process (grey area *sensu* de Queiroz, 2007).

Cuticular compounds (CHCs) mediate recognition and sexual attraction in several insect species (Chung and Carroll, 2015). In *C. cyanellus*, the composition of CHCs varies between sexes and allopatric populations distributed along the Gulf slope of Mexico

TABLE 1 Localities of *Canthon cyanellus* from Mexico and Colombia.

State/ Locality	Locality code	Clade code	Location (Latitude, Longitude)	Elevation (m.a.s.l.)
Tamaulipas, Gómez-Farías	GF	GF	23.0480, −99.1433	379
Veracruz, Tuxpan	Tp	NGM	20.9544, −97.4661	52
Veracruz, Papantla	Pap	NGM	20.4167, −97.4500	200
Veracruz, La Mancha	Man	SGM	19.5688, −96.4092	194
Veracruz, Jalcomulco	Jal	SGM	19.3286, −96.7469	370
Veracruz, Los Tuxtlas	Tx	SGM	18.5833, −95.0667	120
Chiapas, Raymundo Enríquez	Raye	SPS	14.8642, −92.3005	99
Chiapas, El Vergel	Ver	SPS	14.7029, −92.2672	22
Chiapas, Palenque	Nbet	SEM	17.2815, −91.6466	140
Campeche, Calakmul	Cal	SEM	18.3302, −89.8227	225
Oaxaca, Los Chimalapas	Chim	SEM	16.9122, −94.6697	212
Oaxaca, Huatulco	Hua	Hua	15.7800, −96.0900	30
Jalisco, Chamela	Cha	ChaCal	19.4997, −105.0229	90
Guerrero, Ixtapa	Ixt	Ixt	17.6583, −101.5752	120
Natagaima, Tolima, Colombia	Col	Col	3.6483, −74.9997	328

(Ortiz-Domínguez et al., 2006a, 2006b). In the beetle populations of Gómez-Farías such variation has been associated with a change in food preferences for Diplopoda carcasses (Ortiz-Domínguez et al., 2006a). The diet affects the quantity and quality of CHCs preventing sexual recognition and mate selection (Chung and Carroll, 2015). In *C. cyanellus*, the differences in the composition of CHCs are not strong enough to prevent interpopulation matting. Aggressive behavior does occur during sexual recognition at least under laboratory conditions. Interpopulation crosses had low fecundity and fertility, being more evident in couples from populations separated by ≥600 km (Ortiz-Domínguez et al., 2006a). This suggested that the populations throughout its distribution are in an incipient speciation process. Similarly, Grimaldi et al. (1992) observed in heterospecific experimental crosses of allopatric populations of the *Drosophila testacea* that reproductive isolation is asymmetric between some crosses. This is determined by differences in sexual recognition, the lack of transfer of sperm, and hybrid unviability.

In damselflies of the genus *Ischnura* (Sánchez-Guillén et al., 2012, 2014), *Drosophila* flies (Kamimura and Mitsumoto, 2012), and Carabidae beetles (Ishikawa, 1987; Kubota and Sota, 1998), reproductive isolation it is determined by mechanical prezygotic barriers, which prevent the formation of hybrids. Even though the populations of *C. cyanellus* are genetically structured (Nolasco-Soto et al., 2020), the morphology of the aedeagus is similar between individuals and populations (Figures 5, 6). Instead, the morphological differences in the peripheral medial sclerite allowed a possible separation between the different subspecies of *C. cyanellus* (Nunes, 2019; Figure 7). In contrast, in species of beetles: *Phanaeus tridens* group, the morphology of the phallobase, parameres, and endophallite copulatrix are attributes that apparently are in a state of evolutionary stasis (Moctezuma et al., 2021). In *Onthopagus taurus* Schreber, 1759 morphology variation in four of the five endophallic sclerites influenced male's fertilization success in the context of sperm competition (House and Simmons, 2003). In *C. cyanellus*, sperm competition influences paternity success (Favila et al., 2005). Therefore, it is possible, that in *C. cyanellus* the endophallic sclerites may be subject to sexual selection.

3.2. Diversity and genetic structure

Ortiz-Domínguez et al. (2010) quantified the diversity and genetic structure of five allopatric populations of *C. cyanellus* from tropical-forests located on the slope of the Gulf of Mexico. Those populations were structured in two groups, one to the north and one to the south. According to Nolasco-Soto et al. (2017), these groups correspond to the NGM and SGM clades. This might explain the problems of sexual recognition, low fecundity, and fertility, as well as the aggressive behavior, observed between couples from different populations (Ortiz-Domínguez et al., 2006a, 2006b). This genetic structure could be explained by isolation by distance, which restricts gene flow between them (Nolasco-Soto et al., 2017; Figure 8).

Similarly, in the species *Canthon staigi* Pereira, 1953 with wide distribution in the Atlantic forests in Brazil, Paraguay, and Argentina, the effect of habitat loss and fragmentation decreases the genetic diversity of its populations. However, they do not have a fragmented genetic structure due to a high gene flow between populations (Ferreira-Neto et al., 2017). This suggests that the current diversity and genetic structure of neotropical Scarabaeinae populations may be influenced by changes in the landscape caused by anthropic activities. Other factors that can lead to speciation are related to the size of the occupied area, the type of habitat, population demography, life history attributes of the species, as well as historical processes (Nolasco-Soto et al., 2017, Maldaner et al., 2019).

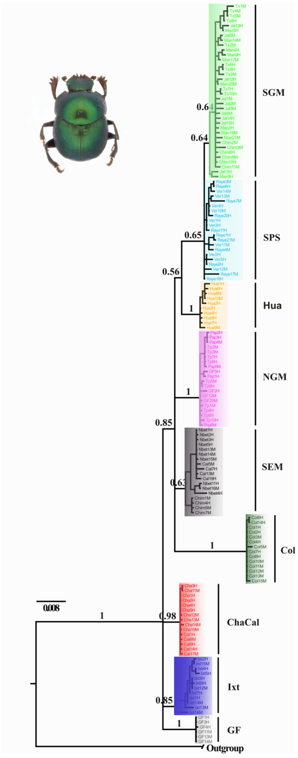

FIGURE 3
Bayesian consensus tree obtained by Nolasco-Soto et al. (2020) inferred from a multilocus dataset (ITS2+16S+COI). SGM, Jalcomulco, Los Tuxtlas, La Mancha, Los Chimalapas; SPS, El Vergel and Raymundo Enríquez; Hua, Huatulco; NGM, Papantla, Tuxpan and Gómez-Farías; SEM, Nueva Betania, Calakmul and Los Chimalapas; Col, Colombia; ChaCal, Chamela and Calakmul; Ixt, Ixtapa; GF, Gómez Farías.

Microsatellite markers indicated that populations of *Canthon staigi*, which have been altered by anthropic activities, presented inbreeding depression and less allelic richness compared to populations in conserved areas (Cruz et al., 2017). Currently, 14 polymorphic microsatellites have been developed (2–16 alleles each) for the populations of *C. cyanellus* that belong to the different clades identified by Nolasco-Soto et al. (2017, 2020). These microsatellites contain private alleles that suggest their potential use to assess the genetic structure and more precise geographic delimitation of clades within *C. cyanellus* (Arce-Valdés et al., 2021).

4. Chromatic variation and cryptic species

In *C. cyanellus* the cuticular color variation does not match with the genetic structure of the populations or with the taxonomic division *sensu* Halffter (1961) (Nolasco-Soto et al., 2017, 2020; Figure 9). Populations with genetically differentiated metallic green individuals along the Pacific slope and the Gulf of Mexico reveal cryptic species in allopatry. The only genetically differentiated populations, which are distinguished by cuticular color, are in the region of Tuxpan and Papantla (i.e., very dark blue and green), and in Gómez-Farías (i.e., bright light green). In the state of Chiapas, there are populations with dark green individuals genetically differentiated from other populations in which individuals with polychromatic and monochromatic colors coexist (Nolasco-Soto et al., 2017, 2020). Solís and Kohlmann (2002) carried out a detailed study for *C. cyanellus* in various locations in Costa Rica, demonstrating the coexistence of several cuticular colors, being an example of a polytopic species, and suggesting genetic differences between populations. Based on that fact, Solís and Kohlmann (2002) do not recognize subspecies. The same coloration patterns as those described by Solís and Kohlmann (2002) can be found in beetles from Chiapas, Mexico. The same can be observed in Nicaragua and Honduras for *C. c. sallei*, but light and dark colors also occur in South American populations (Vaz-de-Mello and Cupello, 2018).

Similarly, in the beetle *Coprophanaeus encifer* Germar, 1821, color variation is not related to cryptic speciation or genetic structure throughout its distribution in South America (Maldaner et al., 2019). On the other hand, *Canthon rutilans* different color morphs were assigned to the subspecies *C. r. rutilans* Castelnau, 1840 and *C. r. cyanescens* Harold, 1868; furthermore, recent studies found that these two subspecies diverge in thermal adaptations (Hensen et al., 2018), reproductive behavior (Hensen et al., 2020), and ecological niche (Hensen et al., 2021). This species indicates that the geographical variation of cuticular color in some species of Scarabaeinae might be related to cryptic speciation or species divergence, nonetheless the assignment of subspecies considering color as the only differentiation character (Solís and Kohlmann, 2002; Cupello et al., 2021).

In some species of Scarabaeinae, the color has been related to the period of activity (Hernández, 2002), thermoregulation (Amore et al., 2017; Alves et al., 2018; Cuesta and Lobo, 2019), phenotypic plasticity (Stanbrook et al., 2021), and Batesian mimicry (Alves et al., 2018). In the geotrupid beetle, *Phelotrupes auratus* local selection affects individuals of different colors that are regulated by multiple loci and correlated with barriers to gene flow (Araki and Sota, 2021). In *C. cyanellus* the metallic green color has a genetic basis (Favila et al., 2000), but it is possible that environmental factors also determine color variation throughout its distribution as has been suggested for other Scarabaeinae (Davis et al., 2008; Scholtz, 2009). Therefore, we do not rule out that stochastic processes such as genetic drift and genetic control by multiple loci may influence geographic color variation in this species.

5. Discussion

The evolutionary scenario that explains the diversification of *C. cyanellus* is associated with historical isolation by distance, which restricted the genetic flow between populations, causing their speciation in allopatry during the Pleistocene. The eight

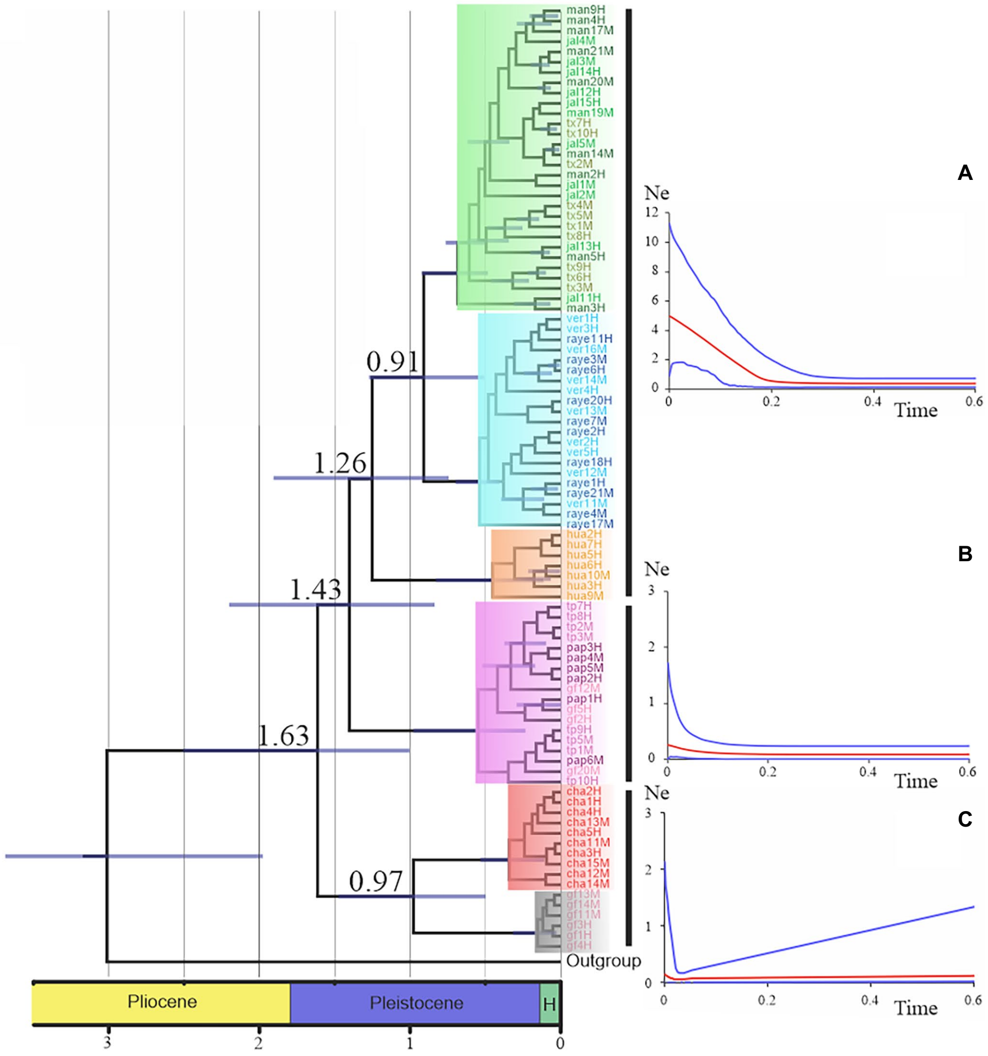

FIGURE 4
Chronogram and demographic history for the major clades were obtained by Nolasco-Soto et al. (2017). Time is in millions of years. Nodes with posterior probabilities above 0.9 show time uncertainty by means of 95% HPD bars. Skyland plots display the historical demographic tendency of the mayor lineages. The red line indicates the trend of the median Ne, whereas the blue lines represent the 95% confidence limits. **(A)** "Great lineage" demographic trend (Fu's *Fs*=−31.01, *p*<0.0001), **(B)** NGM clade demographic trend (Fu's *Fs*=−4.75, *p*<0.01), and **(C)** GF-Cha clade demographic trend (Fu's *Fs*=4.99, *p*<0.01).

historically separate units recovered by Nolasco-Soto et al. (2020) can be identified by nucleotide synapomorphies. Traditional morphological taxonomy for this group was based on the middle peripheral sclerite character. However, based on a phylogenetic species concept, those eight units can be recognized as different species, in which pre-and postzygotic reproductive barriers are developing.

The observed geographic variation in the aedeagus morphology and the body color of *C. cyanellus* is not related to the inferred genetic structure of the populations nor the current taxonomic classification. The latitudinal distribution of color variation in Mexico tends toward monochromatic green. Although the adaptive significance of color variation is unclear, this may suggest some thermoregulatory function or selective pressure imposed by different local environmental conditions (Amore et al., 2017; Alves et al., 2018; Cuesta and Lobo, 2019). It is possible that different evolutionary mechanisms interact to produce geographic variation in body color in this group of beetles (Araki and Sota, 2021).

Studies carried out with microsatellite molecular markers, suggest that the diversity and current genetic structure of populations can be shaped by changes in the landscape caused by human activities (Cruz et al., 2017). This may occur due to habitat fragmentation, favoring in some cases the possibility of allopatric speciation due to geographic isolation and the effect of genetic drift. It is necessary to evaluate to what degree the current genetic structure of *C. cyanellus* populations might be shaped by the effects of fragmentation, extensive use of

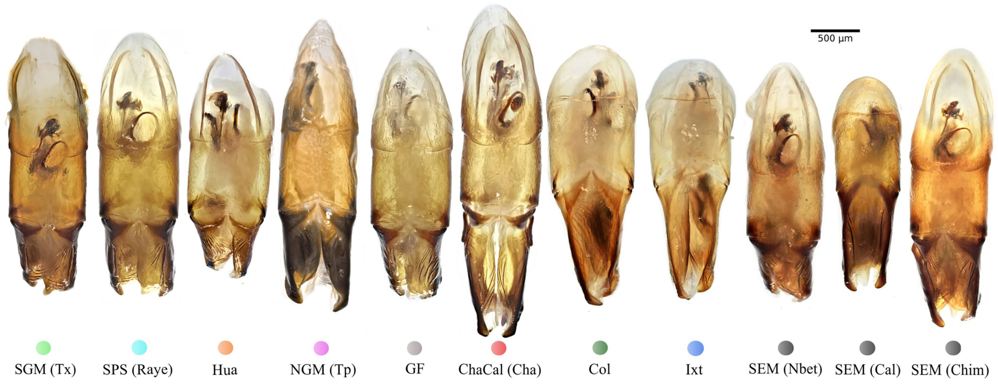

FIGURE 5
Aedeagus lateral view of specimens from the seven Mexican clades and the Colombian clade: Colored dots correspond to the clade color showed in the Bayesian tree on Figure 3.

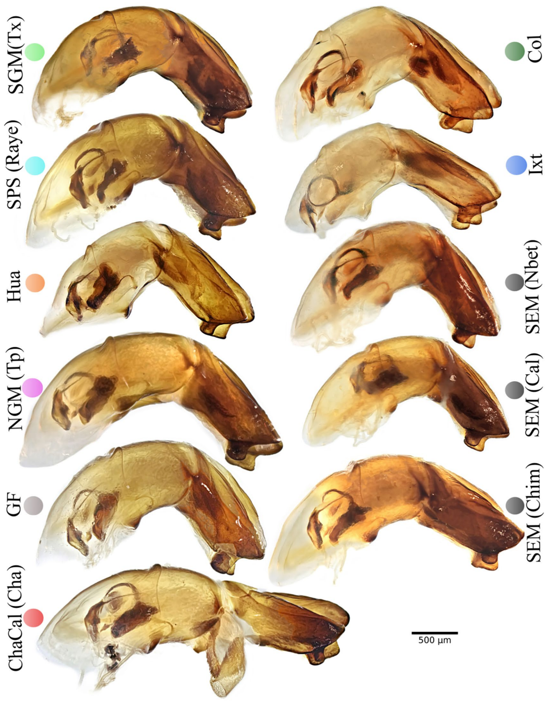

FIGURE 6
Aedeagus dorsal view.

agriculture, and livestock management. This knowledge will make it possible to elucidate if some populations might be susceptible to ecological changes (e.g., Sierra Madre Oriental and in Tapachula, Chiapas).

The current review is part of an effort to understand the evolutionary history of Scarabaeinae beetles in the Mexican Transition Zone. To sort out the cryptic diversity present in this beetle complex represents an important step in understanding its evolutionary interrelationships. New lines of research must be opened to test hypotheses on the evolution of the genitalia, as well as to explore the importance of pre-and postzygotic reproductive barriers in this species.

6. Taxonomic status

Key to the determination of the subspecies of *Canthon cyanellus* (*sensu* Halffter, 1961).

1. Quadridentate clypeus. Hind tibiae markedly arched. The separation between proepisternae and proepimera only with an indication of a keel, limited to the internal part, close to the coxa. Teeth of the anterior tibiae, especially the two most apical ones, notably directed forwards, obliquely: the three tibial teeth are grouped in the most apical part of the piece *C. cyanellus* LeConte.
2. Dorsal surface green, blackish-green or dark blue. Pronotum with fine to evident and dense punctuation. With antescutelar impression. Hind tibiae markedly arched, forming an angle with the point of inflection toward the middle of the tibia. Texas and Mexico. *C. cyanellus cyanellus* LeConte.

Head and periphery of the pronotum dark green, the pronotum, and pygidium disc, except the latero-posterior margins, orange-reddish.

3. With antescutelar impression. Pronotum with very fine but dense punctuation. Dark metallic green elytra. Southwest Mexico *C. cyanellus violetae* n. subsp. Posterior edge of pronotum without antescutelar impression. Pronotum with slight punctuation, perceptible only on both sides and posterior margin. The anterior edge of the elytra, elytral suture line, and elytral epipleura are bright green, the elytral disc is orange-reddish; this coloring manifestly predominates. Central and South America *C. cyanellus sallei* Harold.

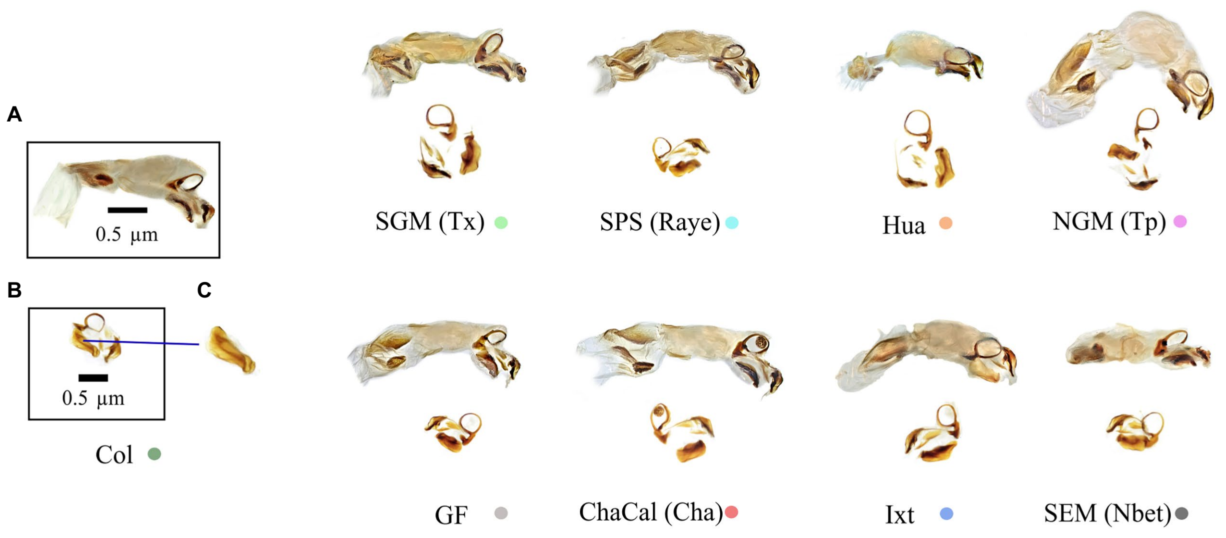

FIGURE 7
(A) Endophallus, **(B)** Endohpallites, and **(C)** Peripheral medial sclerite *sensu* Nunes (2019). The morphology of this structure allows the recognition of *Canthon cyanellus* clades *sensu* Nolasco-Soto et al. (2017, 2020). Colored dots correspond to the clade color shown in the Bayesian tree in Figure 3.

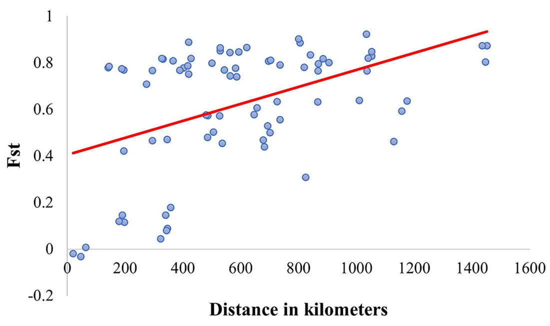

FIGURE 8
Linear regression between F_{st} and the geographic distance (R^2=0.212, p<0.0001) in the Mexican populations of *Canthon cyanellus*. This analysis was carried out based on the paired linear geographic distances between populations and the paired F_{st} values were obtained with DnaSP v6.12.03 (Rozas et al., 2017).

4. Pronotum with a dark triangular spot whose tip reaches the base of the elytra, lateral pronotum spots, separate or absent *C. cyanellus sallei* var. *triangulatus* Schmidt. Upper and lower surface dark green; pronotum with four light spots, one at each angle; pygidium usually dark *C. cyanellus sallei* var. *gutticollis* Schmidt.

On the other hand, Nunes (2019) carried out the most recent taxonomic review for the *C. cyanellus* group. Nunes (2019) assigned a new (but not yet named) subgenus to the group "cyanellus" based on the diagnostic character of the clypeal teeth of the anterior margin of the head. In addition, the morphology of the middle peripheral endophallic sclerite allowed him to separate and give preliminary validity to five of the chromatic forms that had been considered synonyms of *C. cyanellus* to a new species and a subspecies. Some of these chromatic forms have their correspondence with the clades (e.g., GF, NGM) inferred by Nolasco-Soto et al. (2017, 2020). Phylogeography, combined with traditional morphological taxonomy, provides information on species boundaries, populations, and other intraspecific groups; thus, a better understanding of the speciation processes (Table 2).

1. *Canthon cyanellus* LeConte, 1859 *sensu stricto* is the chromatic form used to describe the species. Nunes (2019) designed this as the subspecies, *C. c. cyanellus*. It corresponds to the clade NGM (Nolasco-Soto et al., 2017). A very dark blue with a rough dorsal surface characterizes it. It is distributed at the northern area of Veracruz in Tuxpan, Papantla, and Tancoco. This species may reach its distribution as far as Texas (Robinson, 1948). However, the genealogical relationship among the populations from Texas and Mexico is unknown.
2. *Canthon speciosus* Harold, 1868. This species was considered a synonym of *C. cyanellus*, and it was assigned to the subspecies *C. c. cyanellus* by Halffter (1961). Harold described it as having a bright green and bluish-green body color, with a smooth dorsal surface. This corresponds to the SGM clade *sensu* Nolasco-Soto et al. (2017), which includes populations from the southern area of Veracruz. Nunes (2019) assigned it as a synonym of *C. spinosus* and delimited its distribution in the eastern coastal zone of Mexico from Veracruz, Yucatan, Quintana Roo, Campeche, Chiapas to the border with Guatemala at the Petén area. Some specimens from Los Chimalapas in Oaxaca, all from Nueva Betania in Chiapas, and some from Calakmul in Campeche sequenced by Nolasco-Soto et al. (2020) were

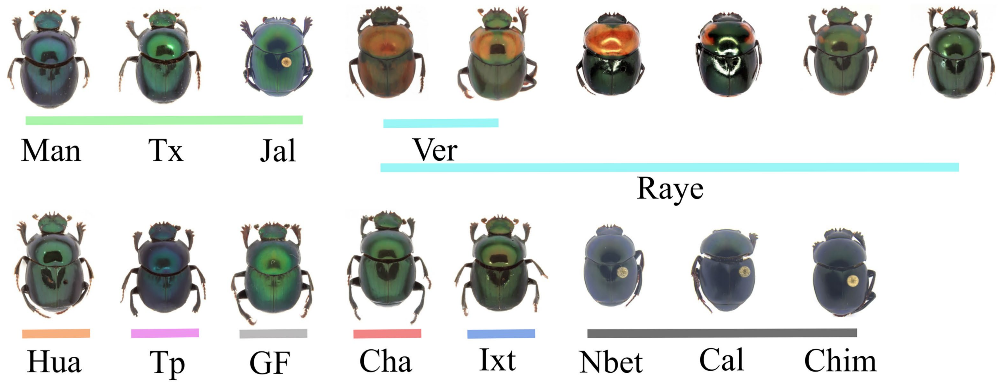

FIGURE 9
Morphological variation of color pattern in *Canthon cyanellus* populations. Colored lines correspond to the clade color shown in the Bayesian tree in Figure 3, (Nolasco-Soto et al., 2020). The genealogy was estimated from Bayesian inference (BI) analysis using the software MrBayes v.3.2.6 (Ronquist et al., 2012) available in the CIPRES portal (Miller et al., 2010).

TABLE 2 Taxonomic division of *Canthon cyanellus* carried out by Nunes (2019) compared to the clades inferred by Nolasco-Soto et al. (2017, 2020)

Nunes (2019)	Nolasco-Soto et al. (2017, 2020)
Canthon cyanellus cyanellus LeConte, 1859	NGM
Canthon cyanellus (undescribed subspecies) Nunes & Vaz-de-Mello	GF
Canthon sallei Harold, 1863 status reviewed	Col
Canthon speciosus Harold, 1868 status reviewed	SGM
Canthon triangulatus Schmidt, 1920 novo status	Col
Canthon violetae Halffter, 1961 novo status	SPS
Canthon (undescribed species) Nunes y Vaz-de-Mello	Ixt
Specimens under review	Hua
Specimens under review	ChaCal

Clade code as in Table 1.

recovered within the SEM clade, therefore, *C. speciosus* would be a polyphyletic group. The SEM clade seems to correspond to the material reviewed by Harold referring to *C. spinosus* from southern Mexico. To resolve this problem material from the localities examined by Nunes should be sequenced, as well as a detailed review of the endophallic sclerites of the SEM clade individuals must be performed.

3. *Canthon violetae* Halffter, 1961. It is characterized by dark-green metallic elytra, as well as reddish-orange pronotum, and pygidium disc, except the lateral–posterior margins. The ventral part of the body is blackish-green and with some abdominal segments reddish-orange. It is endemic to the center and southwest area of the state of Chiapas. This is the SPS clade *sensu* Nolasco-Soto et al. (2017, 2020) that includes individuals from localities as El Vergel (also reviewed by Nunes, 2019), and Raymundo Enríquez, which are genetically differentiated from other populations in Chiapas. At the Raymundo Enríquez locality, there are individuals with completely green or reddish-orange cuticular colors (or a mixed pattern of these colors in different parts of the body; i.e., head, pronotum, abdomen, and pygidium). These color forms have been reported by Solís and Kohlmann (2002) in Costa Rica. This may suggest a possible hybridization zone or a species in which color variation is controlled by several codominant genes.
4. *Canthon sallei* Harold, 1863. Orange color at the cuticula, body, and elytra with black outline, may have a triangular-shaped spot in the center of the pronotum, sometimes it appears as a longitudinal line (Nunes, 2019). Nunes (2019) assigned *Canthon dentiger* Harold, 1968 as a synonym of *C. sallei*. This species is distributed from northwestern Colombia to southern Mexico and may occur in sympatry with *C. triangulatus* at its southern limit and with *C. violetae* at its northern limit (Nunes, 2019). The material reviewed by Nunes came from Nicaragua, Costa Rica, Colombia, and Panama. He also reviewed beetles from El Vergel (Chiapas, Mexico), which corresponds to the SPS clade *sensu* Nolasco-Soto et al. (2017). This clade contains large part of the color variation reported for the "cyanellus" group (e.g., metallic green, orange, and combinations of these colors in different parts of the body). Further molecular analyses of specimens from the localities reviewed by Nunes (2019) should be included, as well as a detailed review of the middle peripheral sclerite morphology must be carried out to determine if all the observed variation represents a polymorphic population or if this is a species complex.

5. *Canthon triangulatus* Schmidt, 1920. Synonyms: *C. sallei guticollis* Schmidt, 1920 and *C. cyanellus havranekae* Martínez, 1988 (Nunes, 2019). The species is distinguished by an opaque dorsal surface, pronotum, and elytra of orange color and black outline. On the pronotum, it has a longitudinal central spot. The pygidium is orange (Nunes, 2019). According to Nolasco-Soto et al. (2020), it corresponds to the Colombian clade. The phenotype corresponded to the one described for the variety that Schmidt called *C. sallei triangulatus*, which Halffter (1961) synonymized with *C. cyanellus sallei*. It is possible that populations from the Natagaima region in Tolima have their own identity and evolutionary history (Nolasco-Soto et al., 2020). These populations are enclosed between the central and eastern Andes Mountains in Colombia.
6. *Canthon cyanellus* (undescribed subspecies) Nunes & Vaz-de-Mello. It is characterized by a bright green color with a rough dorsal surface. According to Nunes (2019), it is an endemic subspecies in the region of "El Cielo" Biosphere Reserve in Tamaulipas (Mexico). This taxon corresponds to the GF clade *sensu* Nolasco-Soto et al. (2017).
7. *Canthon* (undescribed species) Nunes & Vaz-de-Mello. It has bright dark green color. This species corresponds to the clade Ixt located in Ixtapa, Zihuatanejo in the Pacific (Nolasco-Soto et al., 2020). However, it is easily confused with specimens recovered in the SGM, SEM, Hua, and ChaCal clades (Nolasco-Soto et al., 2020). Based on the material reviewed by Nunes (2019), which included specimens from Ixtapa, Zihuatanejo in Guerrero, El Aguacero, and El Vergel in Chiapas, the author concluded that this new species of *Canthon* might be in sympatry with *C. violetae* y *C. sallei*.
8. Other cryptic species. The localities of Huatulco in Oaxaca (Clade Hua) and Chamela Biosphere Reserve (Clade Cha) in Jalisco are monophyletic clades that may represent distinct and new species (Nolasco-Soto et al., 2017).

Author contributions

All authors listed have made a substantial, direct, and intellectual contribution to the work and approved it for publication.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

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The reproductive behavior of Neotropical dung beetles

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Dung beetles display complex reproductive behaviors involving sexual findings, sexual recognition, fighting for mates and food used for nesting, sperm competition, and parental care. Over the past 40 years, significant advances have been made regarding the knowledge of various aspects of the sexual and nesting behavior of Neotropical dung beetles. However, human activities modify the natural habitats of dung beetles at an alarming rate, affecting food availability and altering the ecological functions performed by the species in their different habitats. A deeper understanding of the reproductive behavior of dung beetles may contribute significantly in understanding the evolutionary diversification of these insects and their response to environmental changes. The present study reviews and analyzes studies regarding the sexual and reproductive behavior of Neotropical dung beetle species under field and laboratory conditions. We gathered 132 studies and 146 species; 42% of the available data were based on field observations, 23% on laboratory observations, 30% under both field and laboratory conditions, and 5% unspecified. Our review detected significant knowledge, geographic, and habitat gaps regarding the reproductive behavior of Neotropical dung beetles. Based on our findings, we propose future research goals and alternative methods to measure the behavioral responses of Neotropical dung beetles to the impacts of human activities.

KEYWORDS

sexual behavior, parental care, Neotropical, foraging competition, Scarabaeinae

Introduction

Dung beetles (Coleoptera: Scarabaeidae: Aphodiinae and Scarabaeinae, and Geotrupidae) are evolutionarily related species that use dung, carrion and decomposing fruits as organic sources for feeding and reproduction (Halffter and Matthews, 1966; Halffter and Edmonds, 1982; Hanski and Cambefort, 1991; Scholtz et al., 2009; Simmons and Ridsdill-Smith, 2011). According to how they handle the food resource and the structure of the nests they construct, Halffter and Matthews (1966) established four nesting groups (I-IV). Later, Halffter (1977) and Villalva et al. (2002) mentioned two evolutionary nesting lines closely related to the food resource they consume: burrower and roller beetles, also referred to as paracoprids and telecoprids, respectively. According to Halffter (1977) and Halffter and Edmonds (1982), there are seven nesting patterns in the Scarabaeinae (I to VII), whereas the Geotrupidae displays only the nesting pattern I, and most Aphodiinae are non-nesters.

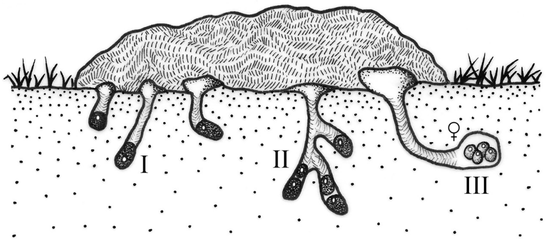

FIGURE 1
Nesting patterns I, II, and III (*sensu* Halffter and Edmonds, 1982).

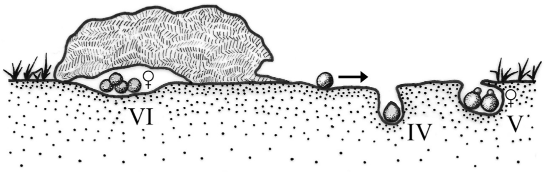

FIGURE 2
Nesting patterns IV, V, and VI (*sensu* Halffter and Edmonds, 1982).

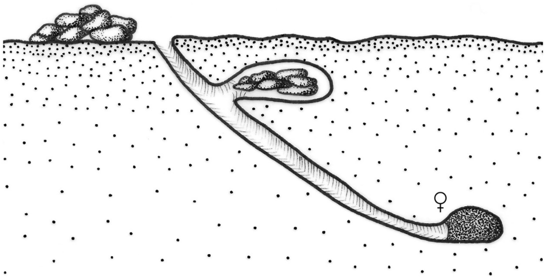

FIGURE 3
Nesting pattern for *Eucranium* Brullé (modified from Monteresino and Zunino, 2003).

Nesting patterns I, II, and III are observed in burrower beetles that construct underground nesting galleries, generally below or to one side of the food source, where they accumulate and manipulate food for their young. Simple underground nests contain only one brood mass or ball in each gallery, while compound nests contain two or more brood masses or brood balls per gallery. Typically, each brood mass or brood ball contains only one egg. In pattern I, the female leaves the nest after the egg is laid in the brood mass; a female can construct several brood masses. In the species showing pattern II, the female adds a layer of soil to the food after oviposition, which can be several millimeters thick, forming a brood ball, and then abandons the nest. The nest can contain up to two or three brood balls. Pattern III includes species in which the female builds nests with several brood balls and cares for them during the larval development of the progeny (Figure 1).

Patterns IV and V (Halffter and Edmonds, 1982) group roller beetles in which the male makes a food ball of dung or carrion from the food source, attract a female and rolls the food ball, with the female transported on the ball some meters away from the food source where the nest will be established. While searching for food, mate, and rolling, males fight for food balls and females. The patterns of roller beetles are differentiated by the complexity of the nesting behavior of both males and females (Figure 2). Pattern IV groups species that build simple nests, formed by one brood ball that may or may not be covered by a layer of soil after oviposition and that are abandoned by the female. In nesting pattern V, the female builds several brood balls from a single ball. Each ball is covered with a layer of soil, and the egg is laid in a chamber built by the female at the apical section of the brood ball (Figure 2; Halffter and Edmonds, 1982; Cambefort and Hanski, 1991; Halffter, 1997; Simmons and Ridsdill-Smith, 2011; Halffter et al., 2013). After brood balls are built, the female takes care of the nest during larval development; the male also stays in the nest, protecting the brood ball and the female, avoiding other males from mating it (Favila et al., 2005). In pattern VI, the female makes brood balls built directly at the food source. Most of the species of the genus *Eurysternus* Dalman belong to this pattern, which usually displays maternal care (Huerta et al., 2003). Within the Scarabaeinae, the members of the Eucraniini tribe, which are endemic to the arid and semi-arid zones of Argentina, were considered rollers by Monteresino and Zunino (2003) (named telephagic and telecoprid by these authors). However, these dung beetles neither make nor roll balls, so they were not grouped in the nesting patterns established by Halffter and Edmonds (1982). Currently, little is known about their reproduction (Figure 3).

After the hatching or emergence from the brood balls or nesting balls, adults are immature (tenerals), and the pre-reproductive period begins, during which adult beetles primarily search and fight for food and also feed. According to Zunino and Palestrini (1986) and Tonelli (2021), young adults feed in different ways: (a) directly above the food source (epiphagic behavior); (b) within the food source (endophagic behavior); (c) under the food source (mesophagic behavior); (d) burying the food in underground galleries to consume it subsequently (hypophagic behavior), and (e) making food balls that are first rolled some distance away from the food source, then buried, and later consumed (telephagic behavior). Throughout the pre-reproductive period, predominate feeding behavior, but there are various aggressive intra- and interspecific interactions, in addition to sexual interactions, including copulation at the end of this period. The pre-reproductive period, which varies according to the species, is followed by the reproductive period. In the subfamily Aphodiinae, some species do not build nests but lay their eggs directly in or under the food; larvae are free-living and directly consume the food source (Halffter and Edmonds, 1982; Hanski and Cambefort, 1991; Nichols et al., 2008; Huerta et al., 2013; Tonelli, 2021). Most Geotrupidae and Scarabaeinae species build nests during this stage. The post-reproductive stage has been little studied in coprophagous beetles, mostly under laboratory conditions; it is known that old individuals have limited activity and ultimately die.

According to Halffter and Matthews (1966), most nesting patterns of Neotropical dung beetle species (non-nesting, paracoprid and telecoprid) are well-represented and can be found in different habitats. However, while the reproductive behavior (including nesting patterns) of some dung beetle species has been studied in great detail, these are usually isolated efforts involving a set of model species (e.g., *Canthon cyanellus*, *Eurysternus*, *Copris incertus*; see Huerta and Halffter, 2000; Huerta et al., 2003, 2005; Favila et al., 2012). Thus, the current state of knowledge on the reproductive behavior of dung beetles in the Neotropics is still to be determined. We aim to review studies regarding the sexual and reproductive behavior of Neotropical dung beetle species under field and laboratory conditions. Our research will contribute to systematizing the information available to date, as well as to guide future research efforts, especially in those tribes or regions with significant information gaps.

Materials and methods

Literature search

The database was constructed through a systematized search of peer-reviewed papers on Web of Science (WoS) regarding the reproductive behavior of Neotropical dung beetles. The search was conducted in the second semester of 2022, covering articles published between 1980 and 2022. We employed the following search terms across the title, abstract, and keywords of each paper: ["dung beetle*" OR Scarabaeinae OR Aphodiinae OR Geotrupidae) AND ("reproductive behavior*" OR reproduct* OR etholog* OR behavior* OR "reproductive success" OR mating* OR "mating success" OR competition OR combat OR contest) AND (nest* OR nesting OR "nesting behavior" OR "resource reloca*" OR "food reloca*" OR "resource reloca*" behavior OR "resource reloca* behavior"].

Inclusion criteria and screening protocol

The WoS search retrieved 117 articles, of which we included only those meeting the following criteria: (1) the study should be based on species of the subfamily Scarabaeinae, Aphodiinae, or the family Geotrupidae; (2) the study should be conducted within the Neotropics, including also the North of Mexico, and the Andean region (*sensu* Morrone et al., 2022), with species native to the region; (3) the study should evaluate behaviors associated with at least one of the three main reproductive stages of beetles: pre-reproduction, reproduction, or post-reproduction. Behaviors associated with the pre-reproductive stage include rolling, construction, excavation of galleries, food relocation, and some reproductive behaviors such as courtship, competition/combat (intra- and intersexual competition), and copulation. Regarding the reproductive stage, we considered female–male behaviors associated with building nests and nesting galleries, as well as rolling and fighting behaviors that may emerge between individuals trying to obtain food resources for nesting, sperm competition, and female selection. The behaviors observed and recorded after reproduction were considered post-reproductive stages. After reviewing the abstracts and titles of the full WoS search results, we selected 35 articles for a full review. The database was supplemented with 97 articles from the authors' library, as these journals lacked a digital repository or the papers were published before 1980 (Supplementary Table S1).

Data extraction

We extracted the following data from the selected literature: (a) the taxonomic identity of each dung beetles species studied (current names of species were used in case of synonyms or new combinations, Supplementary Table S2); (b) study location, including locality and country; the environment and known food resources of each species (Supplementary Table S3); (c) copulation data observed in different Scarabaeinae species, including duration, location relative to the food ball, and life stage; (d) average duration of nest care and preimaginal development (egg, larvae, pupa, and imago emergence) observed in different Scarabaeinae species; (e) fecundity data of different Scarabaeinae species, including the number of nests or galleries during lifetime, the average number of balls or masses per nest and the number of balls or masses during lifetime; (f) nest characteristics of Scarabaeinae and Geotrupidae (structure, complexity, and location relative to the surface and the food source); (g) male/female nesting behavior (food provisioning, excavation, brood construction, and care); (h) nesting pattern (Supplementary Table S4); (i) Aphodiinae reproductive behavior and preimaginal development data.

Results

We reviewed 132 publications and 146 species associated with at least one of the three reproductive stages: pre-reproductive, reproductive, or post-reproductive. Species were evaluated based on the different recording techniques used, of which 42% were field observations, 23% were laboratory observations, 30% were studies performed under field and laboratory conditions, and 5% did not specify the conditions under which the study was carried out.

Observations associated with the pre-reproductive behavior were mentioned in 100 studies containing 101 species records. We found 119 studies with 132 species focused on reproductive observations, such as those associated with nest building and behaviors that may arise from the defense of limited resources (e.g., food and females). Only 40 papers (30%) included observations related to the post-reproductive stage in 18 species.

Study locations

Studies on various aspects of the reproductive behavior of the Scarabaeidae (Aphodiinae and Scarabaeinae) and Geotrupidae were conducted in 15 countries, ranging from Mexico to Argentina (Figure 4). The recorded species were found mainly in three countries: Mexico (38%), Argentina (28%), and Brazil (21%). The remaining countries had less than three species analyzed (Table 1).

The diversity of localities followed the same order mentioned by country. In Mexico, most of the localities referred to in the studies correspond to 16 states, mainly Veracruz, Chiapas, and the State of Mexico. In Argentina, we recorded 11 provinces, including La Rioja, Jujuy, and San Luis. Brazil included seven states, of which São Paulo and Minas Gerais were most frequently mentioned. Colombia and Uruguay had five and four departments, respectively. For each of the remaining countries, only one or two localities are cited (Figure 4).

Considering the family or subfamily of the beetles evaluated, Scarabaeinae was the most studied group in almost all countries, followed by Aphodiinae, studied only in Mexico and Uruguay, and Geotrupidae, studied only in Mexico and Chile. At the level of the Scarabaeinae tribes, Deltochilini was studied in nine countries, followed by Phanaeini in eight countries, and Dichotomiini, Oniticellini, and Onthophagini in six countries. The Eucraniini tribe was studied exclusively in Argentina, and Coprini in Mexico (Table 1).

Among the Scarabaeinae genera, *Canthon* Hoffmannseg was the most represented, with 22 species in five countries, followed by *Onthophagus* Latreille with 13 species distributed in six countries, *Eurysternus* Dalman with 10 species in six countries, *Deltochilum*

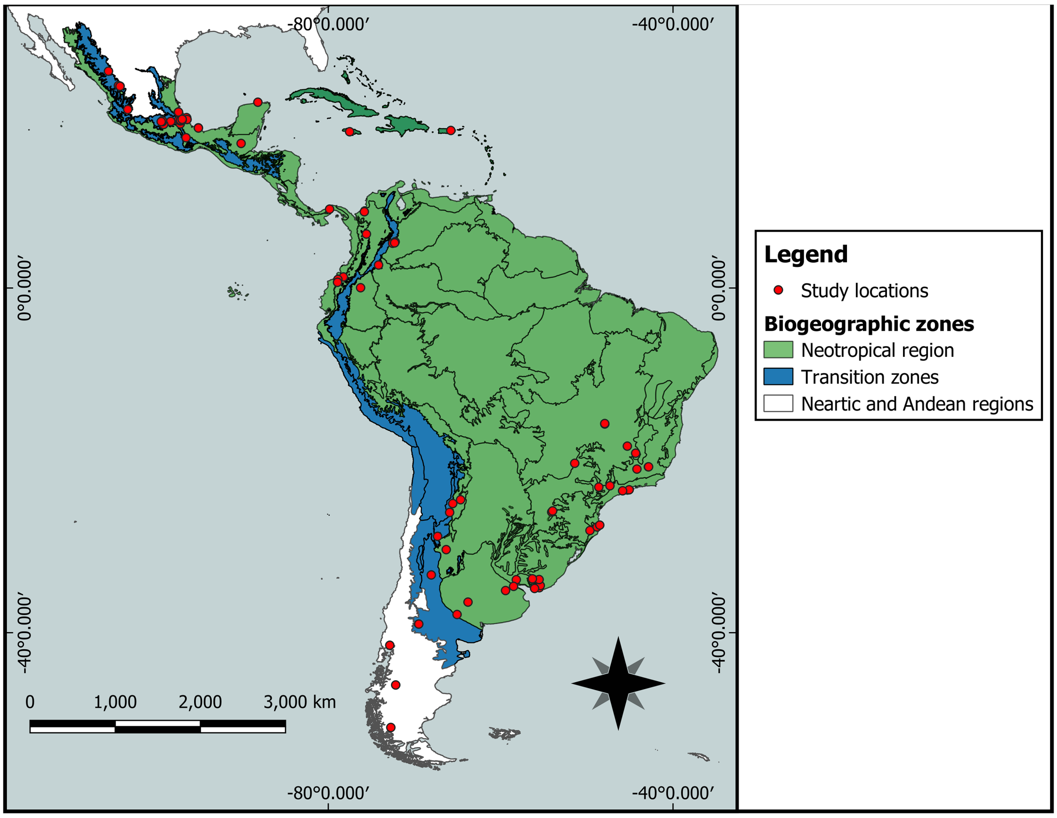

FIGURE 4
Study locations in countries of Latin America regarding the reproductive behavior of Aphodiinae, Scarabaeinae, and Geotrupidae.

TABLE 1 **Paper records on the reproductive behavior of Aphodiinae, Scarabaeinae, and Geotrupidae, according to country, locality, tribe, and study species.**

Tribe	Mex	Arg	Bra	Uru	Col	CR	Chi	Ecu	Pan	Ven	GF	PR	Bol	Gua	Jam
Aphodiinae															
Aphodiini	x		x												
Eupariini	x			x											
Scarabaeinae															
Coprini	x														
Deltochilini	x	x	x	x		x			x	x		x	x	x	
Dichotomiini	x	x	x	x	x		x								
Eucraniini		x													
Oniticellini	x		x		x			x		x	x				
Onthophagini	x	x		x	x	x			x						
Phanaeini	x	x	x	x	x	x		x							x
Geotrupidae															
Ceratotrupini	x														
Geotrupini	x						x								
# locality	16	11	7	4	5	2	3	2	2	1	1	1	1	1	1
# species	54	41	30	8	7	3	2	2	2	2	2	2	1	1	1

Arg: Argentina, Bra: Brazil, Bol: Bolivia, Col: Colombia, CR: Costa Rica, Chi: Chile, Ecu: Ecuador, Gua: Guatemala, GF: French Guiana, Jam: Jamaica, Mex: Mexico, Pan: Panama, PR: Puerto Rico, Uru: Uruguay, Ven: Venezuela.

Eschscholtz with nine species in five countries, and *Dichotomius* Hope with nine species in four countries (Table 2).

Habitats

The habitats where dung beetles display their feeding or reproductive behaviors were mentioned for approximately 97% of the recorded species (Table 2). About half of these species live in native or introduced open environments, such as grasslands in tropical and temperate zones of Mexico, the Pampean region and grasslands of Uruguay, the steppes of Argentina, and the savanna of Brazil. In multiple studies (64%), specimens were collected in fields or pastures dedicated to livestock raising. The species studied within grassland ecosystems were mainly burrower Scarabaeinae (36), with type I, II, or III nesting patterns. Studies on the behavior of roller and non-nesting Aphodiinae species in grasslands were lower (11 and 9, respectively; Table 2; Supplementary Table S3).

Behavioral studies on species collected in forest environments represent one-third of the total; these forest ecosystems include tropical rain forests, temperate mountain forests, or xeric forests, and fruit or forest plantations. Among the species of Scarabaeinae studied in forest ecosystems, 28 were burrower species, and 24 were roller species. A small proportion of all studied species (less than 10%) were recorded in a variety of habitats including native forests, grassland environments, and silvopastoral systems (i.e., *Canthon virens* (Mannerheim) and *Diabroctis cadmus* Harold (Forti et al., 2012; Halffter et al., 2013; Murillo-Ramos et al., 2016). Similarly, *Canthon cyanellus cyanellus* LeConte (Martínez, 1992a,b), and *C. imitator* Brown (Martínez et al., 2019) were collected in both tropical forests and neighboring pastures or crops. The burrower species *Onthophagus curvicornis* Latreille (Montes-Rodríguez, 2017), *Ceratotrupes fronticornis* (Erichson; Ramírez-Restrepo and Halffter, 2016), and *Dichotomius satanas* (Harold; Barretto et al., 2021a,b), which generally occurs in forest environments, also display their activities in pastures dedicated to livestock raising, crops, and even in urban or semi-urban areas. Finally, the tribe Eucraniini represented about 10% of the recorded species studied. These are exclusive burrowers of arid and semi-arid environments, endemic to the northwestern region of Argentina (Zunino et al., 1989; Monteresino and Zunino, 2003; Ocampo, 2005, 2010; Ocampo and Philips, 2005).

Feeding, gallery construction, and food relocation

Coprophagous burrower beetles may feed directly on food or build subterranean galleries to store and later consume the resource during the pre-reproductive stage (Halffter and Matthews, 1966; Halffter and Edmonds, 1982; Halffter et al., 1985; Hanski and Cambefort, 1991; Ocampo and Hawks, 2006; Scholtz, 2009). The pre-reproductive behavior has been studied in detail in eight species of *Phanaeus* (Halffter et al., 1974; Halffter and López, 1977; Price and May, 2009; Huerta et al., 2010). These *Phanaeus* species roll pieces of food some distance away from the source, pushing them with the head and forelegs (butting behavior), then burying them in a feeding gallery for subsequent consumption. According to Huerta and Halffter (2000), in three species of *Copris* Müller (*C. armatus* Harold, *C. lugubris* Boheman and *C. incertus* Say) during the feeding stage, males preferentially store food in sausage-shaped galleries, while females accumulate food masses or nest cakes in subterranean chambers, rather than galleries.

Coprophagous and necrophagous roller species cut and transport a food ball at different distances from the food source, which is used for feeding by sexually immature beetles or nesting by sexually mature beetles (Matthews, 1963; Halffter and Matthews, 1966; Halffter and Edmonds, 1982). During rolling, the beetle pushes the ball with the hind and middle legs; the forelegs are applied on the ground to move the ball. This rolling position is known as the pushing position (Halffter and Matthews, 1966). Most Neotropical species move food by the pushing position. During rolling, the food ball is covered by a layer of soil to avoid its drying out and the arrival of other competitors; in addition, the food ball is protected by chemicals from the exocrine glands of the abdominal and pygidia region of the beetles (Bellés and Favila, 1983; Pluot-Sigwalt, 1988a,b, 1991). The substances released by these glands play multiple functions: defense against competitors such as flies; fungicides or fungistatic; pheromones, and prevention of food decomposition, allowing its consumption by larvae in the brood ball (Favila et al., 2012). However, various species of the genus *Canthon* (e.g., *C. septemmaculatus*, Latterille, *C. tristis*, Harold, *C. obliquus* Horn, *C. edentulus* Harold) and *Deltochilum orbignyi* Blanchard form the food ball but do not roll it; instead, they bury it shallowly below the food source (Halffter and Matthews, 1966; Halffter and Halffter, 1989; Halffter et al., 2013). *Eurysternus* species are considered roller beetles; however, they feed and nest directly below the food source during the pre-reproductive and reproductive stages, respectively (Huerta et al., 2003).

Male competition for food and females

Studies on male competition for food or potential nesting partners are scarce in Neotropical coprophagous dung beetles. Studies on fights between females for food resources are even scarcer. Fight dynamics during the pre-reproductive and reproductive stages have been mentioned or addressed in field and laboratory studies of only six species: *Phanaeus tridens*, Laporte, *Onthophagus acuminatus*, Harold, *Canthon quinquemaculatus*, Laporte, *C. lituratus*, Germar, *C. bispinus* Germar, and *C. cyanellus* (Halffter and Edmonds, 1982; Favila, 1988; Favila and Díaz, 1996; Rodrigues and Flechtmann, 1997; Price and May, 2009; Halffter et al., 2013; Cantil et al., 2014b; González-Vainer, 2015; Salomão et al., 2019).

Pre-reproductive field records on the combat behavior between *Phanaeus tridens* males showed that the winner joins a female, pushing and burying the excrement fragment next to her. Male fights associated with food thievery, gallery invasion and fights between females have been documented in this species (Halffter and Edmonds, 1982; Price and May, 2009). Different fighting strategies for the gallery and the female have been observed in *Onthophagus acuminatus*, where the male owner guards the gallery entrance against intruders and periodically patrols along the tunnel (Emlen, 1997). The owner male fighting to defend the tunnels is horned and mates repeatedly with the occupant female. Intruder males can confront the owner and fight until one of them leaves the tunnel. However, hornless intruder males can also sneak inside, avoiding the guarding male. The intruder male digs side tunnels that intersect guarded tunnels and stealthily

TABLE 2 Number of species by genus in the studied environments.

	Native habitats			Anthropic habitats					
	F	G/OS	Ar/Sar	GG/GOS	C	S	EF	U/Su	Total
Paracoprid									
Anomiopsoides			4						**4**
Ateuchus				1					**1**
Attavicinus	1								**1**
Bolbites				1					**1**
Canthidium	3			2					**5**
Ceratotrupes	1							1	**2**
Copris	3	2		3					**7**
Coprophanaeus	2	2							**4**
Dendropaemon		5							**5**
Diabroctis		1				1			**2**
Dichotomius	2	2		5	1				**10**
Ennearabdus			1						**1**
Eucranium			2						**2**
Eurysternus	11								**11**
Geotrupes	1	1							**2**
Glyphoderus			3						**3**
Gromphas				1					**1**
Liatongus	1								**1**
Ontherus				2			1		**3**
Onthophagus	5	1	1	5			2	1	**10**
Oruscatus				1					**1**
Pedaridium	1	1							**2**
Phanaeus	1	1		3					**5**
Sulcophanaeus	2			4					**6**
Taurocerastes		1							**1**
Tetramereia		1							**1**
Uroxys	1						1		**2**
Telecoprid									
Canthochillum	1								**1**
Canthon	15	4		5	1		1		**26**
Canthonella	1								**1**
Deltochilum	5								**5**
Malagoniella			1	1					**2**
Megathopa				1					**1**
Megathoposoma	1								**1**
Non-nester									
Agrilinellus				1					**1**
Ataenius	1			2			1		**4**
Blackburneus				1					**1**
Cephalocyclus		2							**2**
Gonaphodiellus				1					**1**
Liothorax				1					**1**

(Continued)

TABLE 2 (Continued)

	Native habitats			Anthropic habitats					
	F	G/OS	Ar/Sar	GG/GOS	C	S	EF	U/Su	Total
Planolinellus				1					
Trichaphodiellus	1								**1**
Total	**60**	**24**	**10**	**42**	**2**	**1**	**6**	**2**	**142**

F: Forest; G/OS: Grassland/Open shrubland; Ar/Sar: Arid/Semiarid; GG/GOS: Grazed grassland/Grazed open shrubland; C: Crop; S: Silvopastoril; EF: Exotic forest; U/Su: Urban/Suburban.

copulates with the female of the nest-owning male (Emlen, 1997). The guarding male can catch sneaking males before encountering the female. In this case, sneaking males return to their side tunnels or build new tunnels and remain inactive for several hours, but later they attempt to enter the primary tunnel again in search of the female (Emlen, 1997).

Regarding *Canthon quinquemaculatus* and *C. lituratus,* the theft or splitting of the food ball during rolling has been frequently observed. Specifically, in *C. quinquemaculatus* a case is mentioned where the male rolling the food ball with a female was displaced by the intruder and the female that was rolling with the owner male remained with the thief (Rodrigues and Flechtmann, 1997; Halffter et al., 2013; Cantil et al., 2014b). In *C. bispinus*, intrasexual fights for the food ball were recorded during the food ball rolling and burying by male–female pairs (González-Vainer, 2015).

Fights in *Canthon cyanellus* have been extensively documented in field and laboratory studies. Fights occur mainly between males during the breeding season; intruder males attempt to steal the food ball and the female is transported by an owner male to the nesting site (Favila and Díaz, 1996; Chamorro-Florescano and Favila, 2008). Differences in body size and the reproductive status of females and males (virgins or with previous nesting) influence the fighting success between contestant males for the females transported in the food ball (Chamorro-Florescano and Favila, 2008; Chamorro-Florescano et al., 2011). In *Copris laeviceps* Harold, fights during nesting have also been documented but generated by experimentally placing an intruder female in a nest where brood balls are looked after by a resident female (Klemperer, 1986). Klemperer (1986) also reported cases of a female taking care of brood balls constructed by another female in a foreigner nest.

Mating behavior

Copulation is not easy to observe because it mainly occurs in underground galleries, making it difficult to determine when and how it happens. However, we found information on different aspects of the copulation behavior in 73 species of Neotropical Scarabaeinae beetles (Table 3). The copulation process has been described for only seven species: *Megathoposoma candezei* (Harold; Wille, 1973), *Phanaeus daphnis*, *P. mexicanus* (Halffter and López, 1977), *Liatongus rhinocerulus* (Bates; Halffter and Edmonds, 1982), *Canthon cyanellus*, *C. indigaceus chevrolati* (Martínez and Cruz, 1990), and *Onthophagus acuminatus* (Emlen, 1997).

Halffter and López (1977) defined four stages during copulation: (a) approach of the male to the female, generally near the food source as a meeting place; (b) detection of the female by the male; (c) positive response of the female and male mounting on her and attaching his parameres at the genital opening; (d) insertion of the male aedeagus. During this last stage, males can remain still or include touching or tapping movements with their front legs on the thorax, elytra, or sides of the female, supposedly intended to keep it calm. Although Halffter and Edmonds (1982) considered that there is no elaborate pre-copulatory or courtship behavior among Scarabaeinae, Emlen (1997) interpreted the tapping behavior observed in several species of insects as a copulatory courtship. Finally, at the end of copulation, the male separates and may remain near the female, guarding it against other males, or he may bury himself, searching for food or leaving the nest, depending on the species.

Details related to the site, time, or duration of copulation are only known for 34 species (Table 3), 14 of which are *Canthon* species because these are more easily observed during the rolling of food balls, and for seven *Eurysternus* species next to the food source. The remaining copulation observations correspond to species for which male–female pairs were found at their gallery entrance. A first copulation during the pre-nesting stage, which allows females to complete oocyte maturing and initiate the nesting stage, has only been observed in *Phanaeus mexicanus*, *P. daphnis*, *Canthon cyanellus cyanellus*, *C. indigaceus chevrolati*, *Copris incertus*, and *Eurysternus mexicanus* Harold (Halffter et al., 1976; Halffter and López, 1977; Martínez and Cruz, 1990; Martínez et al., 1996; Huerta et al., 2003). Most copulations observed on the surface at the gallery entrance occur before the nest ball or mass elaboration stage. The copulation duration varied from very short, lasting only one or 2 min in *Coprophanaeus ensifer* (Germar) and *Onthophagus acuminatus* (Emlen, 1997; Lira and Frizzas, 2022), up to maximum times of 75 min in *Canthon cyanellus cynellus* (Martínez and Cruz, 1990) and 84 min in *Eurysternus caribaeus* (Herbst; Huerta et al., 2003). The remaining observed cases ranged from 5 to 40 min (Table 3).

Sperm competition and female selection

Sperm competition in Neotropical dung beetle species has only been studied in *Canthon cyanellus*, observing that the male repeatedly copulates during nesting and before and during the elaboration of nest balls (Favila et al., 2005). It was experimentally demonstrated, with a cuticular genetic marker, that with this behavior, males significantly increase their paternity under a sperm competition scenario (Favila et al., 2005). In another study, Chamorro-Florescano and Favila (2009) found that males regulate copulation frequency during nesting; if the female has already copulated with other males, the latest male increases copulation frequency between the elaboration of nest balls; however, when a male is nesting with a virgin female, he does not mate several times. Besides, only males with previous reproductive experience increase their paternity, contrary to virgin males; that is,

TABLE 3 Copulation data observed in different Scarabaeinae species.

	Copulation			
Tribe / Species	¿Where?	¿When? (DO)	Duration (min)	References[‡]
COPRINI				
Copris incertus	–	10–40 DO /PN	–	Cruz and Huerta (1998), Martínez and Huerta (1997), Martínez et al. (1996)
DELTOCHILINI				
Canthon bispinus	Below food ball	–	30	González-Vainer (2015), Halffter et al. (2013)
Canthon cyanellus cyanellus	–	10–20 DO /PN	30–75	Martínez (1992a), Martínez and Cruz (1990), Halffter et al. (2013)
Canthon edentulus	–	PN / PN care	–	Halffter et al. (2013)
Canthon histrio	–	PN	–	Cortez et al. (2021)
Canthon indigaceus chevrolati	–	20–30 DO /PN	30–40	Martínez (1992a), Martínez and Cruz (1990)
Canthon lituratus	–	post rolling /PN	5.33 to 6.17	Rodrigues and Flechtmann (1997)
Canthon mutabilis	–	PN	–	Halffter et al. (2013)
Canthon obliquus	Near food source	–	–	Halffter and Halffter (1989)
Canthon quinquemaculatus	–	post rolling/PN	–	Cantil et al. (2014b), Halffter et al. (2013)
Canthon rutilans cyanescens	Besides food ball	–	30–40	Carpintero-Hensen et al. (2020), Hernandez et al. (2020)
Canthon rutilans rutilans	–	observed	–	Carpintero-Hensen et al. (2020)
Canthon unicolor	–	PN	–	Cortez et al. (2021)
Canthon virens	–	PN	–	Forti et al. (2012), Halffter et al. (2013)
Megathoposoma candezei	Above food source	–	23	Wille (1973)
DICHOTOMIINI				
Neocanthidium martinezi	In tunnel	–	–	Halffter and Edmonds (1982)
Pedaridium almeidai	In tunnel	PN	–	Verdú and Galante (2001)
Pedaridium brasiliensis	In tunnel	PN	–	Verdú and Galante (2001)
Trichillum externepunctatum	–	observed	–	López et al. (2009)
Uroxys terminalis	Within food source	–	–	González-Vainer and Baruffaldi (2006)
ONITICELLINI				
Eurysternus caribaeus	–	Nuptial feast	19–87	Huerta et al. (2003)
Eurysternus deplanatus	–	PN	–	Huerta et al. (2003)
Eurysternus foedus	–	PN	–	Huerta et al. (2003)
Eurysternus jessopi	–	Forming the ball /PSN	–	Huerta et al. (2003)
Eurysternus marmoreus	–	N	–	Huerta et al. (2003)
Eurysternus mexicanus	–	20–30 DO /pre-infanticice or N	34–40	Huerta et al. (2003), Huerta and Martínez (2008)
Eurysternus plebejus	–	PN	–	Huerta (2012)
Liatongus rhinocerulus	Tunnel entrance	–	15	Anduaga and Halffter (1993), Halffter and Edmonds (1982)
ONTHOPHAGINI				
Onthophagus acuminatus	In tunnel	–	1.4–2.6	Emlen (1997)
Onthophagus lecontei	–	–	17	Arellano et al. (2017)
PHANAEINI				
Coprophanaeus (C.) cyanescens	In tunnel	–	–	Cantil et al. (2015)
Coprophanaeus ensifer	Tunnel entrance	–	1	Lira and Frizzas (2022)
Phanaeus daphnis	Surface	18–64 DO	4–10	Halffter et al. (1974, 1976), Halffter and López (1977)
Phanaeus mexicanus	Surface	14–26 DO	4–10	Halffter et al. (1974, 1976), Halffter and López (1977)
Phanaeus palliatus	Surface	–	–	Halffter et al. (1974)

[‡] The used references used can be found in the Supplementary Table S1.

Days old after emergence (DO); pre-nidification (PN); nidification (N); post-nidification (PSN).

the reproductive experience of the female affects the frequency of mating, and the reproductive status of the male affects its reproductive success during the nesting stage (Chamorro-Florescano and Favila, 2009). In *Canthon edentulus*, copulations have also been observed during the nest care period (Halffter et al., 2013), suggesting that in this species, sperm competition also occurs and that the male can reduce it by repeated mating.

Cryptic choice by females can lead to direct or indirect benefits when choosing the male with whom they will mate (Andersson, 1994). The behaviors of males during combats may be signals allowing females to evaluate and select the most successful males; this, in turn, may be related to attributes indicative of male "quality" (Berglund et al., 1996; Briffa and Sneddon, 2007). Few studies of Neotropical beetles have recorded female behaviors that may reflect the choice or preference towards males with particular attributes. For example, *Canthon cyanellus* females that rolled together with a male were observed to actively participate during male–male combat over attempted ball-stealing by an intruder male, favoring and selecting males with reproductive experience, i.e., with previous mating and nesting (whether intruder or owner) over virgin males (Chamorro-Florescano et al., 2011). Another study found that the combat outcome can significantly affect the reproductive success of both combatants. Winning males increase their acquired paternity under conditions of sperm competition compared to loser males in previous combats (Chamorro-Florescano and Favila, 2016; Chamorro-Florescano et al., 2017).

Sperm competition and cryptic female choices play an essential role for dung beetles during and after copulation. Females copulating with different males may store sperm indefinitely until oocyte fertilization (Halffter and Edmonds, 1982; Eberhard, 1996). However, multiple factors can affect these dynamics. Sexual recognition in dung beetles occurs through cuticular hydrocarbons (Ortiz-Domínguez et al., 2006). These compounds act as short-distance contact pheromones and vary according to several factors, such as the changes at the gonad level in females and males during reproduction (Halffter and López, 1977; Huerta et al., 1981; Martínez and Cruz, 1990; Martínez, 1992b; Martínez and Huerta, 1997; López-Guerrero and Halffter, 2000; Howard and Blomquist, 2005; Huerta and Martínez, 2008; Ginzel, 2010; Favila et al., 2012).

The spermatheca plays a fundamental role in sperm competition and the cryptic choices of females. In Scarabeinae and Aphodiinae, the spermatheca is characterized by a C-shaped sclerotized receptacle with a striated muscle that joins the distal and basal end and a duct. After copulation, sperm migrates through this duct from the spermatophore or seminal fluid to the receptacle, where it is maintained and released until oocyte fertilization (López-Guerrero and Halffter, 2000; Martínez et al., 2001). In the family Geotrupidae, tribe Geotrupini, the spermatheca is pyriform with transverse striations at the base. In most species, it is elongated and has a short duct. Studies suggest that this type of spermatheca is primitive compared to those found in Scarabaeinae (Halffter and Edmonds, 1982; Martínez and Trotta-Moreu, 2010). Although both females and males obtain various benefits by mating with different partners, sperm competition may continue even after copulation under this scenario. However, the female may also perform sperm choice of specific phenotypes by shedding sperm and biasing sperm utilization by muscle contractions, among other possible mechanisms (Eberhard, 1996). These mechanisms have not been explored, but it has been reported that *C. cyanellus* females may benefit certain males having reproductive experience and a successful combat outcome (Chamorro-Florescano and Favila, 2016; Chamorro-Florescano et al., 2017).

Chemical communication at the reproductive stage: Semiochemicals

Chemical communication occurs through semiochemicals, either pheromone for intraspecific interactions or allelochemicals for interspecific interactions (Cortez, 2013). In dung beetles, both compounds are produced by exocrine glands distributed throughout the body, varying according to species and sex, as seen in *Canthon cyanellus*, *C. indigaceus chevrolati* and *C. femoralis* Chevrolat (Favila, 1988, 2001; Pluot-Sigwalt, 1988a,b). However, other attributes influence differences at the glandular level; for example, roller beetles have more exocrine glands than burrower beetles (Pluot-Sigwalt, 1991; Halffter et al., 2013). Glandular asymmetry has evolved in response to the different ecological pressures experienced by roller and burrower beetles, such as the relocation of the food resource competed by conspecific and heterospecific individuals (Hanski and Cambefort, 1991; Favila, 2001).

Since sexually active beetles can also find each other around food to form reproductive pairs, the presence of short- and long-distance sex pheromones during this stage has been suggested (Favila et al., 2012, 2016; Halffter et al., 2013). Recognition in sexually active males and females occurs when both individuals meet, extend their antennae, and touch each other. With this behavior, they can recognize each other through short-distance cuticular compounds. Immature and same-sex individuals will not display cooperative behavior. However, individuals of different sexes or sexually mature collaborate in elaborating and rolling the food ball for subsequent nesting, as demonstrated in *C. cyanellus* (Ortiz-Domínguez et al., 2006).

Long-distance pheromone emission by males has been described in different species of dung beetles, attributed as a strategy to attract females for nesting. However, it has also been suggested that the compounds emitted may repel other males or act as defensive chemicals against potential predators (Favila et al., 2016). During pheromone emission, the male holds the first and second pairs of legs upside down and rubs the abdominal sternites with the hind legs, where several exocrine glands are located. At synchronized time intervals, it rubs its legs and lifts them into the air (Tribe, 1975; Favila and Díaz, 1996; Favila, 2001). This behavior has been reported in different species of dung beetles next to the food source or a food ball, irrespective of whether a female is present, such as *Canthon bispinus*, *C. chalybaeus*, Blanchard, *C. femoralis*, *C. cyanellus*, *C. lituratus*, *C. virens*. However, in all these species, no female was observed arriving (Bellés and Favila, 1983; Favila and Díaz, 1996; Rodrigues and Flechtmann, 1997; Silveira et al., 2006; Vaz-de-Mello and Génier, 2009; Favila et al., 2012; Halffter et al., 2013; Cantil et al., 2014b; González-Vainer, 2015; Martín et al., 2021). In *C. cyanellus* and *C. quiquemaculatus*, the male exhibits this behavior in a nest where a female is already present (Bellés and Favila, 1983; Cantil et al., 2014b). However, two unidentified male species of *Dendropaemon* Perty were observed releasing pheromones, displaying the same behavior described at the chamber entrance. The arrival of a female touching the male's abdomen during the emission behavior, has been described as a recognition behavior in the nesting site, and after this sexual recognition, they enter the gallery (Vaz-de-Mello and Génier, 2009). In *C. femoralis*, once the male buries the food ball, he performs the pheromone emission behavior until the arrival of the female (Favila, 2012).

Allomones are another multifunctional chemical found in dung beetles, related to defense, aggression, and protection of the food resource and the nest. This behavior has been explored in *C. cyanellus*, *C. femoralis* and *Deltochilum furcatum* Laporte (Halffter and Edmonds, 1982; Bellés and Favila, 1983; Favila, 2001; Cortez et al., 2012, 2015; Favila et al., 2012; Ix-Balam et al., 2018). An example of the above is the secretion of the pygidial glands of *C. cyanellus*, which produce chemicals that act as a defensive substance against *Camponotus sericeiventris* Guérin-Méneville (Cortez et al., 2012). When the ant attempts to attack *C. cyanellus*, it approaches the beetle and touches its body with its antennae. However, defensive compounds repel it, such as phenol in *C. cyanellus* and geraniol secreted by the pygidial glands of *C. femoralis*, or guaiacol produced by the pygidial glands of *C. cyanellus* (Favila, 2001; Cortez et al., 2012). In both species, the importance of the compounds released to impregnate and protect the brood balls from fungi has been proven. *Canthon cyanellus* displays nest care during almost all larval development and until the emergence of teneral adults, while *C. femoralis* does not look after the brood ball constructed by the female (Bellés and Favila, 1983; Favila, 2001; Favila et al., 2012). *Deltochilum furcatum* is another species that does not show nest care. It is suggested that pygidial secretions can reduce the oviposition of *Lucilia cuprina* Wiedemann flies on food balls rolled by beetles. However, whether this is due to the effect of secretions on microbial activity or an allomone effect is unknown (Ix-Balam et al., 2018).

The pygidial and abdominal secretions with which dung roller beetles impregnate nest balls during rolling are not only essential to avoid heterospecific competition. The chemicals secreted by the pygidial glands of *C. cyanellus* and *C. femoralis*, such as acetic acid and benzoic acid, have been found to prevent the decomposition of the food with which beetles elaborate nest balls and on which larvae feed until emergence. These compounds also have microbial activities (Favila, 1993; Cortez et al., 2012; Favila et al., 2016).

Nest care and preimaginal development

Subsocial behavior involving nest care by the female until the emergence of offspring is considered a relatively rare behavior within the Scarabaeinae (Halffter et al., 2013). Only 18 species of three genera have been identified in the Neotropical zone, mainly *Copris* and some *Canthon* and *Eurysternus* species, which take care of the nest until a particular stage of preimaginal development. Of special note is the contribution of males during the nest-care phase, albeit for a short time, in five *Canthon* species (Halffter et al., 2013; González-Vainer, 2015) (Table 4).

The nest care duration varies among species, particularly those that have annual cycles and live in temperate zones, such as *Copris armatus* and *C. sierrensis* Matthews, which look after the nest for more than seven and eight months, respectively, until the emergence of the imago, after the winter season ends and temperature improves (Anduaga et al., 1987; Huerta et al., 2010). The other *Copris* species studied are found in more tropical areas, allowing them to have shorter cycles. In these species, care time varies from 47 days on average in *C. laeviceps* to 78 and 88 days on average in *C. lugubris* and *C. incertus*, respectively (Anduaga et al., 1987; Martínez et al., 1996). Four *Canthon* species, *Malagoniella bicolor* (Guerin) and *Megathopa violacea* Blanchard have been identified among the roller dung beetles that perform nest care almost until imago emergence. *Canthon rutilans cyanescens* Harold and *Malagoniella punticollis* (Blanchard) only care for the nest until the larval stage. *Canthon virens* is a particular case, as several studies report that these perform nest-care only during the larval stage, requiring further confirmatory research (Forti et al., 2012; Halffter et al., 2013). In *Canthon mutabilis* Harold, females and males look after the nest only for eight and 5 days, respectively, of the 23 days of preimaginal development (Halffter et al., 2013; Table 4). In *Canthon cyanellus*, the female cares for the nest until the hatching of the offspring, while the male stays in the nest until the female constructs all the brood balls, taking care of both the brood balls and the female to avoid other males mating her (Favila, 1993; Favila et al., 2005).

Among the 11 species of *Eurysternus* studied, seven take care of the nest; in two species, it is undefined whether or not they perform nest caring, and only *E. jessopi* Martínez has been described as not taking care of the nest. The known duration of preimaginal development in this genus varies from 21 days in *E. inflexus* Germar to 83 days on average in *E. marmoreus* Laporte (Huerta et al., 2003, Table 4).

Of all the Neotropical Scarabaeinae species studied, the duration of preimaginal development until the emergence of the imago is known for 43 species. Many species complete their development until emergence within one to two months, as observed in some members of the tribes Deltochilini, Onthophagini, Coprini, Oniticellini, and Dichotomini (Table 4). *Dichotomius (L.) carbonarius* (Mannerheim) and *Attavicinus monstrosus* (Bates) are the only species for which the duration of the larval stage is known. In *Copris sierrensis*, *Dichotomius colonicus* (Say), and *Phanaeus quadridens* (Say), under field conditions, there were still pupae and imagos without emerging 8 months after the onset of preimaginal development, perhaps because they inhabit a temperate zone and were awaiting a more favorable climate to surface (Huerta et al., 2010; Table 4). Therefore, further field or laboratory studies are needed to broaden our understanding of the preimaginal development of multiple dung beetle species, of which little or nothing is currently known.

Fecundity

The fecundity — the number of eggs a female lays over its lifetime — can be considered high in the Aphodiinae (Halffter and Edmonds, 1982). Their nesting behavior is quite simple. The Geotrupidae show a moderate fecundity, with some effort invested in nest building. Finally, in Scarabaeinae, fecundity is relatively low but is compensated by greater reproductive effort or nesting complexity, which may include nest care (Table 5). In this case, some *Copris* species elaborate one to five nests per year or breeding season, with an average of three or four balls per nest (Anduaga et al., 1987; Martínez et al., 1996; Huerta et al., 2010). Also, *Eurysternus* species show a low fecundity, with two to three nests per season and three to five balls per nest, but their nesting behavior can be highly complex. For example, *E. balachowskyi* Halffter and Halffter, *E. caribaeus*, *E. marmoreus*, and *E. mexicanus* build temporary nests that are destroyed before the final nest, implying the likely loss of offspring and a higher fecundity

TABLE 4 Nest care and preimaginal development data observed from different Scarabaeinae species.

Tribe/ Species	Nest care days (mean)	Preimaginal development (days)					References‡
		Egg	Larva	Pupa	Imago pre emergence	Total	
COPRINI							
Copris armatus	175 to 268 (220)	10–29	115–169	50–70	–	175–268	Anduaga et al. (1987)
Copris incertus	72 to 104 (88)	10	45–65	23	–	72–104	Cruz and Huerta (1998), Martínez and Huerta (1997), Martínez et al. (1996)
Copris laeviceps	45 to 49 (47)	6–12	20–35	7–14	–	33–57	Anduaga et al. (1987), Klemperer (1986)
Copris lugubris	(78)	10	40	13	–	63	Anduaga et al. (1987)
Copris sierrensis	Until emergence	–	–	–	+240	–	Huerta et al. (2010)
DELTOCHILINI							
Canthochilum histeroides	–	–	–	–	–	40–50	Matthews (1963)
Canthon bispinus	30–32(♀); 10(♂)	–	–	–	–	40	González-Vainer (2015), Halffter et al. (2013)
Canthon cyanellus cyanellus	25–27 (♀); 5–10(♂)	3	15	10	–	27–28	Martínez (1992a), Martínez and Cruz (1990), Halffter et al. (2013)
Canthon edentulus	26	–	–	–	–	25–28	Halffter et al. (2013)
Canthon histrio	No	–	–	–	–	29–35	Cortez et al. (2021)
Canthon imitator	No	–	–	–	–	30	Martínez et al. (2019)
Canthon indigaceus chevrolati	No	3	15	10	–	27–28	Martínez (1992a), Martínez and Cruz (1990)
Canthon mutabilis	8(♀); 5(♂)	–	–	–	–	22–23	Halffter et al. (2013)
Canthon quinquemaculatus	20 (♀); 5(♂)	–	–	–	–	27–33	Cantil et al. (2014b), Halffter et al. (2013)
Canthon rutilans cyanescens	Until larva	4	18	10	–	33	Carpintero-Hensen et al. (2020), Hernandez et al. (2020)
Canthon rutilans rutilans	–	–	–	–	–	49	Carpintero-Hensen et al. (2020)
Canthon unicolor	No	–	–	–	–	32	Cortez et al. (2021)
Canthon virens	9–11(♀); 4–5(♂) – until emergence	–	–	–	–	26–32	Forti et al. (2012), Halffter et al. (2013)
Malagoniella bicolor	60	–	–	–	–	60	Judulien (1899)
Malagoniella puncticollis	30 d until L3	4.4	24.6	16.7	–	45.7	Palestrini et al. (1994)
Megathopa violacea	60	–	–	–	–	60	Judulien (1899)
DICHOTOMIINI							
Ateuchus aeneomicans	–	–	35–38	25–30	–	60–68	Cárdenas-Castro and Páez-Martínez (2017)
Canthidium moestum	–	6	27	15	–	44	González-Vainer and Morelli (1998)

(Continued)

TABLE 4 (Continued)

Tribe/ Species	Nest care days (mean)	Preimaginal development (days)					References‡
		Egg	Larva	Pupa	Imago pre emergence	Total	
Canthidium sp.	–	–	–	–	–	18–22	Halffter and Halffter (2009)
Dichotomius (L.) carbonarius	–	–	120	–	–	–	Dinghi et al. (2013)
Dichotomius anaglypticus	–	15–25	70–85	180	–	265–290	Alves and Nakano (1977), Cabrera-Walsh and Gandolfo (1996)
Dichotomius colonicus	–	–	–	–	+240	–	Huerta et al. (2010)
Pedaridium almeidai	–	–	–	–	–	63	Verdú and Galante (2001)
Pedaridium brasiliensis	–	–	–	–	–	35	Verdú and Galante (2001)
Trichillum externepunctatum	–	–	–	–	–	30–45	López et al. (2009)
Uroxys terminalis	–	8–14	42–65	11–27	–	67–95	González-Vainer and Baruffaldi (2006)
ONITICELLINI							
Attavicinus monstrosus	–	–	40–45	–	–	–	Anduaga et al. (1976)
Eurysternus balachowskyi	40	–	–	–	–	50	Huerta et al. (2003)
Eurysternus caribaeus	37–71 (54)	–	–	–	–	37–71	Huerta et al. (2003)
Eurysternus inflexus	?	–	15	7	–	21	Huerta et al. (2003)
Eurysternus magnus	52–62 (57)	–	–	–	–	52–62	Huerta et al. (2003)
Eurysternus marmoreus	65–101 (83)	–	–	–	–	65–101	Huerta et al. (2003)
Eurysternus mexicanus	36–58 (47)	–	–	–	–	36–58	Huerta et al. (2003), Huerta and Martínez (2008)
Eurysternus plebejus	33–71 (52)	–	–	–	–	–	Huerta (2012)
Liatongus rhinocerulus	–	10	~90d	~150d	30	~270	Anduaga and Halffter (1993), Halffter and Edmonds (1982)
ONTHOPHAGINI							
Onthophagus batesi	–	6	36	15	–	57	Halffter and Edmonds (1982)
Onthophagus curvicornis	–	2–4	32–39	12–14	–	54–56	Montes-Rodríguez (2017)
Onthophagus hircus	–	6	28	13	–	44	González-Vainer and Morelli (1999)
Onthophagus incensus	–	3–5	22	8–12	–	34–38	Huerta et al. (2010), Martínez et al. (1998)
Onthophagus landolti	–	2–3	20–22	6–8	–	30	Pérez-Cogollo et al. (2015)
Onthophagus lecontei	–	2	22	11	4	39	Arellano et al. (2017)
PHANAEINI							
Phanaeus quadridens	–	–	–	–	+240	–	Huerta et al. (2010)
Sulcophanaeus carnifex	–	9	96	49	21 a 28	154	Klemperer (1983)
Sulcophanaeus menelas	–	11	52	31	–	92	Morelli et al. (1996)

‡The used references used can be found in the Supplementary Table S1.

TABLE 5 Fecundity data of Scarabaeinae species.

	Fecundity			
Tribe/Species	# nests or galleries	# ball or mass / nest (mean)	Balls or mases total (mean)	References[‡]
COPRINI				
Copris armatus	1/year	1–9 (3)	1–9 (3)	Anduaga et al. (1987)
Copris incertus	1–4/ lifetime	3–6	4–18/ lifetime (11)	Cruz and Huerta (1998), Martínez and Huerta (1997), Martínez et al. (1996)
Copris laeviceps	3–5/ year	(9)	27–45/ year	Anduaga et al. (1987), Klemperer (1986)
Copris lugubris	3–4/ year	(4)	12–16	Anduaga et al. (1987)
Copris macclevei		3		Anduaga (2007)
Copris megasoma		2–6 (4.5)		Anduaga and Halffter (1991)
Copris sierrensis	1/ year	4–5	4–5/ year	Huerta et al. (2010)
DELTOCHILINI				
Canthon bispinus	–	2–4	–	González-Vainer (2015), Halffter et al. (2013)
Canthon cyanellus cyanellus	7–8	4–6	30–50	Martínez (1992a), Martínez and Cruz (1990), Halffter et al. (2013)
Canthon edentulus	5	6–14	30–70	Halffter et al. (2013)
Canthon (G.) femoralis	Multiple	1	Multiple	Rivera-Cervantes and Halffter (1999), Favila et al. (2012)
Canthon histrio	–	2–4	2–4	Cortez et al. (2021)
Canthon imitator	–	1 every 4 – 5d	–	Martínez et al. (2019)
Canthon indigaceus chevrolati	30–54	1	30–54	Martínez (1992a), Martínez and Cruz (1990)
Canthon mutabilis	4–5	5	20–25	Halffter et al. (2013)
Canthon muticus	–	6	–	Halffter et al. (2013)
Canthon obliquus	–	1–3	–	Halffter and Halffter (1989)
Canthon quinquemaculatus	1–3	1–5	1–15	Cantil et al. (2014b), Halffter et al. (2013)
Canthon rutilans cyanescens	–	2–11 (6)	–	Carpintero-Hensen et al. (2020), Hernandez et al. (2020)
Canthon rutilans rutilans	–	2–11 (9)	–	Carpintero-Hensen et al. (2020)
Canthon unicolor	–	2–4	2–4	Cortez et al. (2021)
Canthon virens	–	2–3	–	Forti et al. (2012), Halffter et al. (2013)
Delthochilum mexicanum	–	1–3	–	Barretto et al., 2021a
Deltochilum pseudoparile	–	2	–	Halffter and Halffter (2009)
Malagoniella bicolor	–	1	–	Judulien (1899)
Malagoniella puncticollis	Multiple	1–2	Multiple	Palestrini et al. (1994)
Megathopa violacea	–	1	–	Judulien (1899)
DICHOTOMIINI				
Canthidium moestum	–	–	Multiple	González-Vainer and Morelli (1998)
Canthidium sp.	–	1	–	Halffter and Halffter (2009)

(Continued)

TABLE 5 (Continued)

	Fecundity			
Tribe/Species	# nests or galleries	# ball or mass / nest (mean)	Balls or masses total (mean)	References‡
Dichotomius anaglypticus	–	2	–	Alves and Nakano (1977), Cabrera-Walsh and Gandolfo (1996)
Dichotomius colonicus	–	1–2	–	Huerta et al. (2010)
Dichotomius satanas	–	2–9	–	Barretto et al. (2021a)
Neocanthidium martinezi	–	1	–	Halffter and Edmonds (1982)
Ontherus appendiculatus	–	1	–	Cabrera-Walsh and Gandolfo (1996)
Ontherus mexicanus	–	1	–	Cabrera-Walsh and Gandolfo (1996)
Ontherus sulcator	–	1–2	–	González-Vainer et al. (2018)
EUCRANIINI				
Ennearabdus lobocephalus	–	2	–	Monteresino and Zunino (2003)
ONITICELLINI				
Attavicinus monstrosus	–	7	–	Anduaga et al. (1976)
Eurysternus balachowskyi	–	2	–	Huerta et al. (2003)
Eurysternus caribaeus	1–3	2–4	2–12	Huerta et al. (2003)
Eurysternus deplanatus	–	–	Max 5	Huerta et al. (2003)
Eurysternus foedus	–	2–3	–	Huerta et al. (2003)
Eurysternus inflexus	–	3–4	–	Huerta et al. (2003)
Eurysternus jessopi	3–5	4–10	12–50	Huerta et al. (2003)
Eurysternus magnus	–	2–4	–	Huerta et al. (2003)
Eurysternus marmoreus	1–3	3–7	3–21	Huerta et al. (2003)
Eurysternus mexicanus	1–3	2–6	2–18	Huerta et al. (2003), Huerta and Martínez (2008)
Eurysternus plebejus	1–2	2–7	2–14	Huerta (2012)
Liatongus rhinocerulus	1	6–7	6–7	Anduaga and Halffter (1993), Halffter and Edmonds (1982)
ONTHOPHAGINI				
Onthophagus batesi	–	Multiple	"High"	Halffter and Edmonds (1982)
Onthophagus curvicornis	–	2–3	–	Montes-Rodríguez (2017)
Onthophagus incensus	3–5	1–3	3–15	Huerta et al. (2010), Martínez et al. (1998)
Onthophagus lecontei	1–4 galleries	2/ gallery	2–8	Arellano et al. (2017)
PHANAEINI				
Coprophanaeus (C.) cyanescens	–	1	–	Cantil et al., 2015
Coprophanaeus milon	–	2	–	Barattini and Sáenz (1953)
Dichotomius torulosus	–	1	–	Klemperer (1983)
Phanaeus daphnis	–	(3.8)	12 max	Halffter et al. (1974, 1976). Halffter and López (1977)
Phanaeus mexicanus	–	1	12 max	Halffter et al. (1974, 1976), Halffter and López (1977)
Phanaeus palliatus	–	1	12 max	Halffter et al., 1974
Phanaeus quadridens	–	1–2	–	Huerta et al., 2010

(Continued)

TABLE 5 (Continued)

Tribe/Species	Fecundity			References‡
	# nests or galleries	# ball or mass / nest (mean)	Balls or masses total (mean)	
Sulcophanaeus carnifex	–	1	18	Klemperer, 1983
Sulcophanaeus menelas	–	2–3	–	Morelli et al. (1996)

‡The used references used can be found in the Supplementary Table S1.

(Huerta et al., 2003). The species with a simpler behavior and low fecundity include *Liatongus rhinocerulus* Bates, which makes only a single nest per season, consisting of a branched gallery with 6 or 7 nest masses (Anduaga and Halffter, 1993).

Halffter and Edmonds (1982) considered that most Scarabaeinae species produce an average of 20 eggs per female over their lifetime, which still requires significant field and laboratory work to confirm. Although there is plenty of data regarding the nesting behavior of Neotropical species, only 18 species have information on the number of nests or brood balls, brood masses per nest, or galleries built by females over their lifetime or per breeding season. Moreover, 41 species have only partial information. Therefore, there are few species for which the relative fecundity per breeding season is known, obtained from the average number of balls or brood masses produced in each nest. The species known to produce an average of more than 20 eggs over their lifetime or per breeding season include four roller dung beetles: *Canthon mutabilis* (22.5), *C. cyanellus* (37.5), *C. indigaceus chevrolati* (42), and *C. edentulus* (50). On the other hand, those elaborating less than 10 balls or brood masses per breeding season are four species of *Eurysternus*, two of *Copris*, two of *Onthophagus*, and two of *Canthon* (Table 5). In most cases, only the number or type of nest balls or masses found in the field are reported, but further data are required to estimate their fecundity by season.

Nesting behavior patterns: Tunnellers and rollers

Pattern I

The Pattern-I nesting behavior comprises the largest number of records, having been observed in 28 Neotropical species to date, mainly of the genera *Onthophagus* (11 species), *Dichotomius* (6), and *Canthidium* Erichson (4). It has also been occasionally observed in species of *Attavicinus* Philips and Bell and *Liatongus* Reitter (Oniticellini); *Ateuchus* Weber, *Neocanthidium*, and *Uroxys* Westwood (Dichotomiini); *Gromphas* Brullé (Phanaeini) and *Geotrupes* (Geotrupidae; Supplementary Table S4).

The main characteristic of Pattern I is the so-called "brood mass," which is packed in the blind bottom of a simple or branched gallery. The final shape of the brood mass is determined by the cavity, which may be cylindrical (i.e., "sausage-shaped"), oval, or spheroidal (Halffter and Edmonds, 1982). An exception is the nest mass of *Dichotomius carbonarius*, which has a peculiar structure and shape, composed of two connected parts, a lower spherical main structure, and an upper cylindrical protuberance (Dinghi et al., 2013). Also noteworthy is the brood mass of *Neocanthidium martinezi*, Edmonds and Halffter, which is pyriform, resembling a brood ball, resting loosely inside a subterranean cavity. However, it lacks the typical soil cover of brood balls produced by species with a Pattern II nesting behavior (Halffter and Edmonds, 1982).

Pattern-I nests are generally built below the food source. However, individuals of *Canthidium megathopoides,* Boucomont, may cut dung fragments and move them some distance, pushing them with their head and forelegs, before digging a gallery to bury them (Rodrigues and Flechtmann, 1997). This behavior has been extensively observed in several Phanaeini species with a Pattern-II nesting behavior, but not in Pattern-I species. Bisexual cooperation in food provisioning into the nest, whether simple or compound, has been observed in several species with a Pattern-I behavior (Supplementary Table S4). However, only females elaborate brood masses, with a single egg laid in each. *Attavicinus monstrosus* is an exception since the female can oviposit up to three eggs, 10 cm apart, along the sausage-shaped nest (Anduaga et al., 1976; Halffter and Edmonds, 1982).

Regarding the Neotropical Geotrupidae, the nest-building process has been studied in detail only in *Geotrupes cavicollis* Bates in Mexico. This species exhibits a Pattern-I nesting behavior with compound nests and bisexual cooperation, as described above (Halffter et al., 1980b, 1985). Moreover, *Taurocerastes patagonicus* Philippi records showed that they construct galleries up to 35 cm deep stocked with sausage-shaped droppings. These could be only for adult feeding; oviposition was not observed, and larvae of the species were found freely buried, not related to any food mass or gallery (Howden and Peck, 1987).

The majority of the species with Pattern-I behavior studied (72%) elaborate their nests with excrement, mainly bovine, and, to a lesser extent, with feces of other mammals (equines, goats, pigs, rodents, and humans). A considerably lower number of species, which inhabit tropical forests, use various material sources for building their nest masses: fruits, i.e., *Onthophagus rhinolophus* Harold, and *Canthidium* sp. (Halffter and Halffter, 2009; Sarges et al., 2012); decaying leaves, i.e., *Dichotomius carbonarius* (Dinghi et al., 2013); seeds, i.e., *Canthidium laetum* Harold, and *Onthophagus orphnoides* Bates (Halffter and Halffter, 2009); and carrion, i.e., *Canthidium puncticolle* Harold (Halffter and Edmonds, 1982). Other species that live associated with *Atta* Fabricius ant hills in anthropized subtropical and xerophytic scrub environments nest inside or under them, using their detritus as a food source for larvae (i.e., *Ateuchus granigerum* Harold *Attavicinus monstrosus* and *Onthophagus rufescens* Bates; Halffter and Matthews, 1966; Anduaga et al., 1976; Halffter and Halffter, 2009; See Supplementary Table S4). In addition, *Onthophagus browni* Howden and Carthwright, and *Onthophagus coproides* Horn construct their nests exclusively in burrows of the rodents *Neotoma albigula* Hartley and *Thomomys umbrinus* (Richardson), respectively, using their detritus and excrements (Anduaga and Halffter, 1991; Anduaga, 2007).

Pattern II

The Pattern-II nesting behavior has been described in 20 Neotropical species, of which 15 belong to the tribe Phanaeini, genera *Bolbites* Harold (1), *Coprophanaeus* Olsufieff (2), *Diabroctis* Gistel (1) *Oxysternon* Laporte (1), *Phanaeus* (6), and *Sulcophanaeus* Olsufieff (4). The remaining five species belong to Dichotomiini tribe, *Ontherus* Erichson (3) and *Dichotomius* (2) genera (Supplementary Table S4). Regarding the Phanaeini species with incomplete nest descriptions, particularly from the genera *Coprophaneus*, *Phanaeus* and *Sulcophanaeus*, we have considered that their nesting behavior corresponds to pattern II according to Halffter and Edmonds (1982).

In behavioral Pattern II, the excavation and subsequent food provisioning into the nesting gallery usually occur below or to one side of the food source. This characteristic allows classifying these nests as paracoprid. However, the transfer of large food fragments over the surface and a typical paracoprid nest construction has been observed in all the studied *Phanaeus* species. These fragments are pushed and rolled some distance with the head and prothorax or forelegs ("butting" behavior) before being buried. This can be done by the female alone or along with the male, depending on the species (Supplementary Table S4). Upon arrival at the appropriate site, the female starts excavating the gallery. Then the male and the female participate cooperatively in the food provisioning: the male cuts small fragments of food and deposits them at the entrance of the gallery, while the female introduces them into the nest, first by pulling and then pushing them inside (Halffter and López, 1977; Halffter and Edmonds, 1982; Price and May, 2009; Huerta et al., 2010). This butting behavior has also been recorded occasionally for *Oxysternon conspicillatum* Weber (Halffter and Matthews, 1966).

Bisexual cooperation in gallery construction and food provisioning occurs in 15 Phanaeini species of the genera *Bolbites, Coprophanaeus, Phanaeus* and *Sulcophanaeus*, but not in *Oxysternon* or Dichotomiini species with nesting pattern II. In *Coprophanaeus ensifer, Sulcophanaeus leander* (Waterhouse), and several species of *Phanaeus*, both sexes cooperate in both gallery excavation and food storage (Noriega, 2002; Price and May, 2009; Lira and Frizzas, 2022; Supplementary Table S4). In *B. onitoides,* Harold, *S. carnifex* (Linnaeus) and *S. imperator* (Chevrolat), the male introduces food fragments into the upper part of the gallery and the female carries them to the nest chamber to elaborate nest balls; males never enter the nest chamber (Klemperer, 1983; Cabrera-Walsh and Gandolfo, 1996). However, in several of these species, females can also nest alone. Nest care has not been observed in any species with a Pattern-II nesting behavior; the female leaves the nest after elaborating the last ball.

Finally, most species displaying Pattern-II build their nests with herbivorous mammal droppings. Exceptions are *Phanaeus halffterorum* Edmonds, which uses fungi and carrion in pine and oak forests in Mexico (Price and May, 2009), and *Coprophanaeus* species that use omnivorous and carnivorous mammal droppings or carrion in tropical forests and grasslands in South America (Barattini and Sáenz, 1953; Cantil et al., 2015; Lira and Frizzas, 2022).

Cases worth highlighting are the species of the tribe Eucraniini, endemic to the arid and semi-arid region of northwestern Argentina (South American Transition Zone). These burrowing species display a unique behavior: they carry dung pellets with their front legs and move forward with their middle and hind legs to bury them in a deep gallery excavated in advance; this operation is repeated several times. It has been suggested that this telephagic behavior is a strategy to exploit the scattered dry dung, mainly from rodents and camelids, by gathering and rehydrating it in the wetter bottom of tunnels (Zunino et al., 1989). The previous gallery excavation is a typical behavior of burrowing species (paracoprids); therefore, they have been considered paracoprids in this work (Supplementary Table S4).

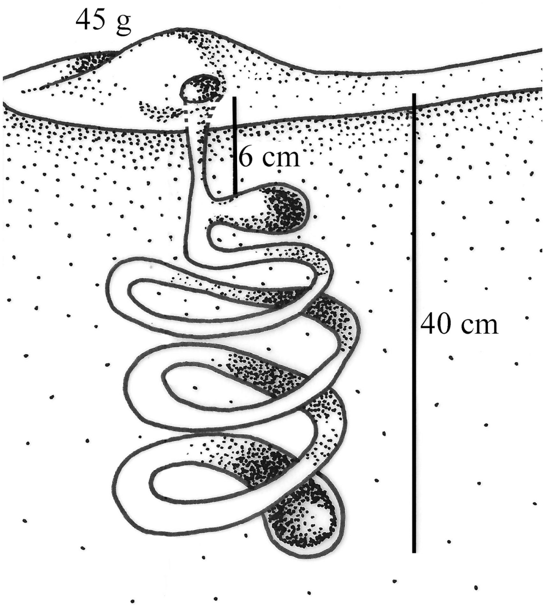

FIGURE 5
Anomiopsoides heteroclyta (Blanchard) nest (modified from Monteresino and Zunino, 2003).

Behavioral studies within the tribe Eucraniini have been conducted in 11 species of the genera *Anomiopsoides* Blackwelder, *Ennearabdus* Lansberge, *Eucranium* Brullé, and *Glyphoderus* Weswood (Zunino et al., 1989; Monteresino and Zunino, 2003; Ocampo, 2004; Ocampo and Philips, 2005; Ocampo, 2005, 2010; Supplementary Table S4). Bisexual cooperation in gallery construction and food provisioning has been recorded in eight species; brood-ball elaboration, only in two: *Anomiopsoides heteroclyta* (Blanchard; unpublished observation by A. Martínez, cited by Monteresino and Zunino, 2003; Figure 5) and *Ennearabdus lobocephalus* (Harold) (Monteresino and Zunino, 2003; Ocampo, 2010). The final nest structure for the other species is unknown. In *E. lobocephalus*, a composite paracoprid nest was built below bovine excrement under experimental conditions. The tunnel was filled like a sausage, and it bifurcated at the distal end, communicating with a lateral gallery containing stored food and a chamber containing two brood balls (Monteresino and Zunino, 2003). The observed characteristics of this paracoprid nest may correspond to a Pattern-II behavior. However, brood balls are not housed in separate chambers, as is typical in the nests corresponding to this pattern. On the other hand, Ocampo and Philips (2005) proposed that *Eucranium arachnoides* Brullé and *E. planicolle,* Burmeister, as well as others of the related genus *Anomiopsoides*, do not elaborate masses or brood-balls, but that larvae develop by feeding freely on fragmented and fermented pellets stored at the bottom of tunnels. These authors observed pupae of *Anomiopsoides* (species not indicated) under laboratory conditions, enclosed in cells made of organic material and sand. Undoubtedly, it is necessary to advance in the knowledge of the nesting behavior of Eucraniini species to define their behavioral patterns in further detail, considering that there may be significant differences in behavior between genera and species of this group.

Pattern III

The Pattern-III nesting behavior has been described for eight species of Neotropical dung beetles of the genus *Copris* (Tribe Coprini) and one species of the genus *Eurysternus* (Oniticellini; Supplementary Table S4) in studies conducted in Mexico. All *Copris* species are paracoprid and subsocial, and their behavior is highly uniform. Females make a nesting cake placed in a spacious chamber built at the end of a gallery. From the cake, brood balls are cut to build compound nests, which are taken care of until the emergence of the offspring. During the nest-care stage, the female adds an outer layer of soil to each brood balls; this, together with the care, protects the progeny from desiccation and fungal attack. There are slight variations between species, particularly regarding nest depth (Anduaga et al., 1987; Huerta and Halffter, 2000). *Copris megasoma* Matthews and Halffter and *Copris macclevei* Warner breed exclusively on gourd excrement (Anduaga and Halffter, 1991; Anduaga, 2007).

The nesting behavior of *Eurysternus foedus* Guérin-Méneville was classified as Pattern III by Huerta et al. (2005). This species builds underground nests where the female store food in a brood mass in a chamber. This mass is not divided into balls, but the female oviposits two to six eggs, where larvae develop. The female takes care of the brood mass until the progeny emerges. All studies on this species have been conducted in Mexico.

Patterns IV and V

Nesting Patterns IV and V correspond to roller species, which belong exclusively to the tribe Deltochilini in the Neotropics. Nesting Pattern IV has been recorded for 15 species, mainly in the genera *Canthon* (8) and *Deltochilum* (4) and occasionally in *Canthochillum* Chapin, *Malagoniella* Martínez, and *Megathopa* Eschscholtz. Nesting Pattern V has been recorded in nine species of *Canthon* and one of *Malagoniella* (Supplementary Table S4).

In most roller species, during the reproductive season, males and females meet at the food source, where they cut and elaborate balls which are rolled together; sometimes, the male initiates the rolling of a ball alone and attracts a female, completing the rolling and burial together. In Pattern IV, the resulting nest is simple, made up of a single brood ball shaped by the female, which she abandons after oviposition. In contrast, Pattern-V nests are compound, cared for by the female for some time, occasionally almost to the emergence of the offspring. Bisexual cooperation in nest care has been observed in some species. The male may remain with the female for nearly the entire duration of preimaginal development (i.e., *Canthon cyanellus cyanellus, C. edentulus* and *Malagoniella puncticollis*), while in other species, the male stays for a shorter time (i.e., *Canthon bispinus, C. rutilans rutilans* Laporte, *C. rutilans cyanescens* Harold and *C. virens virens*). During nest care, the beetle pair does not feed.

Behavior Patterns IV and V have recorded exceptions concerning nest care. Judulien (1899) described the nests of *Malagoniella bicolor* (cited as *Megathopa bicolor*) and *Megathopa violacea* (cited as *Malagoniella intermedia*) in detail, pointing out that these nests are simple and cared for by the female over approximately 2 months. It is necessary to confirm the simple condition of the nests of these species through further studies since this may vary. *Malagoniella puncticollis* normally builds simple nests but occasionally builds compound nests; in all cases, the female cares for them over up to 30 days. *Canthon rutilans cyanescens* builds a simple nest that is cared for by the couple until the larva hatches (Hernandez et al., 2020). *Canthon bispinus*, which makes characteristic Pattern-V nests, also cares for simple nests under laboratory conditions (González-Vainer, 2015). In contrast, in *Canthon mutabilis*, the pair separates and leaves the compound nest after the last oviposition. Males and females can build up to five nests in the same reproductive period under laboratory conditions (Halffter et al., 2013).

Parental care of the nest dramatically increases the survival of the offspring; in *C. cyanellus cyanellus*, brood balls that are left with no parental care are attacked readily by fungi (Favila, 1993). In *C. bispinus*, the female guards the nest for 30 days, resulting in a high progeny survival rate (92%; González-Vainer, 2015). Male *C. c. cyanellus* secretes chemicals in their abdominal glands that prevent the development of fly larvae, saprophagous and entomopathogenic fungi, and phytopathogenic bacteria in brood balls where the female lays the eggs (Favila et al., 2012). Chemical protection of the brood in roller beetles does not necessarily require the presence of the female or both parents in the nest. *Canthon femoralis femoralis* builds simple nests and leaves them on the surface; however, it probably has a defense and protection mechanism for brood balls by depositing more stable chemicals than those produced by *C. c. cyanellus* (Favila et al., 2012). In *C. rutilans cyanescens,* it was observed that the female defecates on the chamber walls before placing the egg and that the couple often walks on the ball, probably applying protective chemical secretions, until the larva hatches (Hernandez et al., 2020).

Brood balls of roller species are typically pear- or teardrop-shaped, usually covered by thick layers of soil, except for *C. edentulus*, which lacks a cover (Halffter et al., 2013). However, several studies do not indicate this aspect of the brood ball structure. The nests of most species are housed either in surface chambers covered with soil or leaves or underground, reaching 60 cm depth, as in the case of *Deltochilum orbignyi* (Halffter and Matthews, 1966).

Some species of roller dung beetles do not roll the brood balls but make them, whether simple or compound, in underground or surface chambers below the food source or at the soil-excrement interface. These species are *Canthochilum histeroides,* (Harold) *Canthon edentulus, C. mutabilis, C. obliquus* and *D. orbignyi* (Matthews, 1963; Halffter and Matthews, 1966; Halffter and Halffter, 1989; Halffter et al., 2013). In the case of *C. mutabilis,* this condition is facultative and depends on the size of the food source: if it is large, beetles make paracoprid nests; if it is small, beetles build telecoprid nests (Halffter et al., 2013).

Approximately 70% of the nests described for roller species are made exclusively with dung, mostly from herbivorous mammals. Nests built preferably with feces of omnivorous mammals have been recorded to a much lesser extent, as are the cases of *C. femoralis femoralis*, which displays a clear preference for monkey feces (Rivera-Cervantes and Halffter, 1999) and *C. rutilans cyanescens* which prefers *Cerdocyon thous (crab-eating fox)* dung to make the brood balls (Hernandez et al., 2020). Another species, *Canthon rutilans rutilans* build nests exclusively with dung from omnivorous and carnivorous mammals (Carpintero-Hensen et al., 2020). Only four species were found to build their nests with carrion: *Canthon bispinus, C. cyanellus cyanellus, C. virens virens* and *C. virens aff.*

paraguayanus Balthasar (Halffter and Edmonds, 1982; Favila and Díaz, 1996; Halffter et al., 2013; Cantil et al., 2014a; González-Vainer, 2015). *Canthon mutabilis* has been the only recorded species capable of successfully building its nests with carrion and dung (Halffter et al., 2013), while *Deltochilum pseudoparile* Paulian builds nests with both feces and decomposed *Brosimum alicastrum* Swartz fruits (Halffter and Halffter, 2009; Halffter et al., 2013; Supplementary Table S3).

Concerning necrophagous species, most experimental studies have used beef or fish as food resources with which the species studied have built their nests. However, in the field, *C. c. cyanellus* has occasionally been observed feeding on carcasses of crickets and other dung beetles of the genera *Phanaeus* and *Copris* (Villalobos et al., 1998). In laboratory conditions, *C. c. cyanellus* can make food balls with the abdominal contents of crickets; even more, it can successfully build nests with the body of the diplopod *Orthoporus ornatus* (Girard) (Villalobos et al., 1998).

Another necrophagous species, *Canthon virens virens*, has been observed in the field feeding on the bodies of different arthropods such as Diplopods, Heteroptera, Coleoptera, and Lepidoptera. Under laboratory conditions, it can build nests with the bodies of crickets and cockroaches, both alive and dead, being an opportunistic predator (Halffter et al., 2013). In addition, several field studies have recorded that *C. v. virens* is an active predator of female ants of the genus *Atta* Fabricius during the short period of their nuptial flight after the ants clip their wings (Hertel and Colli, 1998; Vaz-De-Mello et al., 1998; Silveira et al., 2006; Forti et al., 2012). The female of *C. v. virens* catches an ant, decapitates it, rolls its body, buries it superficially, and makes two or three brood ball with it (Silveira et al., 2006; Forti et al., 2012).

Another necrophagous roller species that is an opportunistic predator is *Canthon chalybeus,* which preys on the snail *Bulimulus apodemetes* d'Orbigny (Martín et al., 2021). Males and females can kill a healthy snail, cut its shell, and roll its body into a ball. This beetle can also use snail carcasses. *Canthon morsei* has also been observed feeding on a wounded, still-living specimen of the diplopod *Rhysodesmus dasypus* (Gervais) (Villalobos et al., 1998), and it has been caught in pitfall traps baited with carcasses of the millipedes *Amplinus bitumidus* and *Anadenobolus putealis* (Bedoussac et al., 2007). Necrophagous species likely use the bodies of dead or dying invertebrates found in their habitat to build their nests. The capability of feeding and nesting with the flesh of wounded invertebrates could have been an evolutionary step before the development of the predation behavior of some Deltochilini (Villalobos et al., 1998; Martín et al., 2021).

Pattern VI

Pattern VI groups most species of the genus *Eurysternus* (Halffter, 1977; Halffter and Edmonds, 1982) with known reproductive behavior. This Neotropical genus includes a total of 53 species (Génier, 2009); the feeding and nesting behavior has been studied only in 10 of these, mainly in Mexico (Génier, 2009; Supplementary Table S3). Except for *E. foedus,* whose female builds brood masses, the known behavior of this genus consists of building balls solely for nesting. Males of the species studied have never been observed performing this behavior (Huerta et al., 2003). Adults feed directly above or below the food source. No straightforward relocation of food has been observed during nesting; the female builds the balls by getting under the food and moving within it, using her middle legs as oars (see Halffter et al., 1980a).

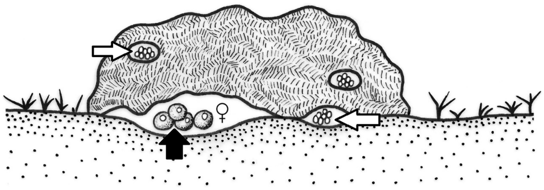

FIGURE 6
Oviposition sites of the Aphodiinae within the dung mass or at the dung-soil interface (white arrows), as also observed in some *Eurysternus* species (black arrow).

The *Eurysternus* species studied show several differences (Supplementary Table S4; Huerta et al., 2003). Some supposed subsocial species do not care for their offspring. The morphological characteristics of this genus are directly related to their nesting behavior and cannot be related to any of the evolutionary lines of the Scarabaeinae (paracoprids and telecoprids), nor can they be considered endocoprids because they do not nest within the dung mass but at the dung-soil interface (Figure 6; Halffter et al., 1980a).

Aphodiinae reproductive behavior

Studies on the reproductive behavior of the subfamily Aphodiinae are few, consisting of scarce data on eight species of Aphodiini and three of Eupariini, mainly from Mexico. They are coprophagous dwellers that do not build nests but lay their eggs in the dung or at the dung-soil interface, depending on the species (Figure 6). The knowledge state of gonad maturity in both sexes helped to distinguish young from already mature individuals, as in *Gonaphodiellus opisthius* (Bates), *Cephalocyclus hogei,* (Bates) *Planolinellus vittatus* (Say), and the three *Ataenius* Harold species studied (Cruz et al., 2002; Martínez and Suárez, 2012; González-Vainer et al., 2018). The other species practically emerge mature and ready to reproduce. Most of the lifetime of Aphodiinae beetles is spent in the preimaginal stages or diapause; when adults emerge, they have a short period of activity lasting two or 3 months to reproduce, and then they die (Table 6).

Although there are data available on the phenology and reproductive cycles of several species of Mexican Aphodiini (see Martínez et al., 2022), information on their reproductive behavior is scarce, including mating and oviposition, since they are not easy to observe given their small size and because they spend most of their time inside the dung pats. Martínez et al. (2022) synthesize the available information on the reproductive cycles of some Aphodiini: *Agrilinellus ornatus* (Schmidt), *G. opisthius*, and *Liothorax levatus* (Schmidt), by characterizing mature, maturing, or immature individuals by ovary size variations, and the presence or absence of spermatozoa in the female spermatheca once they have already copulated. While in males, it is mainly due to the size of the glandular reservoir. In Eupariini, besides the anatomical variations mentioned to characterize the maturity state of individuals, in *Ataenius perforatus* Harold was possibly observed copulating inside the dung mass, at the end of which a spermatophore is formed in the vagina of females. This structure

TABLE 6 Pre-reproductive and reproductive behavior data, and preimaginal development time (days) for Neotropical Aphodiinae species.

	PR	RP			Preimaginal development				
Tribe/ Species	Inmature individual	Copula	Spm	Egg number	Egg (d)	Larva (d)	Pupa (d)	Total (d)	References‡
APHODIINI									
Agrilinellus ornatus	N.O.	N.O.	N.O.	–	–	–	–	–	Martínez (2005)
Gonaphodiellus opisthius	O	N.O.	N.O.	15–18	–	–	–	–	Martínez and Alvarado (2001), Cruz et al. (2002), Martínez and Suárez (2012)
Blackburneus salylorea	N.O.	N.O.	N.O.	8	4–5	16	5	15–26	Martínez and Suárez (2012)
Cephalocyclus durangoensis	N.O.	N.O.	–	–	–	–	–	–	Martínez and Suárez (2012)
Cephalocyclus hogei	O	O	O	–	–	–	–	–	Cruz et al. (2002), Martínez (2005)
Liothorax levatus	N.O.	N.O.	N.O.	–	–	–	–	–	Martínez (2005), Martínez and Suárez (2012)
Planolinellus vittatus	N.O.	N.O.	N.O.	–	3–4	7–8	7–8	18–20	Martínez (2008), Martínez and Suárez (2012)
Trichaphodiellus brasiliensis	–	–	–	–	–	43	12	55	Verdú and Galante (1997)
EUPARIINI									
Ataenius apicalis	O	N.O.	O	16–18	–	21	14	28–35	Martínez and Cruz (1990), Cruz and Martínez (2002)
Ataenius perforatus	O	O	O	10–12	5–7	38.7	10.5	45–66	González-Vainer (2015)
Ataenius sculptor	O	N.O	O	16–18	–	28	7	35	Martínez and Cruz (1990), Cruz and Martínez (2002)

Pre-reproductive period (PR), reproductive period (RP), (O: observed; N.O.: not observed; Spm: spermatophore; d: days).
‡The used references used can be found in the Supplementary Table S1.

was also observed in the other two *Ataenius* species studied and only in a single Aphodiini species (*Cephalocyclus hogei*; Cruz et al., 2002). The number of eggs laid is known for some species, such as *G. opisthius*, which lays 15 to 18 agglutinated eggs in an underground chamber under the manure, and *Blackburneus saylorea* (Robinson), which lays eight eggs per nesting chamber in the two to three chambers it builds over its lifetime (Cruz et al., 2002). In *Planolinellus vittatus*, each egg is deposited in a laying chamber built within the manure still wet from the manure crust, although the total number of eggs laid per female is not reported (Martínez, 2008). On the other hand, in the three studied *Ataenius* species, eggs may be laid either under the manure or at the manure-soil interface; the number of eggs laid varies from 10 to 18 eggs per clutch. Finally, the time elapsed from preimaginal development to imago formation is known for only three Aphodiini species and all three Eupariini species. This time varies from 19 days to 66 days. The development time of each preimaginal stage is known for only four species; most of this time is spent in the larval stage (Table 6).

Geotrupidae breeding behavior

Studies on the reproductive behavior of Geotrupidae species are also scarce in the Neotropics. There are data on only four species belonging to two tribes — Ceratotrupini and Geotrupini —of which three are Mexican, and one is Chilean (Supplementary Table S4). All these species are coprophagous and paracoprid; the exception is *Taurocerastes patagonicus*, considered roller or telecoprid for moving food with its front legs; it is also a rare species that does not fly (Howden and Peck, 1987).

The species with the best-known reproductive behavior is *Geotrupes cavicollis*, observed under laboratory conditions (Halffter et al., 1980b, 1985); there is less information for the other species

(Supplementary Table S4). This species also undergo maturation after emerging, and immature individuals build simple feeding galleries near or under the manure at a maximum depth of 10 cm. This period lasts 35 to 40 days after emergence; the reproductive period begins when the male and the female copulate at the gallery entrance for 10 min. Food is stored in galleries with the couple's collaboration during this period. The nest comprises a maximum of five galleries, each with one egg in the distal end. In rare cases, two eggs can be laid per gallery, with soil in between the two eggs; the second was laid 24 h after the first. The subsequent oviposition took place 10 to 15 days later. Geotrupidae nest range between eight to 21 cm in depth, depending on the galleries and their radial or parallel distribution, with an average length of 21.5 cm. According to Halffter et al. (1980b, 1985), for the female to continue laying more than one or two eggs, the male must copulate and help with nest provisioning. Within each brood mass, preimaginal development starts with the embryo, and it takes 10 days for the larva to hatch; the larval stage lasts 210 days, followed by pupae, which take 44 days, and then the adult or imago remains in the nest for 30 to 40 days before emerging to the surface. Females die after 80 to 90 days (maximum 140 days) and only lay five eggs over their lifetime. However, females of *G. cavicollis* still have large oocytes not laid, differing from Scarabaeinae and Aphodiinae species, in which females show the reduction of their oocytes before dying (Martínez, 1992a,b; Martínez et al., 1996; Martínez, 2008; Martínez and Suárez, 2012).

Regarding the other species, *Ceratotrupes fronticornis* (Erichson) buries dog feces to build nests, but the type of the nest is not mentioned (Ramírez-Restrepo and Halffter, 2016). In *Geotrupes (Halffterius) rufoclavatus* Jekel, females oviposit in February because they have matured or maturing ovaries; however, no information is available on their oviposition behavior or the type of nest (Trotta-Moreu et al., 2007). Finally, in *Taurocerastes patagonicus*, one study describes that food is moved as pellets, then buried in simple, winding galleries inclined 70° and measuring 10 to 35 cm long (Howden and Peck, 1987). At the bottom, they accumulate food, forming a mass 5 to 7 cm long by 2 to 3 cm high. Nevertheless, it is not mentioned whether this food is only for adults or also for the young. Although male–female pairs were observed inside the gallery with food, no eggs were found. In another site, larvae were observed buried at 35 cm depth, although not associated with any food reserve or mass (Howden and Peck, 1987). Further studies are required to clarify this peculiar behavior.

Discussion

This review found that behavioral studies on dung beetles have been carried out on a low number of species (146), considering that the estimated richness of Scarabaeinae alone in the Neotropical region is approximately 1,250 species (Escobar, 2000). If the Aphodiinae and Geotrupidae are also included, behavioral studies have been conducted on less than 10% of the total dung beetle species. These studies are more abundant for Scarabaeinae (85%) compared to Aphodiinae (9%) and Geotrupidae (6%). The above is partly due to the number of Scarabaeinae species recorded in the Neotropics; more specifically, because only in the subfamily Scarabaeinae food relocation and nest construction are key features of the adult behavior in the vast majority of their species (Halffter and Edmonds, 1982); therefore, they constitute interesting model for behavioral studies. The pre-nesting stage has been studied in 101 Scarabaeinae species, the reproductive stage in 128 species, and the post-reproductive stage in only 18 species. Forty-two percent of the behavioral studies were based on field observations, 23% on laboratory observations, 30% under both field and laboratory conditions, and 5% were unspecified.

Behavioral studies on Neotropical Scarabaeinae species have been performed in 15 countries, mainly Mexico, Brazil, and Argentina. For the subfamily Aphodiinae, behavioral studies have been carried out only in Mexico and Uruguay, whereas some species of Geotrupidae have been studied only in Mexico and Chile. This review highlights the need to conduct further behavioral studies in several Central-South American and Caribbean countries, including Guatemala, El Salvador, Honduras, Nicaragua, Cuba, Haiti, Paraguay, Peru, Guyana, and Suriname. Isolated studies have been carried out in Venezuela, Bolivia, Ecuador, Chile, and Jamaica. The lack of behavioral studies for the Amazon rainforest has also become evident, particularly in Brazil, where such studies have addressed the southern area of this country. Although it is necessary to continue behavioral studies on Neotropical species from a biogeographical point of view, studies should also address the species inhabiting the Caribbean and Amazonian subregions (*sensu* Morrone et al., 2022). The above is increasingly urgent, given the accelerated loss of tropical rainforests. It is also necessary to fill the information gap on species inhabiting some provinces within the Chacoan subregion (e.g., Caatinga and Chaco), as well as on species living in the South American Transition Zone and the Andean region.

Another critical aspect is that at least one-half of the studied species were collected in open habitats (i.e., grasslands of temperate zones of Mexico, the Pampean region, and steppes of Argentina, or grasslands of Uruguay and the savanna in Brazil). These species are related to livestock and are burrowing species, with nesting Patterns I, II, and III. Only one-third of the studies have been conducted on both tropical and temperate forest species, mostly on burrowing species. Human activities profoundly modify native Neotropical environments; records of the dung beetle species studied indicate that only a small proportion of them (less than 10%) are habitat generalists that live in native forests, grasslands, and silvopastoral systems. Therefore, few dung beetle species may adapt to the continuous changes occurring in this region.

Feeding is crucial for dung beetles because it allows them to perform all their functions, including sexual maturation and reproduction. Intraspecific and interspecific male competition for food and females, which occurs during the pre-reproductive and reproductive stages, has been studied in a few burrowing and roller species. Although most of these studies have focused on fights between males, few have evaluated fights for these resources between females. Mate selection by males and females is fundamental for the reproductive success of dung beetle species. Fights have been analyzed in detail only for *Canthon cyanellus*. Evaluating the factors involved in the ability to win or lose a fight for limited resources and once this competition is transferred to the sperm level or the cryptic selection by females is still limited. Comparative studies will be highly relevant to explore the behavioral patterns within the context of evolutionary and ecological pressures the species have been exposed to during the pre-reproductive, reproductive, and post-reproductive stages.

Copulation has been described only in seven species. The duration of copulation has been recorded only in roller species because it generally occurs during the ball-rolling phase or in shallow nests. Few species have records regarding courtship before and during copulation and its incidence on reproductive success. Likewise, chemical communication has been investigated only in roller species; however, the effect of pheromones on intraspecific interactions and allelochemicals on interspecific interactions has been studied in a few roller species.

Although studies on nesting behavior in Scarabaeinae have been carried out on few species, most are representative of all the behavioral patterns proposed by Halffter and Edmonds (1982) and belong to almost all Neotropical tribes (e.g., Deltochilini, Coprini, Phanaeini, Dichotomiini, Oniticellini, and Onthophagini). Over the past 40 years, these studies have deepened our knowledge of behavioral patterns in dung beetles and revealed their plasticity. Subsocial behavior, the degree of development that varies among species, has also been studied in detail. This behavior has been analyzed mainly in *Copris* and some *Canthon* and *Eurysternus* species, which take care of the nest until a particular stage of preimaginal development. Conversely, the incipient knowledge about the nesting behavior of the Eucraniini has evidenced that it does not conform to any known patterns, highlighting it as a group of great interest for study.

This work has identified a few species for which there is a considerable accumulation of knowledge, ideal for answering questions or testing particular hypotheses. *Canthon cyanellus* is a good model for behavioral studies (Favila, 2001), also known as a model system (Dugatkin, 2001). Undoubtedly, studying the reproductive behavior of dung beetles in their environment, where their behavior is displayed naturally, is fundamental for understanding the ecological processes surrounding the variation in the reproductive behavior of each species. Transferring these studies to the laboratory allows us to have controlled conditions and test hypothesis that can be quantified regarding the effect of previously identified variables that affect or regulate behavioral patterns. Both field and laboratory data are essential for understanding the ecological processes and evolutionary contexts of Neotropical dung beetles. However, laboratory studies can only be conducted for some species, whereas only some are sound model systems for behavioral studies. The above depends on several conditions that must be controlled to maintain the reproductive behavior of the studied dung beetle species, which is hard to achieve. This is one of the main reasons why conclusive laboratory results have yet to be obtained for some species of dung beetles.

Finally, it is necessary to continue studying the behavioral biology and ecology of dung beetles in their original habitats in Neotropical forests since these habitats are being heavily anthropized, and information on many species is still lacking (about 88% of the richness estimated of Scarabaeinae). We risk losing species or altering behavioral patterns due to the effects of these macro and micro environmental changes on the Neotropical region, which are likely to affect species' survival and the environmental services provided by this group of beetles.

Author contributions

All authors listed have made a substantial, direct, and intellectual contribution to the work and approved it for publication.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

Supplementary material

The Supplementary material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2023.1102477/full#supplementary-material

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Toward a standardized methodology for sampling dung beetles (Coleoptera: Scarabaeinae) in the Neotropics: A critical review

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Introduction: The standardization of sampling protocols is imperative for robustly studying any taxonomic group. Replicable methods allow the comparison of data between different spatial and temporal studies. In the case of dung beetles, one of the best-studied indicator groups in analyses of environmental disturbance, a wide range of collection methodologies are used, from basic pitfall traps to more complex or complementary methods such as mini-Winkler extractor. Also, different types of attractive baits, sampling effort, durations, and designs are used in dung beetle studies. Variations in methodological approaches are particularly noted in the Neotropics, which may be related to the vast number of biological strategies and behavior of dung beetles that inhabit this region. A lack of methodological unification for the Neotropical region makes a cross-sectional analysis of the information impossible.

Methods: We performed a compilation and analytical review of the existing literature for dung beetle sampling in the Neotropics, discussing the most used methodologies, their advantages and disadvantages, and specific cases in which particular models are more efficient.

Results: Pitfall traps baited with human excrement are the most common sampling method, but there is a wide range of models and variations in the structure of this trap. The complementary effect generated by flight interception traps, light

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traps, and direct collections, particularly within microhabitats, is exciting for the potential of finding new species. Some methodologies, such as mini-Winkler extractor, fogging, or very specific baits, are infrequently used.

Discussion: There was a lack of inclusion of spatial and temporal variation among studies. Therefore, it is necessary to consider broader sampling windows, which include different spatial scales, seasons, and years. Finally, we propose a standard protocol for sampling dung beetles in the Neotropics, depending on each objective, and including a basic methodology for obtaining complete local inventories.

KEYWORDS

collecting methodology, flight intercept traps, monitoring protocol, tropical America, Scarabaeidae, survey

Introduction

Biodiversity, a somewhat loosely delineated concept in the ecological literature, needs defining for every case where it is used. In many situations, it is meant to describe all the species in an area; in others, it is restricted to one group of organisms. The latter is probably a more precise measure if one is trying to compare different habitats or locations. Defining biodiversity as a metric for a group of similar and related species allows a more accurate picture of the effect of geography, habitat, altitude, or other comparisons among species comprising these locations. It has been well-documented that there is declining species abundance and richness across the globe, which is why these studies are so critical. The diversity of birds (Fujisaki et al., 2008), amphibians (Becker et al., 2007), and mammals (Spooner et al., 2018), among many other groups, were documented as declining, with causes ranging from climate change, overhunting, and the introduction of exotic species. Nevertheless, fewer investigations have examined insect declines in the Neotropics (Scheffers et al., 2012; Cardoso and Leather, 2019; Cardoso et al., 2020). In order to clearly assess biodiversity within a biological group, robust and standardized surveying methodologies are required. However, many different methodologies have been employed to study each biological group, and this issue may pose challenges regarding the comparisons among studies.

The Neotropics comprise multiple ecosystems that are biodiversity hotspots for many taxa (Myers et al., 2000; Durães et al., 2013; Ríos-Touma and Ramírez, 2019). While controversy remains about the species extinction risk of tropical deforestation (Laurance, 2007), the current increase in habitat loss has become a critical concern for many vulnerable species and the environment as a whole (Barbosa et al., 2021). The Neotropics are particularly vulnerable because of uncontrolled logging, cattle ranching, mining, and farming (Gibbs et al., 2010; Ferreira et al., 2014). Numerous studies have documented the effect of anthropic activity, with declines in many species and extirpation of others (e.g., Noriega et al., 2021a). These works often examine species that are especially vulnerable to habitat change and are considered indicators. Such bioindicators are plants or animals that are thought of as "canaries in the coal mine," meaning they may be the initial species to show declines or actual physiological changes with disturbance (Salomão et al., 2019a). These species are often considered bioindicators because they also have important roles in the local ecology (Vulinec, 2002; Valente-Neto et al., 2021). Different insect groups are often referred as bioindicators because of their relative ease of capture and standardized methodology, rapid response to environmental degradation, and cost efficiency ratio (Gardner T. et al., 2008). Recent studies have included dragonflies (Silva et al., 2021), ants (Pérez-Espona, 2021; da Silva W. B. et al., 2022), and butterflies (Doré et al., 2021) as bioindicators, among others.

Dung beetles (Coleoptera: Scarabaeinae) feature as one of the best-studied indicator groups in the analysis of environmental disturbance (e.g., Nichols et al., 2007; Gardner T. et al., 2008). Most of the studies have shown significant changes in dung beetle richness and abundance with even small changes in intact forests (Nichols et al., 2007). The presence of dung beetles also indicates that large mammals are present, providing the food source for dung beetles (Vulinec et al., 2006; Raine and Slade, 2019; Correa-Cuadros et al., 2022). There are, however, a wide range of sampling methodologies for dung beetles, from basic pitfall traps to more complex or complementary methods such as mini-Winkler extractor (Iannuzzi et al., 2021). These varied methodologies and sampling efforts make comparisons difficult among the many studies. In this scenario, the standardization of sampling protocols is an imperative need for studying any taxonomic group. Replicable methods allow for comparing data between different spatial and temporal studies. Nevertheless, no consensus allows a methodological unification, presenting works with different sampling designs that make a cross-sectional analysis of the information impossible. Among the biogeographic domains, Neotropical regions comprise one of the best-studied areas regarding dung beetle ecology, thus serving as a model region to depict the dynamics of ecological studies in dung beetles. In this paper, we thus focus on the Neotropical region to make a cross-sectional analysis of the importance of different types of traps, baits, sampling efforts, durations, and designs in sampling dung beetles. We also reviewed several studies to determine the most employed methodologies for the analysis of the effect of habitat alteration on dung beetle richness and abundance. Finally, after reviewing the existing literature, we propose a protocol for the group aiming for standardizations in dung beetle sampling in the Neotropics.

Materials and methods

Literature search and inclusion criteria

We performed a literature search following the PRISMA methodology (Page et al., 2021) to identify articles dealing with dung beetle trap sampling published from 1968 to 2021 (maximum time search window). Firstly, we conducted bibliographic queries in Web of Science (WoS) and Scientific Electronic Library Online (SciELO) databases using the keyword string: ("scarab*" OR "escarab*" OR "dung beetle*") AND ("neotropic*" OR "tropic*") AND ("trap*" OR "tramp*"), looking for matches in the title, abstract, and/or keywords. Therefore, from the initial search (updated on February 2022), we retrieved 4,799 records (WoS = 4,632 and SciELO = 167). We then eliminated duplicate records, studies out of the boundaries of the Neotropics (see Morrone et al., 2022), experimental, meta-analysis, revision, taxonomical or without richness data associated with trapping (i.e., articles that appeared more than once in the different search engines or the same platform due to typographical errors). All references not related to any dung beetle species of the subfamily Scarabaeinae were also excluded.

The following information was collected from each selected publication: year of publication, author(s), title, journal, language, country, biomes, ecosystems, if the study is about disturbances and what type of disturbance it is, geographic coordinates, elevation, trap type, the number of traps used, time active of each trap, bait, study approach (i.e., taxonomic or ecological), number of samples in space (spatial replicates), number of samplings in time (temporal replicates), seasonality, and any relevant additional observation. It is important to clarify that an article can represent more than one item for the analysis. For more detailed information from each of the analyzed studies, please see Supplementary Annex 1. To keep consistency with the literature, we used the biogeographical proposal by Morrone et al. (2022) to standardize and unify the biomes.

Publication bias

This literature search type has several limitations, which were carefully considered when analyzing the data and interpreting the results. First, the search may miss some relevant papers simply because either the title, abstract, or keywords did not contain the focal keywords. Other authors have previously identified these limitations using similar search approaches (see Prather et al., 2013). It is evident that the language, especially in the Neotropical region, is a limiting factor in the search and that articles in Spanish and Portuguese could have been left out. Finally, we may have failed to include some works that were not indexed by the platforms used here. Despite these limitations, we believe that the data retrieved gives us enough relevant information to examine general trends in dung beetle trapping research in the Neotropics. With our current literature revision, we may identify knowledge gaps that could help us to develop future research strategies to build more precise methodological approaches.

Results

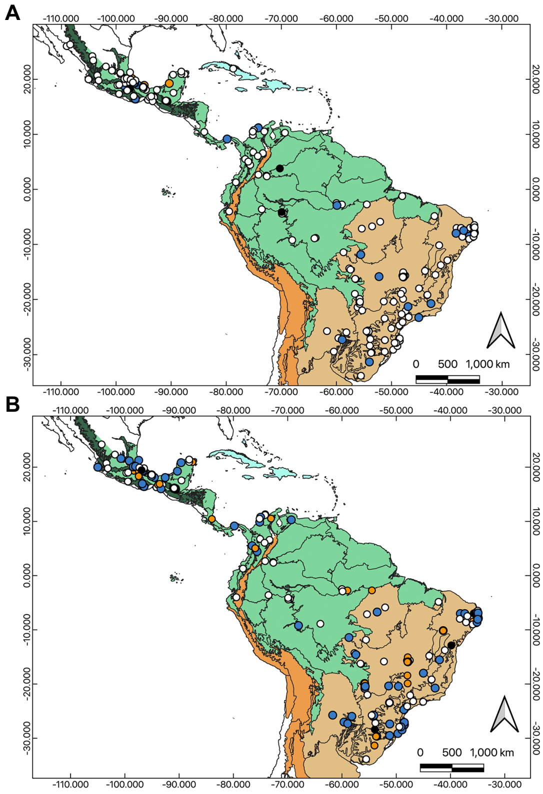


FIGURE 1
Distribution of published studies of dung beetles sampling compiled in our dataset in the biogeographical regions in the Neotropics. Each dot corresponds to one paper. **(A)** Studies using only pitfall trap (open diamonds), and other complementary traps. One trap (open dots), two traps (light gray dots), three traps (dark gray dots), and four traps (black dots). **(B)** Studies using different types of baits. One bait (open dots), two baits (light gray dots), three baits (dark gray dots), and four baits (black dots).

As a result of our bibliographic search, we found 241 articles studying dung beetles in the Neotropical region (Figure 1; Supplementary Annex 1). We recorded evidence of a marked trend toward an increase in publications on dung beetles in the last three decades (Figure 2A). We registered very few works in the 90s and none before 1990, which is related to the restrictions of the search method and the words used. Most of the registered articles are in English (*n* = 194, 80.5%), followed by Spanish and Portuguese (Figure 2B). We find a wide variety of registered journals, with more than 74 different journals. The journals with the highest number of articles included are Revista Brasileira de Entomologia, Journal of Insect Conservation, Revista Mexicana de Biodiversidad, Neotropical Entomology, and PLoS ONE (Figure 2C).

Biogeographical evaluation (regions and countries)

Twelve countries are represented in our dataset, comprising almost the full range of the Neotropical region, with the southernmost study being carried out in Uruguay and the northernmost in Mexico (Figures 1, 2D). The studies included South, Central, North America, and the Caribbean. Brazil had the largest number of studies (*n* = 122, 50.6%), followed by Mexico (*n* = 80; 33.2%), and Colombia (*n* = 19, 7.9%; Figure 2D). Data from these three countries represented 91.7% of our

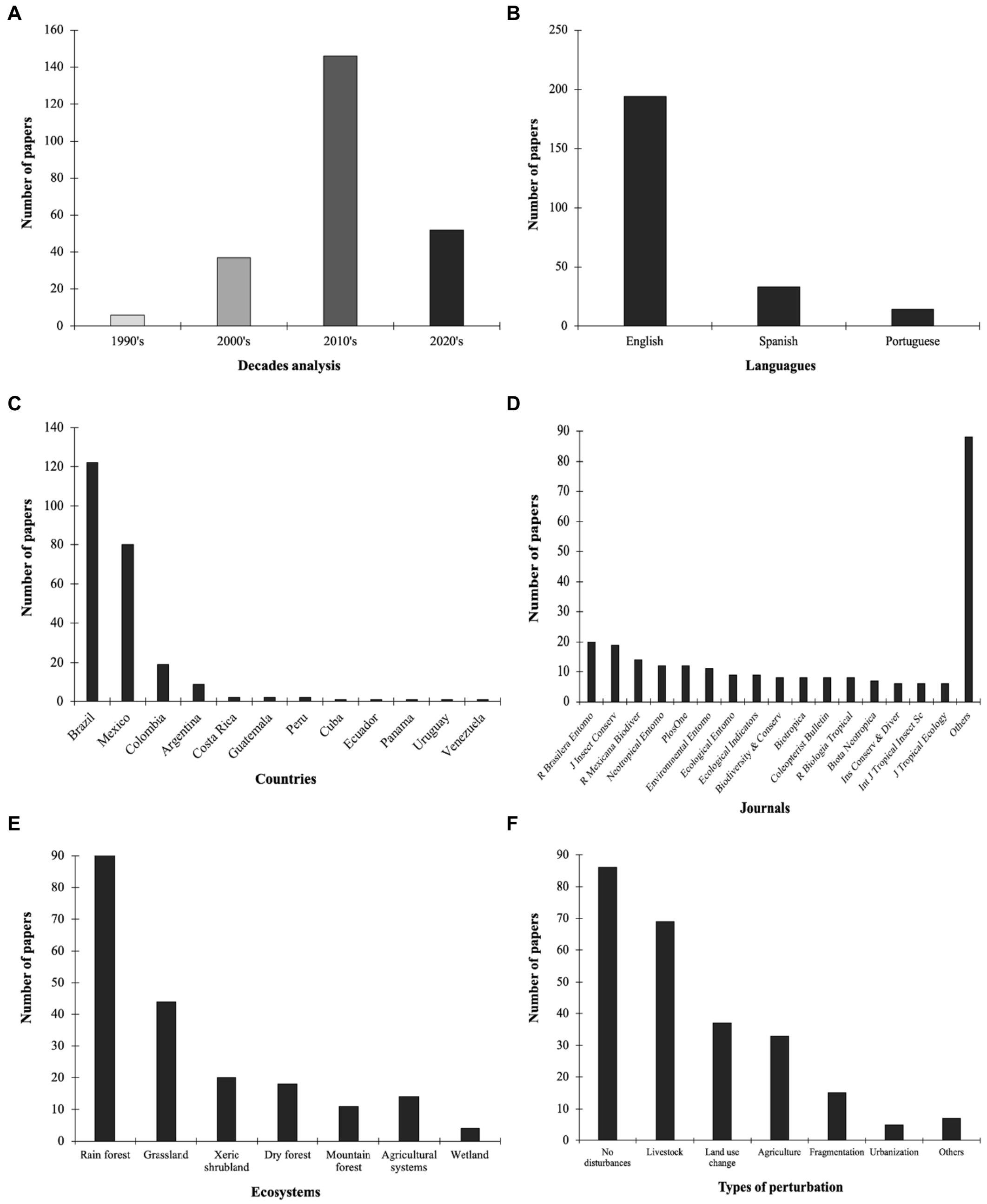


FIGURE 2
Number of published papers on dung beetle sampling compiled in the Neotropics according to different variables: **(A)** Decades analysis; **(B)** Languages; **(C)** Journals; **(D)** Countries; **(E)** Ecosystems; and **(F)** Types of perturbation.

dataset. Argentina was represented by nine papers (3.7%). Among the countries with the lowest number of publications in this review, Costa Rica, Guatemala, and Peru were represented by two papers each (0.8%); Cuba, Ecuador, Panama, Uruguay, and Venezuela were represented by only one study each (0.4%). Nine countries, within the Neotropical region had no studies recorded in this review. In Brazil, most studies took place in the Paraná dominion (Atlantic province, Araucaria Forest province, and Paraná Forest province) and Chacoan dominion (Caatinga province and Cerrado province). In Mexico, most studies were conducted in the Mexican Transition Zone (Trans-Mexican Volcanic Belt province) and the Mesoamerican dominion (Veracruzan province and Yucatán Peninsula province). In Colombia, most studies belonged to the Pacific dominion (Guajira province, Magdalena province). To cite some prolific researchers in Mexico: G. Halffter, M.E. Favila, A. Estrada, L. Arellano, and R.P. Salomão; in Brazil: J.N.C. Louzada, F.Z. Vaz-de-Mello, M.I.M. Hernández, P.G. da Silva, and C.M.A. Correa; and in Colombia: L.C. Pardo-Locarno, F. Escobar, and J.A. Noriega.

Researched ecosystems, natural, and unnatural

Natural forests were the most studied ecosystem, with 62.6% of the reviewed studies (n =151; Figure 2E). Among them, tropical rainforests showed the highest number of papers (*n* =122, 50.6%), followed by dry forests (*n* =18, 7.5%), and mountain forest (*n* =11, 4.5%). Other natural ecosystems, such as xeric shrubland and wetlands, represented together 9.9% of the total number of studies. Research on Neotropical dung beetles also showed a high number of papers in other non-forested ecosystems. Among these papers, some of the most studied include grassland (including both natural and anthropic, with 18.2%) and agricultural systems (5.8%; Figure 2E) which encompassed coffee, corn, or oil palm plantations. In addition, around two-thirds of the studies evaluated dung beetles under the effects of anthropic disturbance (Figure 2F). Among them, livestock was the most studied anthropic impact (*n* =69, 28.6%), but other agriculture or fragmentation were also common.

Type and number of traps

Pitfall traps were used in the majority of studies (*n* =206, 85.48%), while manual capture (*n* =21, 8.71%), light traps (*n* =13, 5.39%), flight interception traps (*n* =11, 4.56%), and NTP-80 (permanent necro trap model 80, *n* =7, 2.90%) were less frequently used. Carp traps, dung pats, Malaise traps, aerial traps, Shannon traps, and platform traps were used in very few studies (totaling *n* =17, 7.05%; Figure 3A). None of the typical techniques were used in a small number of studies (*n* =5; 2.07%); instead, other observations or experimental methodologies were used. Most studies (*n* =208, 86.31%) surveyed dung beetles using only one trap type, two trap types were simultaneously used in 21 studies (8.71%), while three trap types were used in one study (0.41%) and four different types were used in four studies (1.66%; Figure 3B). Pitfall traps were used as the only surveying method in 182 (75.52%) studies; samplings using exclusively manual capture was performed in eight studies (3.32%), and light traps were only used in seven studies (2.90%). Studies using only flight interception traps to sample dung beetles comprised four studies (1.66%).

Overall, studies that used more than one sampling method always used pitfall traps (e.g., pitfall and light traps, pitfall and NTP-80, pitfall and platform traps, pitfall and Shannon traps, pitfall and carp traps). In very few studies, pitfall traps were combined with flight interception traps (*n* =6, 2.49%) and direct collection (*n* =5, 2.07%). Among the studies that used pitfall traps, the number of traps ranged from four to more than 300 traps. Almost one-third of the studies (*n* =62, 30.10%) had a sampling effort ranging from four to 20 traps. In 42 of the analyzed studies (20.39%), there was a sampling effort ranging from 21 to 60 traps; in 73 of the studies (35.43%) from 61 to 300 traps were used; 300 or more traps in 26 studies (12.62%; Figure 3C). In three studies (1.46%), the number of traps used was not reported.

Type, number, and quantity of bait

Baited techniques to sample dung beetles were used in most of the studies analyzed, and only 2.9% used non-baited collecting methods. Human dung was the most used bait, corresponding to 56% of the papers evaluated (*n* =135). Secondly, carrion was used in 41.5% of the studies (*n* =100), followed by cattle dung (*n* =42, 17.4%) and pig dung (*n* =34, 14.1%; Figure 3D). In a smaller number of studies, other dung types were used as baits, including horse, wild vertebrate [native and exotic species, e.g., waterbuck – *Kobus ellipsiprymnus* (Ogilby, 1833) and jaguar – *Panthera onca* (Linnaeus, 1758)], and combinations of different types of dung, such as human and pig dung. There was no consensus concerning the number of baits used in the sampling protocols. Almost half of the papers (*n* =110, 45.6%) used only one bait type, whereas 35.2% (*n* =85) of them used two types of bait and 9.1% used three types of bait (*n* =22; Figure 3E). The amount of bait used varied and ranged from 25 g to 35 g (*n* =48, 19.9%), followed by 40–50 g (*n* =41, 17.0%), and 5–25 g (*n* =31, 12.8%; Figure 3F). Nonetheless, a significant number of analyzed papers (*n* =86, 35.6%) did not include this information.

Time, distance between traps, and spatial sampling

A considerable number of studies did not present a clear temporal (*n* =48, 19%) and spatial (*n* =52, 21.6%) distribution of traps. This included studies with unclear sampling techniques or studies with sampling techniques that did not comprise the use of traps *per se* (e.g., direct collection in dung pats). The time length during which traps were kept active in the experiments varied greatly, ranging from 24 h (1 day) to more than 480 h (20 days; Figure 4A). Among the studies that reported the time in which traps were kept active in the field, most of them had traps installed for 48 h (*n* =114, 47.3%), followed by 24 h (*n* =40, 16.6%), with fewer choosing 480 h or more (*n* =28, 11.6%). Three studies (1.2%) let traps remain active for <24 h. Distances between traps varied widely, from 2 m to 1,000 m (Figure 4B). From the studies in which trap spacing was reported, most of them had traps spaced 50 m apart (*n* =76, 40.2%). A considerable number of studies used the spacing intervals 2–20 m (*n* =52, 27.5%) and 25–40 m (*n* =25, 13.2%), while a few studies spaced traps more than 50 m (from 60 m to 100 m, *n* =13, 6.8%; 150 m or more, *n* =11, 5.8%). In terms of spatial sampling, of the 241 articles reviewed, the majority (>55%) used between 1 and 3 replicates per study, however a single replica was used by most of the authors (Figure 4C). Forty percent used more than four replicates, of these less than half (45%) used more than 10 replicates. A minority of studies (4%) did not give sufficient information on the sampling.

Seasonality and temporal sampling

Concerning temporal variation, research conducted throughout the year corresponded to only 22.8% (*n* =55) of the papers reviewed (Figure 4D). In general, research was carried out only in the rainy season (*n* =89, 36.9%), while other works also include the dry season with 20.3% of the total (Figure 4E). There are very few studies carried out only in the dry season, as well as papers that do not present explicit information about the time of year in which the study took place.

Discussion

Biogeographical evaluation and researched ecosystems

The large number of studies found in Brazil, Mexico, and Colombia reflects the pioneering aspect and growth of research centers and researchers aimed at studying the biology, ecology, and

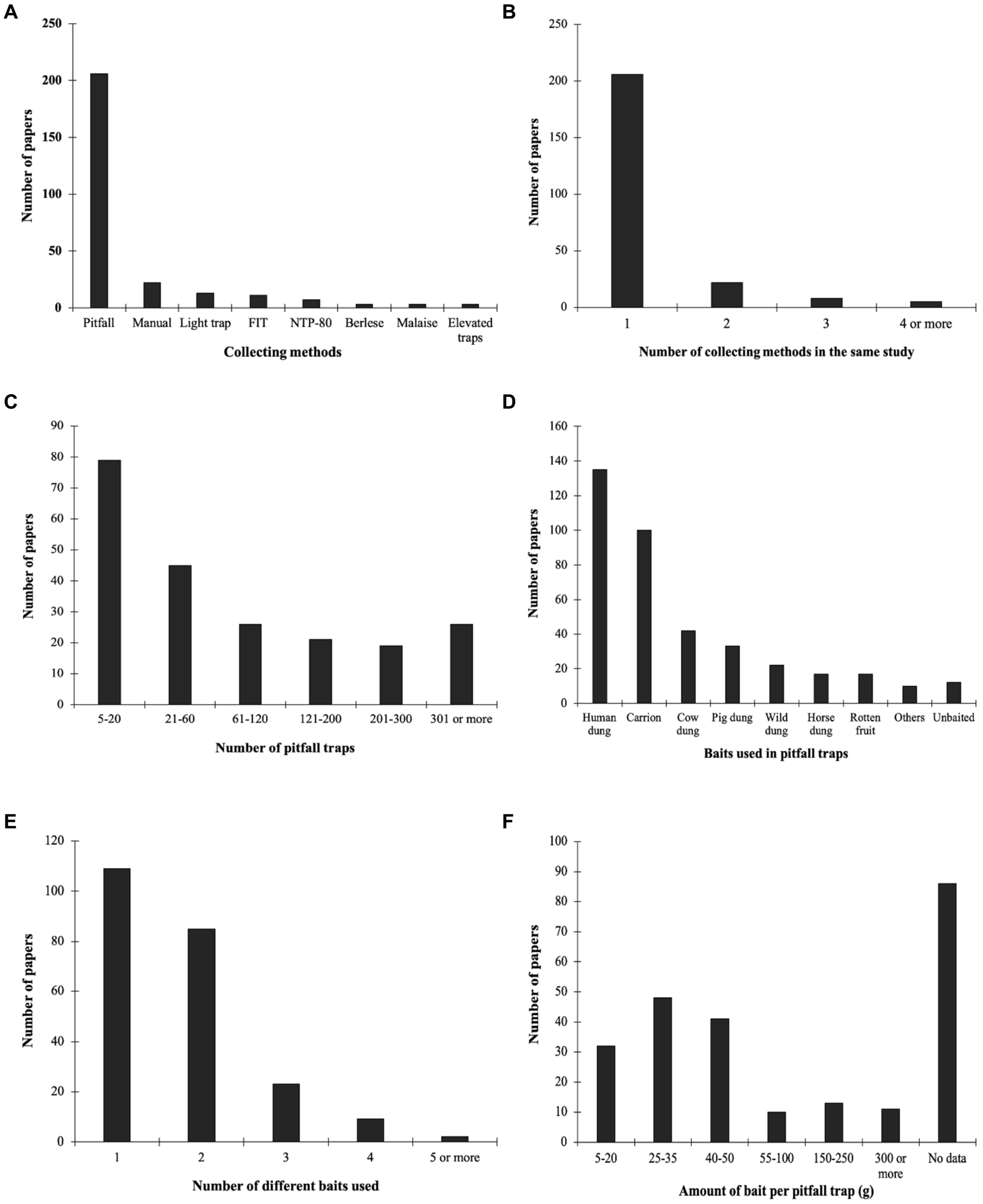


FIGURE 3
Number of published papers on dung beetle sampling compiled in the Neotropics according to different variables: **(A)** Collecting methods; **(B)** Number of collecting methods in the same study; **(C)** Number of pitfall traps; **(D)** Baits used in pitfall traps; **(E)** Number of different baits used; and **(F)** Amount of bait per pitfall trap.

taxonomy of Scarabaeinae in these countries. Most of the work carried out with dung beetles in the Neotropics is carried out in natural forest environments, likely due to the large coverage of Neotropical forest biomes, but also strongly influenced by the geographical location of researchers throughout history, initially focused on Mexico with the pioneering work carried out by Halffter and collaborators. After the proposal on using dung beetles as ecological indicators (Halffter and Favila, 1993), many works emerged comparing communities in pristine and anthropized environments (e.g., Gardner T. A. et al., 2008; López-Bedoya et al., 2021, 2022). When comparing multiple environments (i.e., natural vs. anthropic), it is necessary to carefully standardize the sampling methodology, to avoid collecting bias. For example, baits placed in environments with high direct solar incidence can quickly lose efficiency due to water loss (Lobo et al., 1998) representing a potential bias on capture rates between environments. Several classical studies of the 90's or previous were not included; these papers are found in local or not indexed journals. These are located in Mexico and Brazil, but this does not alter the general pattern. Almost 14 provinces do not show any studies in this work, which suggest low or null effort, particularly in the Subregion called the South American

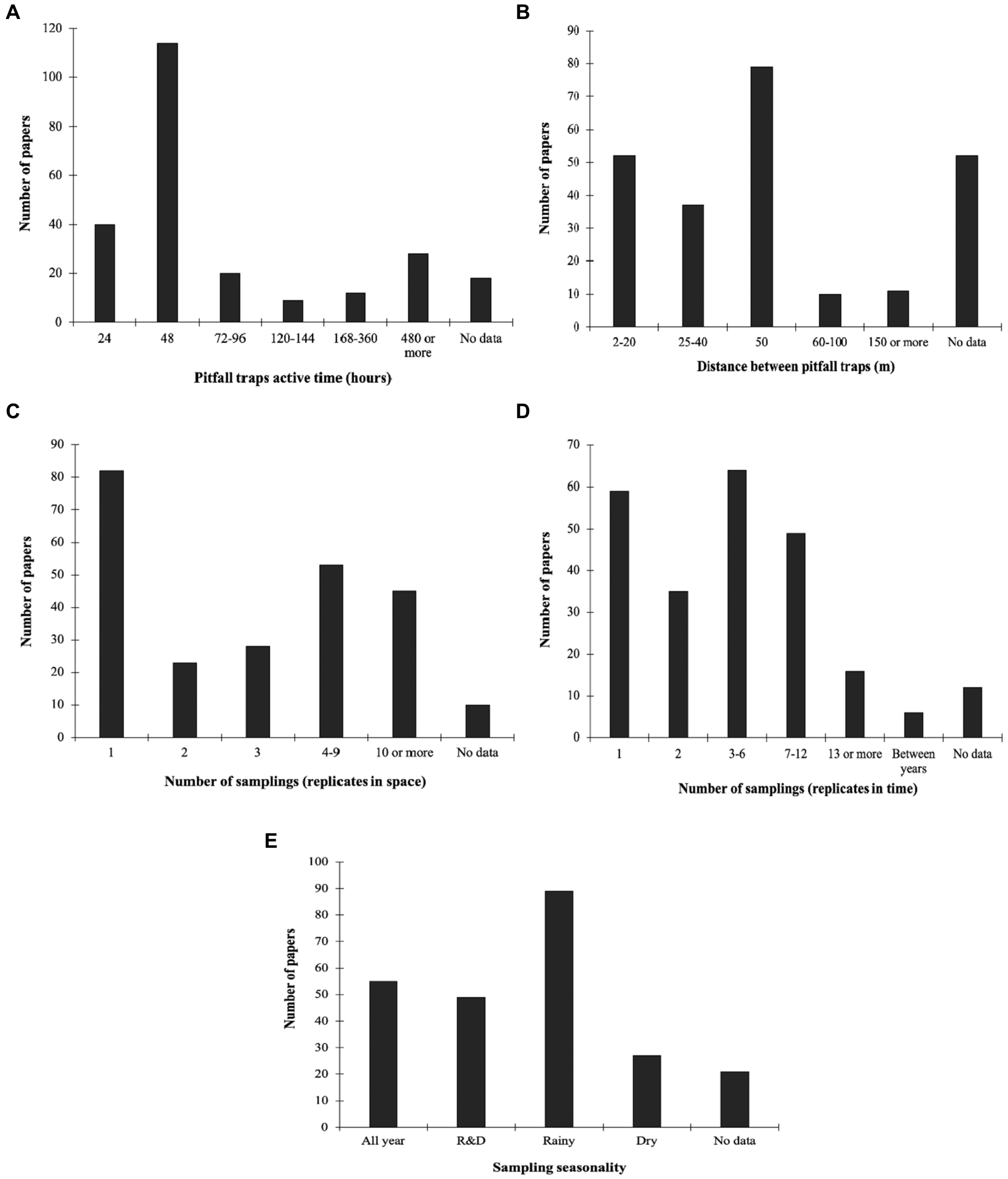


FIGURE 4
Number of published papers on dung beetle sampling compiled in the Neotropics according to different variables: **(A)** Pitfall traps active time; **(B)** Distance between pitfall traps; **(C)** Number of samplings in space; **(D)** Number of samplings in time; and **(E)** Sampling seasonality.

Transition zone. In the following paragraphs, we will discuss the findings of this revision and suggest trends encompassing sampling protocols, aiming to improve and guide future ecological studies with dung beetles.

Type and number of traps

Pitfall traps consist of a container buried at ground-surface level filled with liquid (soapy water or ethanol), allowing crawling animals to fall in but preventing them from leaving (Southwood, 1978; Brown and Matthews, 2016). Our results show that pitfall traps are the dominant method for capturing dung beetles. However, there is a great diversity of models of this trap (Lobo et al., 1988; Veiga et al., 1989; Halffter and Favila, 1993) that have been implemented throughout history to capture a great diversity of taxa (e.g., Newton and Peck, 1975; Spence and Niemelä, 1994; Buchholz and Möller, 2018). The use, adaptation, and importance of pitfall traps for dung beetle capture were described by Lobo et al. (1988), Veiga et al. (1989), and Halffter and Favila (1993). Pitfall traps are popular because they are inexpensive and relatively simple to construct, install, collect, and are efficient in capturing beetles, especially when combined with bait suspended above the trap (Lobo et al., 1988; Halffter and Favila, 1993; Kočárek, 2000; Hohbein and Conway, 2018). The design of pitfall traps is not universal (Lobo et al., 1988), being contingent on the creativity of researchers (e.g., Porter, 2005; McKnight et al., 2013; Buchholz and

Möller, 2018), availability of resources, and characteristics of the ecosystem where they are deployed (e.g., Spence and Niemelä, 1994; Porter, 2005; Noriega and Fagua, 2009). This is the main reason why a clear description of the trap adaptations used is essential, so methodologies are replicable, and results are comparable (Brown and Matthews, 2016; Hohbein and Conway, 2018); rather than simply stating that "pitfall traps were used to capture beetles" (e.g., Sarges et al., 2012; Trujillo-Miranda et al., 2016; Salomão et al., 2019a). On the other hand, we must also consider that the current trends that focus on publishing shorter and more precise publications often results in articles with limited methodological descriptions, removing details of trapping methods.

The number of traps set has not been contemplated in most studies evaluating different aspects of the methodological design of studies using pitfall traps (Boetzl et al., 2018). In the few studies that have considered it, the number of traps was identified as one of the most critical factors in the sampling design (Engel et al., 2017). However, there has been and continues to be a considerable variation in the number of traps used in studies (Brown and Matthews, 2016), and dung beetles are no exception (see Supplementary Annex 1). In most studies, 10–40 pitfall traps were placed per sampling event. However, there are studies in which the number of traps implemented exceeded one thousand (e.g., Estrada et al., 1999; Sarges et al., 2012; Bourg et al., 2016), and the most extreme case evaluated is 2,400 active traps per sampling event (Estrada and Coates-Estrada, 2002). However, some studies do not include the number of pitfall traps used (Martínez and Suárez, 2006; Morón-Ríos and Morón, 2016; Salomão et al., 2019a); providing this information is critical to calculate capture rate and ensure replicability. The spatial distribution and number of traps across habitat gradients should also aim to be standardized to ensure unbiased evaluation of the impact of anthropogenic activities.

In a recent study, Rivera and Favila (2022) demonstrated that ecological studies in the Neotropics often collect more dung beetle individuals than necessary to obtain a representative diversity sample. They suggest that we are currently oversampling the dung beetle community. In future studies, it is crucial to assess the optimal number of traps between effort and efficiency (richness, abundance, and diversity of captured dung beetles), which is the most widely used criterion for selecting the sampling methodology (Noriega and Fagua, 2009). Finding this optimal number is important since the potential impact on dung beetle populations has not been quantified, and it is possible that with fewer traps, the species asymptote will be reached, avoiding over-capture. Also, the optimal number of traps is important, especially considering that dung beetle sorting and identification can be time-demanding activities that limit the development and conclusion of ecological studies.

The use of direct collection and active searching for beetles in dung pats is based on how easy it is to find fresh excrement and insects (e.g., Morelli and Gonzalez-Vainer, 1997; Mendes and Linhares, 2006; Lopes et al., 2020). In our work, manual capture was the most used method for collecting dung beetles after pitfall traps. Its main limitation is that it is especially useful for capturing endocoprids (i.e., *Eurysternus* spp., beetles that nest inside the excrement) and not for collecting paracoprids or telecoprids. Light traps have been primarily used to capture phytophagous and saprophytophagous beetles that are photophilic (Ratcliffe and Cave, 2009). Nonetheless, their use to capture Scarabaeinae is based on the fact that light trap can catch species that do not fall into other types of traps (Hill, 1996; Abot et al., 2012), such as some species of *Dichotomius* Hope or *Digitonthophagus* Balthasar. Flight interception and Malaise traps are also used, intended to intercept insects randomly as they move through the air without avoiding or attracting into the trap (Southwood, 1978; Boiteau, 2000). The effectiveness of flight interception traps is limited because flying adults avoid them and may bounce off the trap without being picked up (Boiteau, 2000). We noted that these traps were among the most used after manual capture and light traps (e.g., da Costa et al., 2009; Rodrigues et al., 2010; Otavo et al., 2013; Puker et al., 2020; de Moura et al., 2021). The popularity of their use is based on the active flight displayed by dung beetles, which allows them to be intercepted if the traps are appropriately located (Puker et al., 2020). Flight intercept traps allow the capture of dung beetles not attracted by omnivore bait, as some species of *Onthophagus* Latreille, *Deltochilum* Eschscholtz, *Phanaeus* MacLeay, *Canthidium* Erichson, *Cryptocanthon* Balthasar, or *Anomiopus* Westwood, which have other food preferences (i.e., carrion, predatory, fugivory, mycetophagy).

The other most commonly used trap to capture dung beetles was NTP-80 (a model invented by Miguel A. Morón), a modification of the pitfall traps designed for the collection of insects with an affinity for decaying organic matter of animal origin, which can remain active for extended periods, and that has the main advantage of preventing looting by mammals attracted by the bait (Morón and Terrón, 1984). All the papers citing this trap were performed in Mexico (e.g., Trevilla-Rebollar et al., 2010; Deloya et al., 2013; González-Hernández et al., 2015), suggesting that it is a local modification that is not commonly used in other countries. Other types of complementary traps (e.g., aerial traps, light traps, flight interception traps, mini-Winkler extractor) for the capture of dung beetles are extremely limited because they usually incur extra expense and time, and generate discrete results in the effort and efficiency ratio. However, it has been mentioned by several authors that these traps can be used to capture rare species that do not usually fall into pitfall traps (e.g., Hill, 1996; Noriega, 2011; Abot et al., 2012; Touroult et al., 2017; Silva et al., 2020; Ong et al., 2022) and so helpful to taxonomical approaches to get rare and/or small species (e.g., Mora-Aguilar and Delgado, 2018, 2019). Therefore, studies with these traps are more relevant for taxonomic research and not for bioindicator studies. Thus, studies that evaluate these aspects in the future should be conducted.

Type, number, and amount of bait

It is virtually impossible to collect all species in a taxonomic group with only one sampling technique or bait type (e.g., Missa et al., 2009). However, a high sampling efficiency of the assemblage is vital to any research involving the biodiversity of dung beetles (e.g., Marsh et al., 2013; Noriega, 2015; Correa et al., 2018) since they are widely used as bioindicators of environmental changes (Halffter and Favila, 1993; Nichols et al., 2007). Human dung is the most used bait to sample dung beetles in the Neotropical region. Indeed, the feeding preference of dung beetles for omnivorous mammal dung usually attracts a more significant number of species and individuals relative to herbivore dung, carnivore dung, rotten fruits, or carrion (Filgueiras et al., 2009; Bogoni and Hernández, 2014; Correa et al., 2016, 2018; Salomão et al., 2018). Human dung is one of the most attractive baits for the dung beetle sample (Martín-Piera and Lobo, 1996) and is a resource available worldwide wherever the researcher travels (Marsh et al., 2013). For these reasons, human dung features as the bait type most used to sample a high abundance and species richness of dung beetle in ecological studies at the assemblage scale (Howden and Nealis, 1975; Gardner T. A. et al., 2008; Correa et al., 2016). Marsh et al. (2013) suggested using human-pig dung mixes in different proportions, with this mixed dung bait (human:pig) exhibiting efficiency comparable to human dung (see Marsh et al., 2013) and is used in more recent studies (e.g., Braga et al., 2013; França et al., 2020; Noriega et al., 2021a; see Supplementary Annex 1), demonstrating a possible tendency for future studies in the Neotropical region. In contrast, omnivorous dung can be an ineffective bait for species with a preference for open areas and/or herbivorous dung (Noriega *personal observation*).

Most of the studies used a single bait type in their sampling protocol, usually human dung which allows standardized comparisons among different habitats (see Howden and Nealis, 1975; Gardner T. A. et al., 2008; Correa et al., 2016). Using a single bait has clear logistical advantages, such as reduced time to set up traps in the field, reduced physical effort, and fewer financial resources (Gardner T. et al., 2008). Nevertheless, due to the trophic specialization of dung beetles (Halffter and Matthews, 1966), using multiple baits may attract a more diverse group of beetles and thus result in a better characterization of assemblages (e.g., Larsen et al., 2006; Noriega, 2015; Correa et al., 2016; Chamorro et al., 2019). Although, carrion was widely recorded in studies that used two or three bait types, mainly together with a dung type (e.g., human, cattle, or pig dung) but almost never used as the only bait in a study. The use of carrion is important due to the possibility of sampling generalists and necrophagous species (Halffter et al., 2007). Still, contrasting to dung there is no standardized carrion type to sample dung beetles, and studies use different carrion types, including fish, chicken, bovine, and pig (see Supplementary Table S1). Pivotally, the use of baits (individual or combined) will depend on the main objective of the research (see Correa et al., 2018).

The amount of bait used ranged from 5 g to 50 g. Indeed, there is no consensus in the literature on the amount of bait needed to sample dung beetles effectively, even though it has been reported that the amount (e.g., size and volume) of bait has a positive effect on the number of species and individuals captured (see Peck and Howden, 1984; Gill, 1991; Raine et al., 2020; Martínez-Hernández et al., 2022). The most commonly used dung type, human dung, can be in short supply, with a single person generating fresh dung for about 8–10 traps per day, based on a standard bait size of 20 g proposed by Marsh et al. (2013). This reduced the number of traps per day and severely limited sampling effort, and because of the high sampling effort employed in dung beetle ecological research (Gardner T. et al., 2008), larger amounts of human dung are required. This fact may drive the researchers to use lower amounts of bait per trap, aiming to increase the number of traps in their studies. To understand better how the collection method can affect the quantification of the community, further studies should assess the efficiency of different amounts of baits in sampling dung beetles in the Neotropical region (Martínez-Hernández et al., 2022). Furthermore, to our knowledge, it is relatively unknown how the amount of bait may affect the attractiveness of dung beetle assemblages in scenarios with distinct environmental and landscape conditions. In dry ecosystems, such as in tropical dry forests in the Neotropics, dung dries more quickly compared to wet ecosystems (e.g., tropical rainforests). Regarding ecosystem types, the amount of feces could be considered and modulated in order to maintain a similar attractiveness during the sampling period among different regions. Thus, this information may help researchers to use a standardized and/or ideal amount of bait per trap in future studies.

Time and distance between traps

Most studies using pitfall traps ranged from 24 to 48 h of active trapping. Previous studies state that dung beetles have a high colonization rate on decaying material during the first 48 h of resource availability (Kessler and Balsbaugh, 1972; Sullivan et al., 2017; Wassmer, 2020). There are two important factors related to the time in which baited traps are active: (i) the decrease in the potential of the attractiveness of the resource with the advance of time (Hanski and Cambefort, 1991), and (ii) decaying organisms that fall in the pitfall produce odors that may attract or repel organisms other than those attracted to the bait used in the experiment (Schmitt et al., 2004; Fletchmann et al., 2009). In tropical rainforests, 48 h comprises the optimal time-lapse to obtain the most bait-attracted dung beetles. Nonetheless, in tropical dry forests, there is a high evapotranspiration dynamic (Sampaio, 1995; Velloso et al., 2002), which results in the rapid drying out of food resources. In dry-forest ecosystems, it is relatively common to install pitfall traps for 24 h (e.g., Barraza et al., 2010; Rangel-Acosta and Martínez-Hernández, 2010; Salomão et al., 2018). Decaying organisms in pitfall traps may attract insect-feeding vertebrates (e.g., *Caracara plancus* (Miller, 1777), Oliveira-Ribeiro *personal observation*; Young, 2015), resulting in the consumption of dung beetles within pitfall traps. Considering the decrease of attractiveness after 48 h and the biased attractiveness caused by decaying material, the time duration of 48 h is the most appropriate for dung beetle surveys at the assemblage level, although it is also possible to re-bait traps every 24 or 48 h, eliminating the problem of attractiveness decline. However, it would lead to an increase in the time spent on collecting.

Trap spacing had an astonishing range, from two to 1,000 m apart. Nonetheless, most studies (more than 80%) spaced traps up to 50 m. Standardized trap spacing guarantees accurate ecological comparisons among ecological studies (Larsen and Forsyth, 2005; Noriega and Fagua, 2009; da Silva and Hernández, 2015; but see Moctezuma, 2021). Dung beetle trap spacing relates to the study sampling unit: studies in which traps are treated as individual samples require spatial independence, while studies that consider a set of traps as a sample need spatial independence among samples. To determine the appropriate trap spacing that avoids pseudo replication issues (i.e., guaranteeing spatial independence among traps or set of traps), previous studies tried to assess the optimal distance among sampling units (Larsen and Forsyth, 2005; da Silva and Hernández, 2015). According to these studies, trap spacing from 50 to 150 m (depending on the mobility of the species and environmental conditions) would be an adequate distance to avoid interference between samples. In studies that evaluate the landscape process, it is most beneficial to distribute traps in a way that allows effective regional sampling, which is limited by the smallest study sites (e.g., islands, forest fragments, see Filgueiras et al., 2015; Storck-Tonon et al., 2020; Rodriguez-Garcia et al., 2021). Whenever a habitat is spatially limited, traps need to be clustered spatially, and thus trap spacing can be relatively small (e.g., Arellano et al., 2005; Costa et al., 2013). Traps can be installed close to each other to evaluate bait attractiveness or food preference (e.g., 2–3 m; see Louzada and Carvalho e Silva, 2009; Correa et al., 2018), while ecological studies that do not aim to sample the diversity of a region (e.g., studies of seed dispersal or to obtain a focal species), optimum trap spacing is not necessarily a rule.

Spatial, seasonality, and temporal sampling

The highest percentage of studies used only one sample (space-for-time replicates), due to several reasons. Some large-scale studies (i.e., comparing bioregions) use few samples, either to randomize a large number of sites avoiding pseudoreplication or to study biogeographical patterns (e.g., da Silva P. G. et al., 2022). Other studies focused more on behavior, natural history, or ecosystem services (e.g., Salomão et al., 2018; Noriega et al., 2021a), do not usually include gradients or a spatial analysis comparison. In addition, studies that are not necessarily large-scale will choose small sampling replicates to avoid spatial autocorrelation (Leather et al., 2014; Negrete-Yankelevich and Fox, 2015) or to study spatiotemporal diversity (e.g., Ferreira et al., 2018). Twenty percent of the reviewed studies used two or three samplings, most of which used spatial controls or replicas of the same habitat (Gómez-Cifuentes et al., 2019), while ~22% of studies used from four to nine replicates, including works with spatial replicability, studying beetles at the landscape level (e.g., Ramírez-Ponce et al., 2019; Correa et al., 2021). Studies with a larger number of samples (>10) are mainly due to studies with multi-year sampling (e.g., Salomão et al., 2020; Noriega et al., 2021b), studies in wider areas with multiple sites and replicates, or analyzing longer gradients (e.g., Vulinec, 2002; Correa et al., 2019). Lastly, the absence of detailed information on sampling or replication in some articles is a widespread pattern in other sub-themes, where the description of the methodological component is very incomplete, especially when the articles are concerned with details of natural history, food preferences, phenology, etc.

In terms of seasonality and temporal sampling, the rainy season may be ideal for collecting a higher abundance of adults that can be attracted to baited traps (Halffter and Matthews, 1966; Andresen, 2005; Correa et al., 2018). This is due to the behavior of dung beetles, which is strongly influenced by the rains (Halffter and Matthews, 1966; Doube, 1991; Hanski and Cambefort, 1991) and temperatures throughout the year (Verdú et al., 2006; Hernández and Vaz-de-Mello, 2009; da Silva et al., 2018). These activity peaks in rainy periods (mainly in environments with slight thermal variation throughout the year) are related to the physiological characteristics of insects, which must be able to survive by minimizing the loss of body water (Verdú et al., 2019), extracted from the trophic resources (e.g., excrement or other types of organic matter). In addition, the moisture of the resource, or the amount of water that the excrement can hold, is an important factor both in the spread of smell over long distances and the water availability provided by these beetles (Fletchmann et al., 2009; Dormont et al., 2010; Holter, 2016). Baits in traps for dung beetles suffer intense dehydration in dry periods, which produces a lower attractiveness (Lobo et al., 1998). Nonetheless, it is important to consider that seasonality among insects in the tropics is still uncertain (Kishimoto-Yamada and Itioka, 2015), mainly in ecosystems that are evergreen and that do not have a marked dry season. Such an argument is often used in ecological studies of dung beetles in the Neotropics that are performed during the dry season (e.g., Salomão et al., 2019b).

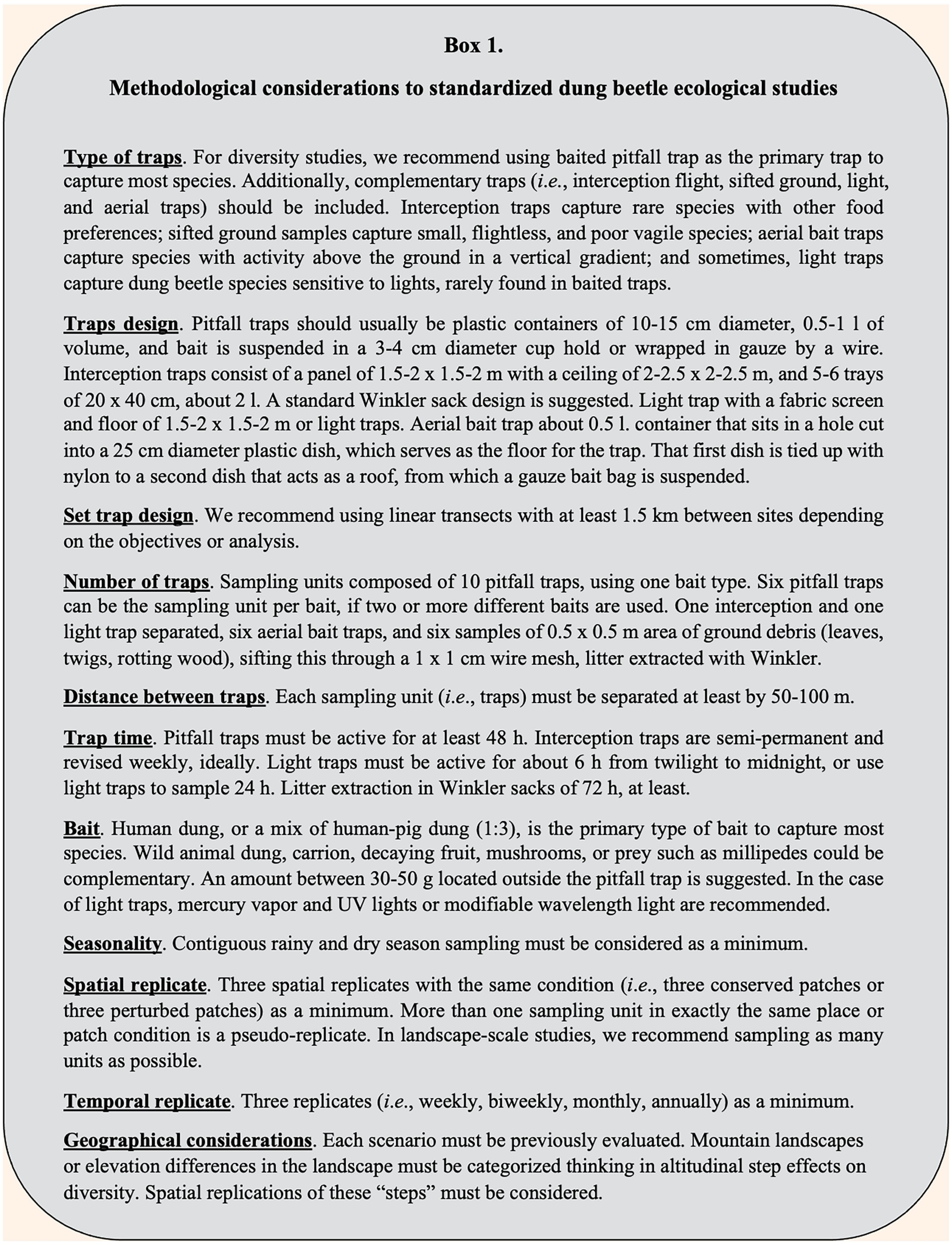
Ambient temperature is an excellent variable in predicting Neotropical dung beetle species richness (Lobo et al., 2018). Although some dung beetle species can slightly control their body temperature (e.g., Verdú and Lobo, 2008; Gallego et al., 2018); they are animals that depend on environmental temperature to perform their physiological functions, with an ideal temperature range (Chown, 2001; Sheldon et al., 2011). As humidity and temperature are strongly associated, spring or rainfall periods are suitable for these individuals to leave the nests for feeding or reproductive purposes. In this sense, it is important to take into account that the dispersion of individuals at these times can mask the dependence that many species have on their habitat since, during these favorable periods, it is possible to capture species in habitats where they would not survive during the dry season (Hernández et al., 2014). Another relevant issue is that unfavorable environmental conditions are less critical in burrowing species since they are less subject to seasonal climatic variations, remaining in the tunnels for long periods, where they have sufficient food for themselves and their offspring (Halffter and Matthews, 1966; Hanski and Cambefort, 1991; Scholtz et al., 2009).

Gaps, potential questions, things to improve, and recommendations

In this review, we examined the various methods used to depict dung beetle assemblages, diversity, and abundance in 241 papers published in peer-reviewed journals. We limited our search to the Neotropics, and those papers focused on dung beetle biodiversity. We analyzed several variables related to trapping design. Based on our analysis, we made a series of recommendations for the optimal procedures to examine dung beetle diversity and abundance, and we propose some minimum requirements for a standard protocol (see Box 1). In the interest of staying within our stated scope in this paper, we did not delve into other issues of importance for dung beetle diversity studies. We did not examine the methods for collecting beetles once they are in the trap, such as what kill solution is preferred (for example, the old technique of using ethylene glycol is no longer recommended because of its toxic effect on mammals). We also did not discuss live-trapping versus kill-trapping, labeling, storage, or identification (still problematic due to the many beetle species and the low number of taxonomists). In addition, several concerns in dung beetle studies were not discussed here, including the definition of diversity, the best metrics to use in describing dung beetle assemblages, and what statistical methods should be employed in comparing two or more habitats, to name a few. These are more complex and controversial subjects and need to be examined further.

Box 1. Methodological considerations to standardize a sampling protocol for dung beetle ecological studies

One of the critical aspects of scientific studies is the possibility of replicating them. In ecological studies, the sampling design (i.e.,



Box 1.

Methodological considerations to standardized dung beetle ecological studies

Type of traps. For diversity studies, we recommend using baited pitfall trap as the primary trap to capture most species. Additionally, complementary traps (*i.e.*, interception flight, sifted ground, light, and aerial traps) should be included. Interception traps capture rare species with other food preferences; sifted ground samples capture small, flightless, and poor vagile species; aerial bait traps capture species with activity above the ground in a vertical gradient; and sometimes, light traps capture dung beetle species sensitive to lights, rarely found in baited traps.

Traps design. Pitfall traps should usually be plastic containers of 10-15 cm diameter, 0.5-1 l of volume, and bait is suspended in a 3-4 cm diameter cup hold or wrapped in gauze by a wire. Interception traps consist of a panel of 1.5-2 x 1.5-2 m with a ceiling of 2-2.5 x 2-2.5 m, and 5-6 trays of 20 x 40 cm, about 2 l. A standard Winkler sack design is suggested. Light trap with a fabric screen and floor of 1.5-2 x 1.5-2 m or light traps. Aerial bait trap about 0.5 l. container that sits in a hole cut into a 25 cm diameter plastic dish, which serves as the floor for the trap. That first dish is tied up with nylon to a second dish that acts as a roof, from which a gauze bait bag is suspended.

Set trap design. We recommend using linear transects with at least 1.5 km between sites depending on the objectives or analysis.

Number of traps. Sampling units composed of 10 pitfall traps, using one bait type. Six pitfall traps can be the sampling unit per bait, if two or more different baits are used. One interception and one light trap separated, six aerial bait traps, and six samples of 0.5 x 0.5 m area of ground debris (leaves, twigs, rotting wood), sifting this through a 1 x 1 cm wire mesh, litter extracted with Winkler.

Distance between traps. Each sampling unit (*i.e.*, traps) must be separated at least by 50-100 m.

Trap time. Pitfall traps must be active for at least 48 h. Interception traps are semi-permanent and revised weekly, ideally. Light traps must be active for about 6 h from twilight to midnight, or use light traps to sample 24 h. Litter extraction in Winkler sacks of 72 h, at least.

Bait. Human dung, or a mix of human-pig dung (1:3), is the primary type of bait to capture most species. Wild animal dung, carrion, decaying fruit, mushrooms, or prey such as millipedes could be complementary. An amount between 30-50 g located outside the pitfall trap is suggested. In the case of light traps, mercury vapor and UV lights or modifiable wavelength light are recommended.

Seasonality. Contiguous rainy and dry season sampling must be considered as a minimum.

Spatial replicate. Three spatial replicates with the same condition (*i.e.*, three conserved patches or three perturbed patches) as a minimum. More than one sampling unit in exactly the same place or patch condition is a pseudo-replicate. In landscape-scale studies, we recommend sampling as many units as possible.

Temporal replicate. Three replicates (*i.e.*, weekly, biweekly, monthly, annually) as a minimum.

Geographical considerations. Each scenario must be previously evaluated. Mountain landscapes or elevation differences in the landscape must be categorized thinking in altitudinal step effects on diversity. Spatial replications of these "steps" must be considered.

number of samples, spatio-temporal distribution of the samples, detailed sampling technique) configure as a primordial aspect that will allow replicability in further studies. Under such rationale, it is essential to note that a considerable number of ecological studies in this review did not correctly detail their sampling methodology. For example, some studies do not include the number of pitfall traps used, which is a determinant in calculating capture rate and ensuring replicability. Besides, the absence of detailed information on sampling or replication in some articles is a widespread pattern in other sub-themes. It is often expected that the characterization of methodological components is very poor, especially when the articles are concerned with details of natural history, food preferences, phenology, etc. Such practices may come together with the requirements of ecological journals for manuscripts to present a concise description of methods. With the data presented in this study, we reinforce the importance of adequately detailing sampling methodology in ecological studies encompassing the dung beetles.

In this context, we found different information gaps in both geographical and methodological contexts. This investigation shows how multiple countries of the Neotropical region present limited knowledge on dung beetles (evidenced by the few researches found). For this reason, an increased research effort is recommended on dung beetles in countries with high biodiversity potential, such as Ecuador, Peru, and Venezuela. In this context, dung beetles have been used in different meta-analyses (e.g., Nichols et al., 2007; López-Bedoya et al., 2022). However, a substantial limitation of interpretation of results when evaluating global patterns is the standardization of methodologies between investigations included in a meta-analysis. To provide better conclusions on global patterns, it is necessary to start with methodological standardization on dung beetles. The idea of standardizing a sampling methodology is to allow comparisons on a large scale (continental, neotropics, etc.), allowing for studying global changes. However, we understand that we are still some ways away from standardization, as the more crucial things while developing a methodology are the question we want to answer and the material and financial resources available to answer it. In saying that, we acknowledge that much of the research carried out in Latin America has limited funding, so the methodology followed is subject to the financial and human resources available to researchers.

Standardization in models and size of other types of traps (including pitfall) is poorly evaluated. In some cases, the experience in the right location, orientation, selection of corridors or gaps, and the number of this type of traps and samples (e.g., mini-Winkler, interception) could be an essential factor in efficiency in obtaining favorable results in rare species of scarabs. This inexperience could be derived from the fact that this type of trap is more commonly used by taxonomists o to other groups of beetles or insects. Collaboration between experts in ecology and taxonomy should be mandatory for the correct determination of species, better analysis of data, and a deep study of the numerous specimens collected and frequently stored. This way, several of these specimens or a synoptic sample should be preserved, pinned, and deposited in public collections. The standardized methodology for sampling dung beetles suggested in this study (see Box 1) may be helpful for studies directed toward the knowledge of dung beetle fauna that can support data on the species distribution in the Neotropical region. Here, we offer a methodological guideline that can be replicated in studies at local scales in the Neotropics or other regions of the world with a high diversity of dung beetles (e.g., Afrotropical, Oriental).

Considering the time, financial and logistical resources, which in many cases are scarce, we suggest a standardization for the dung beetles sampling. The use of transect for dung beetle sampling is widely used (e.g., Gardner T. et al., 2008; Gardner T. A. et al., 2008; Macedo et al., 2020; Noriega et al., 2021a), being suitable because it presents a greater amplitude in the dispersion of the odor plume of the baits when compared with other denser configurations of traps. Considering that most forest areas in the Neotropics are small (e.g., Ribeiro et al., 2009), very long transects are not possible due to the edge effect (see Laurance and Bierregaard, 1997); therefore, the distance of 100 between traps within the same site is more feasible, considering the configuration of the areas, especially forest areas in the Neotropics. However, if it is not possible to use 100 m, at least a minimum distance of 50 m is recommended. We suggest five or six traps per site (see Rivera and Favila, 2022), therefore considering a transect of 400 m, with five traps spaced at 100 m by type of bait, considered as a replica, and at least three replicas, regarding the distance between sites.

We suggest that the distance between sites should not be <1.5 km since large species can disperse, covering a distance of 1 km in 2 days (Peck and Forsyth, 1982). This distance between areas ensures that traps installed for 48 h do not receive dung beetles from other areas studied. Small traps can limit the capture of beetles, especially in tropical forests, which within 48 h, can attract large numbers of insects. Therefore, we suggest traps with a capacity of at least 0.5–1 L, and around 1/3 of their liquid capacity can be added (water + salt + neutral detergent). The short period (48 h) makes the salt efficient for preserving the dung beetles and does not interfere with the attraction of the beetles. The detergent helps to break the surface tension of the water. For bait, plastic coffee cups (50 mL) are easy to find in any country, so we suggest their use, with the bait supply in at least 1/3 of its capacity, with a mix between pig-human dung bait, due to the ease of use, wherever the researcher is (Marsh et al., 2013). As a suggestion for the pitfall traps, plastic plates can be used to avoid the bait's desiccation and prevent its contents from leaking due to rain. We also suggest installing the traps in places with little solar radiation; for this, the researcher can find more suitable places as far as possible. These suggestions aim at the bait's attractiveness during the entire period of trap activity.

In terms of potential research areas, there are several future studies. One topic that has not been fully explored is the attraction of dung beetles to specific chemicals. In order to know and determine the volatile organic compounds (VOCs) to which beetles are most attracted may evaluate the best baits to use in the field. This multi-disciplinary research area requires chemical analysis of the VOCs, followed by lab and field behavioral trials. Another aspect to explore is experimental approaches focused on diversity complementarity by comparing different types of traps, types of baits, and proportions of bait mixes need to be explored. It is essential to include and evaluate several types of baits and species or groups of mushrooms, fruits, carrion, dung, and mesofauna, as myriapods and gastropods are necessary. In addition, sample coverage estimators may be considered in future meta-analysis studies aiming to propose the most appropriate sampling effort in dung beetle studies in different Neotropical ecosystems.

In terms of potential aspects to improve is the omission of information on the richness and abundance captured in each trap in ecological studies related to dung beetles. Providing this information as Supplementary material in future studies would not mean any additional effort because it is an essential step in organizing and analyzing the information in this type of study. Henceforth, we recommend providing this information as the best way to improve our understanding of the efficiency of the methodologies implemented (e.g., type of trap, the number of traps, the type of bait, the distance between traps) in research related to dung beetles. Analyzing this information will let us propose standardized, efficient sampling protocols for dung beetles in the upcoming years.

Due to the decrease in biodiversity due to anthropic causes, we believe it is crucial to think about pitfall traps that can keep the specimens alive after their identification in the field. Many species that fall into the traps are easily identifiable, and after being counted (and perhaps marked to avoid counting them in the following capture), these specimens could be released and returned to nature, thinking that they can continue to perform their ecosystem functions. Those species that are not easily identified or of which there are few specimens in scientific collections can be captured and deposited, as well as vouchers for each species. The need for intensive work on the biodiversity of many taxa is becoming more essential as climate change and habitat destruction increase, and surveys of organisms over time will enhance our understanding of the detrimental effects of these factors on our biodiversity (Brodie et al., 2012). Whatever way one defines biodiversity, it is still well known that the wealth of species once seen on this planet is rapidly declining. Documenting this decline may give us clues to ameliorate it if we can do this quickly. Dung beetles are a suitable ecological indicator species, have essential roles in the ecosystem, and are a proxy for surveying large mammalian fauna, especially in the Neotropics. This is why it is critical to standardize our survey methodology and promote solid techniques across the landscapes where we collect these valuable insects.

Data availability statement

The original contributions presented in the study are included in the article/Supplementary material, further inquiries can be directed to the corresponding author.

Author contributions

EM-A and JN conceived the idea, designed the research, and structured the manuscript. EM-A, AA-J, CC, PS, VK, PL-B, MH, JP-C, RS, GV, and JN gathered and analyzed the data. All authors interpreted the results, contributed to the writing of the paper, and approved the last version of the document.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

Supplementary material

The Supplementary material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2023.1096208/full#supplementary-material

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Dung beetles (Coleoptera: Scarabaeidae) in grazing lands of the Neotropics: A review of patterns and research trends of taxonomic and functional diversity, and functions

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Dung beetles are one of the most representative groups of insects associated with livestock, as they take advantage of the manure of livestock for food and reproduction. They have been widely used as a bio-indicator group to evaluate their responses to land-use change and other environmental disturbances by analyzing species diversity at different spatial and temporal scales. However, the impacts of livestock management practices, forms, and history on dung beetle diversity are still poorly understood. This paper is an exhaustive and systematic review of the existing peer-reviewed and indexed literature on the taxonomic diversity (species richness and composition), functional diversity, and ecological functions of dung beetles from different provinces and biogeographic domains in tropical grazing lands of the Neotropics. We analyzed the timeline of the studies conducted so far, and we detected increasing literature produced mainly in South America. We included the most frequent objectives, tendencies, software, and statistical analyses. Given the significant heterogeneity of livestock landscapes in the Neotropics, the reviewed studies have conceptualized broadly what a pasture is, and the authors have used different descriptions of other grazing lands. Additionally, management data and livestock practices vary widely among studies, and management history is poorly described. In future research, it is relevant to include as much information as possible and the consequences of different livestock management practices on additional ecological attributes of dung beetle assemblages at different landscape scales (spatial and temporal) to predict how ecological processes change in Neotropical landscapes. Considering the importance of the data to be included in future work, we propose a collection format to unify the information collected in the field when conducting ecological studies in grazing lands. Moreover, we define a classification system to homogenize the features that distinguish the multiple tropical grazing lands reported in the literature. Preserving dung beetle diversity and associated ecological functions is urgent for maintaining ecosystem services in grazing lands. The challenge for research institutions is to continue filling gaps

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in knowledge to help those who work in transferring knowledge, to help ranchers exercise better options for more sustainable livestock farming, and to publish results for conservation decision-making.

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cattle ranching, ecosystem functions and services, functional groups, management history, traits, Scarabaeinae

1. Introduction

Livestock activities have transformed natural ecosystems into landscapes dominated by semi-open grazing areas associated with original vegetation for breeding several species of domesticated livestock (Guevara and Lira-Noriega, 2004). Projections for 2050 warn that the need for food will increase, such that land area destined for food production will increase (Herrero et al., 2015; FAO, 2017). Intensive and sustained land management over time has caused a cascading loss of native vegetation. There are, therefore, many overgrazed areas in the Neotropics that require special attention for biodiversity conservation purposes (Mellink and Riojas-López, 2020).

Biodiversity supports essential life-support services (Summers et al., 2012). Ecosystem services are the conditions and processes which provide ecosystem goods to sustain and fulfill human life and ecological continuity (e.g., food, medicine, firewood, freshwater; Daily, 1997; MEA [Millennium Ecosystem Assessment], 2005). Improving our knowledge of biodiversity conservation and its relationship with ecosystem services is critical in identifying humankind's main ecological problems and finding solutions (Brand and Vadrot, 2013). According to Yu et al. (2017), there are several common indicators to monitor biodiversity loss and the implications for the sustainable provision of ecosystem services, and one of them is biodiversity *per se* because it has a substantial impact on ecosystem functions through the different functional traits presented among species in the community. An ecological indicator is a biological group sampled under various habitat conditions resulting from human activities (Calow, 1987; Moreno et al., 2007).

Dung beetles (Coleoptera: Scarabaeidae) are a valuable ecological indicator group for biodiversity assessment (Halffter and Favila, 1993; Spector, 2006; Nichols et al., 2007; Numa et al., 2009; Otavo et al., 2013), because they are well known taxonomically and ecologically, and susceptible to changes in habitat management (Favila and Halffter, 1997; Martínez et al., 2017; Barragán et al., 2021). Moreover, they exhibit wide variation in life history strategies and body sizes that are reflected in functional traits (Halffter and Edmonds, 1982; Hanski and Cambefort, 1991), as well as ecological functions that can be measured (e.g., dung removal, seed dispersion, soil bioturbation; see Andresen, 2002; Braga et al., 2013; Noriega et al., 2021a; Barragán et al., 2022). Therefore, dung beetles are adequate models for functional diversity and ecosystem functionality studies (Barragán et al., 2011; Braga et al., 2013), and they are essential for the maintenance of ecosystem functioning in grazing lands (Louzada and Carvalho e Silva, 2009). In this context, dung beetles are one of the most representative taxonomic groups of insects associated with grasslands and livestock. Most adult coprophagous beetles in grazing lands use fresh dung of mammalian herbivores (native, introduced, and domestic) for feeding and nesting; hence, dung removal has been one of the most measured ecological variables to evaluate dung beetle functionality (Holter, 2016). Consequently, dung beetle diversity is crucial for dung degradation; without them dung accumulates, leading to various health problems for human populations and ecological issues in ecosystems (Pecenka and Lundgren, 2018). Thus, the services performed by dung beetles reduces the use of financial resources to treat livestock health and soil fertilization (Lousey and Vaughan, 2006; Lopez-Collado et al., 2017).

We conducted an exhaustive and systematic evaluation of the peer-reviewed and indexed literature on the taxonomic (species richness and composition) and functional diversity, as well as the ecological functions of dung beetles in Neotropical grazing lands. We analyzed the timeline of the studies conducted to date and defined a classification system to homogenize the features that distinguish the multiple Neotropical grazing lands reported in the literature. Our review consists of several sections. First, we analyzed the regional and local changes in taxonomic dung beetle diversity (e.g., species richness, abundance, biomass), as well as the effect of grazing lands and livestock management on biodiversity from different provinces and biogeographic domains in tropical grazing lands of the Neotropics. Second, we discuss the meaning, importance, and vision of functional diversity studies on dung beetles. We considered functional groups and traits (both effect and response traits), including their selection, the most used, and the justification, in addition to analytical methods and relevant case studies. Third, we argued the relationship between biodiversity and ecosystem function (BEF). This relationship and its consequence for ecosystem services have predominantly been studied by controlled, short-term, and small-scale experiments under standardized environmental conditions and constant assemblage compositions. We discuss in the three sections the grazing land types and changes over time and we described these lands for understanding the dynamics of dung beetle assemblages. We describe livestock management practices and forms of management reported in the literature on dung beetle ecology and suggest some additional practices that we believe should be added to works on the subject. The history of land use is very important in this context. Finally, this article synthesizes the main findings, new research frontiers, and answers some open questions, current research gaps, potential developments in the field, and future challenges.

2. Methods

2.1. Literature search and inclusion criteria

We used the Scopus and Web of Science databases to search for literature on the taxonomic and functional diversity and functions of dung beetles in pasture habitats, following the PRISMA methodology (Moher et al., 2009), which only considers indexed articles. The following search terms were used for the taxonomic diversity of dung beetles: ((“Dung beetle*” OR Scarabaeinae) AND disturb* AND (“Species richness” OR diversity OR Abundance) AND (Communit* OR Assemblage*) AND (“Tropical Forest*” OR Tropic*)). For functional diversity, we employed the following search terms: ((“Dung beetle*” OR Scarabaeinae) AND (disturb* OR “habitat disturb*” OR “land-use type*” OR “land-use change*” OR “land-use disturb*” OR anthropic* OR modification OR fragmentation OR “natural grassland*” OR Grassland* OR margeland* OR meadow* OR steppe OR “grazed rangeland*” OR Llanos OR Pampa OR savanna* OR Woodland* OR brushland* OR shrubland* OR Campos OR Cerrado OR Agroforestr* OR silvopastor* OR “forest grazing” OR “graz* forest*” OR Agriculture OR Pasture OR “livestoc* graz*” OR “cattle graz*” OR grazed OR “Open fores* “OR Temperature OR Microclim*) AND (“functional diversity” OR “functional trait*” OR “functional group*” OR Thermoregulation OR “ecological function*” OR “dung removal” OR “manure removal”) AND (Communit* OR Assemblage*) AND (“Tropical Forest” OR Tropic*)). Regarding dung beetle functions, we used the following search terms: ((“scarab*” OR “dung beetle*”) AND (remov* OR func* OR disper* OR biotur*) AND graz*). The search window of time covered articles published between January 1980 to February 2022.

Our search returned 272 taxonomic diversity articles, 109 functional diversity articles, and 81 articles regarding dung beetle functions. We complemented the taxonomic diversity search by including articles published in Spanish and Portuguese from the authors’ collection. We also surveyed among the three topics covering all articles obtained to add potential complementarity. The relevant articles for taxonomic and functional diversity and dung beetle functions were selected using the following criteria: i) the study includes species from Aphodiinae and/or Scarabaeinae subfamilies, ii) the study is based partly or entirely in grazing lands (pastures, cattle systems, agroforestry systems, and similar habitats), iii) the study evaluates taxonomical and/or functional diversity and/or dung beetle functions (e.g., dung burial, soil removal, fly control), and iv) the study is conducted in the Neotropics. Under these criteria, 76 taxonomic diversity articles, 26 functional diversity articles, and 18 dung beetle function articles were retained for data extraction (Figure 1; see Supplementary Table S1).

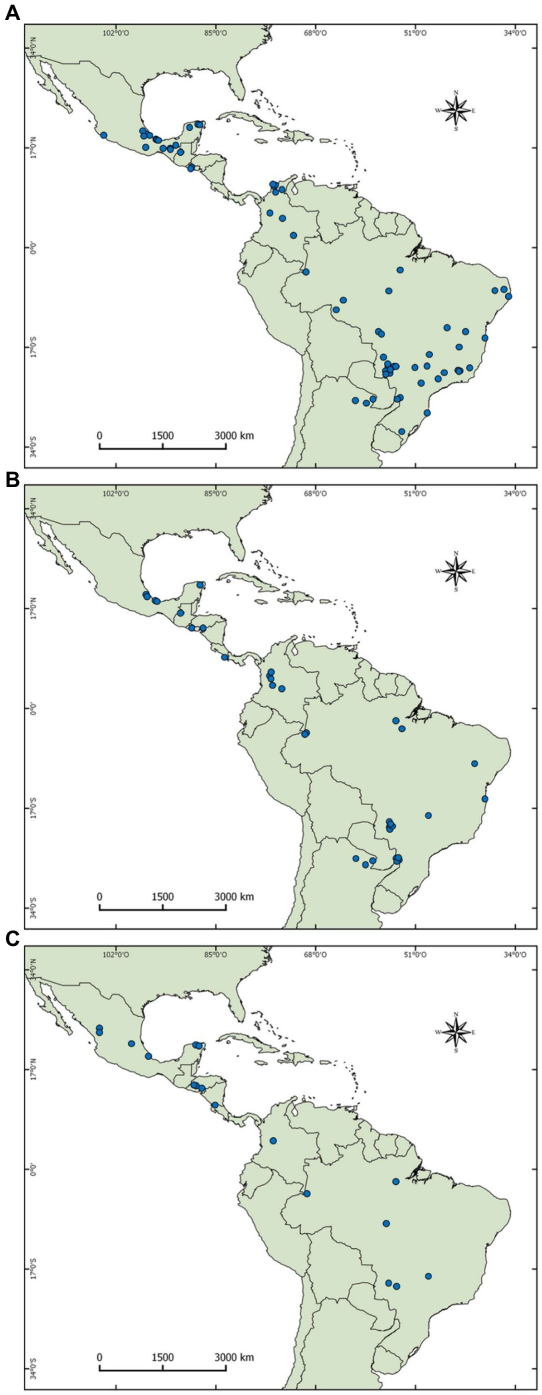

FIGURE 1
Maps with locations of dung beetle studies (Coleoptera: Scarabaeidae) in grazing environments included in the analytical review. **(A)** Taxonomic diversity studies, **(B)** functional diversity studies, **(C)** ecological functions studies.

2.2. Data extraction and synthesis

We extracted the following information for all articles: (a) Neotropical biogeographic domains and provinces (*sensu* Morrone, 2017), including the year in which the study was published, the spatial and temporal scale, elevation (m a.s.l.) of the sampling sites, including sociopolitical divisions such as Town, County, State, and Country; (b) grazing land descriptions (e.g., grassland type), livestock management scheme and history, its surrounding matrix (at landscape scales) and whether cattle are present; (c) functional groups and traits of the dung beetle species; and (d) analytical methods and software used (Supplementary Table S2).

2.3. Grazing land (concepts, classifications, and descriptions)

In this review, grazing land is any vegetated land that is grazed or that has the potential to be grazed by animals. Pasture lands are

TABLE 1 Grazing land classification.

1. Grasslands: Grasses, weeds, and forbs	2. Woodlands: mix of herbs, grasses, and woody species	3. Agroforestry: intentional integration of trees and woody shrubs into crop and animal farming systems
1.1 Pasture lands (pasture): non-native, cultivated, improved grasses (Supplementary Figure S1A)	2.1 Brushlands, shrublands: areas covered with bushes and/or woody shrubs (Supplementary Figure S1D)	3.1 Agro-silvo-pastoral: woody perennial plants with agricultural crops, fodder crops and livestock production (Supplementary Figure S1H-J)
1.2 Rangelands: indigenous natural grasslands, margelands, meadows, steppe (Supplementary Figure S1B) 1.2.1 Grazed rangelands. Rangelands with livestock presence (Supplementary Figure S1C) 1.2.2 Llanos. Extensive system of grasslands, seasonally flooded, with infertile and acidic soils (Examples: plains east of the Andes in Bolivia, Colombia, and Venezuela) 1.2.3 Pampa. Treeless grasslands on flat and fertile plains (eastern and central Argentina)	2.2 Campos. Grasses, herbs, small shrubs, occasional trees, on undulating and hilly landscape, with variable soil fertility. Differs from Cerrado in having a longer and more severe winter and a relative abundance of native legumes. The Campos are the northern part of the Pampa. The sub-tropical climate is humid, warm in summer and mild in winter (Examples: Uruguay, southern Brazil, and north-eastern Argentina). Includes "campo limpo" and "campo rupestre" (Supplementary Figure S1E)	3.2 Forest grazing: combined use of forested or wooded land for timber production and animal production (grazing of native forage; Supplementary Figure S1K)
	2.3 Cerrado *sensu stricto*. Savanna with varying amounts of trees and shrubs along rivers and in valley bottoms (Example: central Brazil; Supplementary Figure S1F)	3.3 Grazable forest land: Forest land that produces, at least periodically, sufficient understory vegetation that can be grazed. The forages are usually native (Supplementary Figure S1L)
	2.4 Savanna: Grassland characterized by precipitation between 375 and 1,500 mm/year, variable proportions of trees or large shrubs, especially in tropical and sub-tropical regions (South America, sub-tropical and tropical regions of North America; Supplementary Figure S1G)	

complex and globally diverse agricultural systems that vary in vegetation types (i.e., land cover) and management. Land cover in pasture systems can consist of (i) natural grasses alone, (ii) include naturally occurring shrubs and/or trees, or (iii) be entirely planted either in monocultures or as a component of mixed crop-live-stock systems. To analyze how authors have handled the concept of pasture and the description of grazing land and the cattle-grazed landscape, we have classified grazing lands (based on information from Butler et al., 2003; Allen et al., 2011; Holechek et al., 2011; Longland, 2013; Dixon et al., 2014; Costa et al., 2015; Hasanuzzaman, 2020; Oliveira et al., 2020; Jurado-Guerra et al., 2021). In Table 1, we show the grazing land definitions, descriptions, and categorizations (supported with pictures: Supplementary Figure S1) currently in use. We have classified grazing lands and proposed this classification for use in future studies by analyzing how different authors have handled the concept of pasture and the description of grazing lands and the cattle-grazed landscape.

Grazing land management, in turn, varies in animal density, from animals moving freely over large areas (often called 'extensive grazing'), to concentrated and rotated over small areas (termed 'intensive rotational grazing'). Grazing land use also varies in terms of animal occupancy, with some systems primarily reliant on grazing and most others using pasture and feed lots (Oliveira et al., 2020) and livestock rotation. Other aspects in livestock management are livestock breed, production objective, types of grasses, water management for livestock, mating for livestock breeding, and infrastructure. Landowner management practices associated with grazing lands in this review are related to agrochemical use (herbicides, insecticides, dewormers), fertilizers, livestock feed supplements, fire, tillage, vitamins, and vaccines.

3. Results

3.1. Dung beetle taxonomic diversity studies in grazing lands

Seventy-six articles were analyzed in this section (Supplementary Table S1A). Publication numbers increased over time, where 8% ($n=6$) were published in the 1990s, 24% ($n=18$) in the 2000s, and 68% ($n=52$) in the 2010s where the highest values were reached, and it seems that this trend will continue into the 2020s (due to the number of articles already available for publication in 2021 and 2022; Figure 2A). The most significant number of published papers came from Brazil ($n=45$, 59.21%), followed by Mexico ($n=20$, 26.31%), Colombia ($n=7$, 9.21%), El Salvador-Nicaragua ($n=2$, 2.63%) and Argentina ($n=2$, 2.63%; Figure 2B). These tendencies are reflected in the biogeographic domains in which these studies were carried out; mainly in the Chacoan, Mesoamerican, Parana, and South Brazilian domains (Figure 2C). Brazil and Mexico have published papers on taxonomic diversity and grazing lands during the analyzed period, but Brazil increased its production of articles on this topic from 2010 onwards ($n=31$).

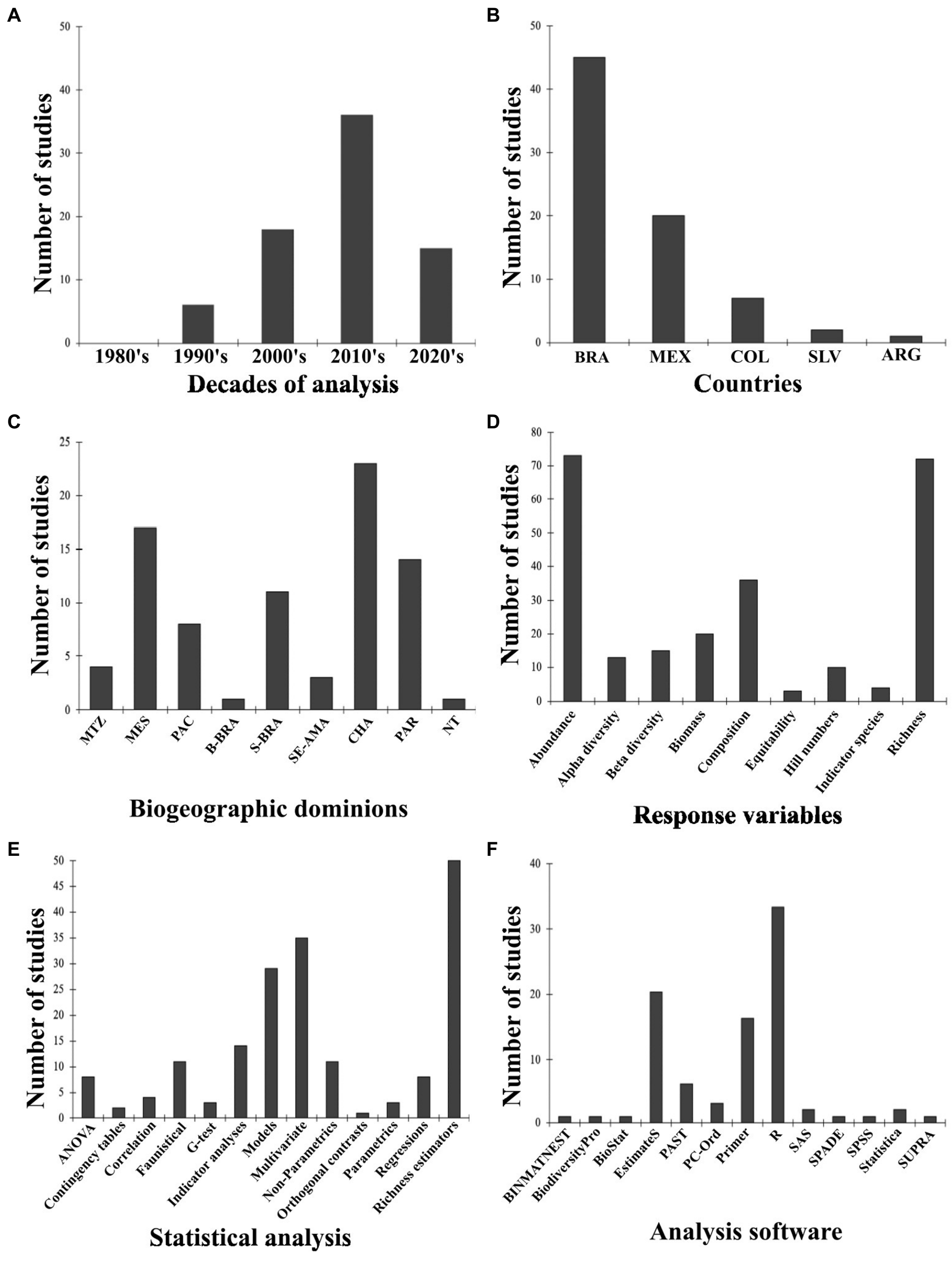

FIGURE 2
Number of taxonomic diversity studies. **(A)** Over time (decades). **(B)** Per country. Countries: Brazil=BRA, Mexico=MEX, Colombia=COL, El Salvador=SLV, Argentina=ARG. **(C)** Per biogeographic dominion. Mexican Tranzition Zone=MTZ, Mesoamerican=MES, Pacific=PAC, Boreal Brazilian=B-BRA, S-BRA=South Brazilian, South Eastern Amazonian=SE-AMA, Chacoan=CHA, Parana=PAR, Not tropical=NT. **(D)** Per response variable. **(E)** Per statistical analysis. **(F)** Per software protocol.

Most articles described grazing lands as grasslands (75.21% of the 91 sampling sites), woodlands in only 8.26% ($n = 10$), and agroforestry systems in 15.70% ($n = 19$). The proportions of each type of grassland, woodland and agroforestry system in the reviewed articles are shown in Supplementary Table S3. Pasture lands included exotic pastures and treeless pastures. The most common species of grasses (mainly African) are shown in Supplementary Table S4. The woodland systems essentially belonged to South America grazing lands like Cerrado *sensu stricto*, Pampa, Campos ("campo rupestre," "campo limpo"), and Savanna (Supplementary Table S3). The principal agroforestry systems included silvopastoral systems with leguminous fodder plants (*Vachellia* spp., *Guazuma ulmifolia* Lam., *Leucaena leucocephala* (Lam.) de Wit, *Brosimum alicastrum* Sw.) and pastures, silvopastoral systems with native trees and fruit species, and silvopastoral systems with exotic species (e.g., *Pinus* spp.) and living fences (Supplementary Table S3).

Livestock management was included in the reviewed studies mainly for grazing description, animal information, production objective, water aspects, and infrastructure (Supplementary Table S5). Grazing information included animal rotation, type of grazing system, and fodder levels. Animal information included livestock stocking rate data and breed description. The main production objectives were meat and dual-purpose livestock (Supplementary Table S5). Information about water use only included irrigation and some aspects of water supplies. In terms of infrastructure, only the construction of stables is mentioned. We found that 43.63% of the reviewed manuscripts do not include livestock management aspects (Supplementary Table S5). Regarding the general objectives of the reviewed articles, the most common was the analysis of the effect of land use changes on taxonomic diversity (50% of all reviewed papers), followed by the impacts of surveys on distribution (26.32%), pasture management (13.16%), disturbance gradients (11.84%), fragmentation (9.21%), and silvopastoral systems (2.62%). The most used comparison type among the studies was diversity changes along management gradients (e.g., among forest, plantation, pasture, crops; 26.32% of the studies), followed by the forest vs. pasture diversity comparisons (19.74%), native vs. exotic pastures (13.16%), pastures (11.84%), exotic pasture diversity assessment (9.21%), vegetation gradients (e.g., primary forest, secondary forest, and pasture; 7.89%) and other comparisons representing the remainder (cattle presence or absence, restored gradients, living fences vs. pastures, natural fields, traps and bait functioning). The most important analyzed response variables were species richness and abundance, followed by the analysis of changes in species composition and biomass (Figure 2D). The more relevant tendencies were the decrease in species diversity from forest to pastures or along vegetation gradients from forest to pasture, or along management gradients. Species composition generally changed among conditions, mainly between wooded and open areas. In comparisons between native pastures or vegetation and exotic pastures, richness was higher in the native environments. In seasonal comparisons, the rainy season showed the highest richness.

Among the 76 articles evaluated, the most frequent analyses used were richness estimators ($n = 50$, 66.6%), multivariate analysis ($n = 35$, 46.6%), and models ($n = 29$, 38.6%). Richness estimator groups include Chao 1 and 2, Jackknife 1 and 2, Bootstrap, and Sample coverage. Multivariate analysis included Canonical Correlation Analysis (CCA), Principal Coordinate Analysis (PCO), Principal Component Analysis (PCA), Redundancy Analysis (RDA), and Permutational multivariate analysis of variance (PERMANOVA). Model group analyses consisted of Linear Models (LMs), Generalized Linear Models (GLMs), Generalized Linear Mixed Models (GLMMs), and Generalized Additive Models (GAMs; see Figure 2E, Supplementary Table S1). In relation to Software programs, R was the most used ($n = 33$, 44%), followed by Estimate*S* ($n = 20$, 26.6%) and Primer ($n = 16$, 21.3%). Finally, the R packages most used were iNext ($n = 18$, 24.0%), vegan ($n = 17$, 22.6%), and Betapart ($n = 6$, 8%; Figure 2F). Most of the studies that analyzed taxonomic diversity in grazing lands in the Neotropics have been carried out using a local spatial approach (~ 74%). It should be noted that 7.6% of the total articles reviewed had a scope at the local and landscape level; authors reflected on the variables affecting diversity at the local, landscape, and/or regional scales. Finally, very few studies ($n = 7$) make comparisons using a temporal approach (six were short-term and one was long-term).

3.2. Functional dung beetle diversity studies in grazing lands

The study of dung beetle functional diversity in Neotropical livestock systems began with Halffter et al. (2007) in Mexico. Moreover, Mexico is the only country that performed functional studies over the last three decades, with two studies per decade (Figure 3A). In the next decade, more than twice as many papers were published compared to the 2000s, with 60% of them conducted in Brazil. After 2020, the greatest number of functional studies have been published ($n = 9$, 34.62%; Figure 3A) in Brazil, the country with the most functional studies published to date, while El Salvador and Costa Rica showed opposite patterns, with one article published per country (Figure 3B). Additionally, the study of dung beetle functional diversity in livestock systems has been relatively new in countries such as Argentina (2019), Colombia (2020), and Costa Rica (2021; Figures 3A,B). Almost 40% of the reviewed papers were performed between two biogeographic provinces: 20% in Parana (between Brazil and Argentina) and 17% in Rondônia (Brazil). Moreover, 60% were divided among the remaining 13 provinces, most of them with only one published paper (Figure 3C). Approximately 57.70% of the articles were performed in the Parana ($n = 8$, 30.77%) and Chaco ($n = 7$, 26.92%) biogeographic domains. Mesoamerica ($n = 6$, 17.65%) and southern Brazil ($n = 6$, 17.65%) had equivalent numbers of studies, followed by the Mexican transition zone ($n = 2$, 5.88%), the Pacific ($n = 2$, 5.88%) and southeastern Amazon ($n = 2$, 5.88%), and the South American transition zone ($n = 1$, 2.94%; Figure 3C).

Grazing lands were described in most articles on functional diversity as grassland (71.79%, $n = 28$), woodland (5.13%, $n = 2$), and agroforestry system (23.08%, $n = 9$). The proportion of each type of grassland, woodland, and agroforestry system in the reviewed articles are shown in Supplementary Table S3. Pastureland included exotic pastures and treeless pastures. The most common species of grasses are shown in Supplementary Table S4. Rangelands comprised native grassland of *Andropogon* spp. and *Axonopus* spp. without cattle presence, and grazed rangelands having the same species, but with cattle presence (Supplementary Table S3). The woodland systems belonged to South America grazing lands like Cerrado *sensu stricto*, and Grota (Supplementary Table S3). The principal mentioned agroforestry systems included silvopastoral systems (SPS) with leguminous fodder plants [*Vachellia pennatula* (Schltdl. & Cham.) Seigler & Ebinger, *Leucaena leucocephala* (Lam.) de Wit] and pastures; SPS with commercial species and native trees, SPS combining fruit species (*Psidium guajava* L.) and native trees (*Quercus insignis* M. Martens & Galeotti), and SPS with exotic species (e.g., *Pinus* spp.; Supplementary Table S3). Livestock management information is included in the reviewed studies about functional diversity, mainly about grazing, but including animal information, water aspects, and total surface (Supplementary Table S5). Grazing information contains animal rotation aspects, food surveys, plant successional information, grass type and management, description of the silvopastoral design and/or silvopastoral grass cover, pasture age, and grazing system management (Supplementary Table S5). Animal information

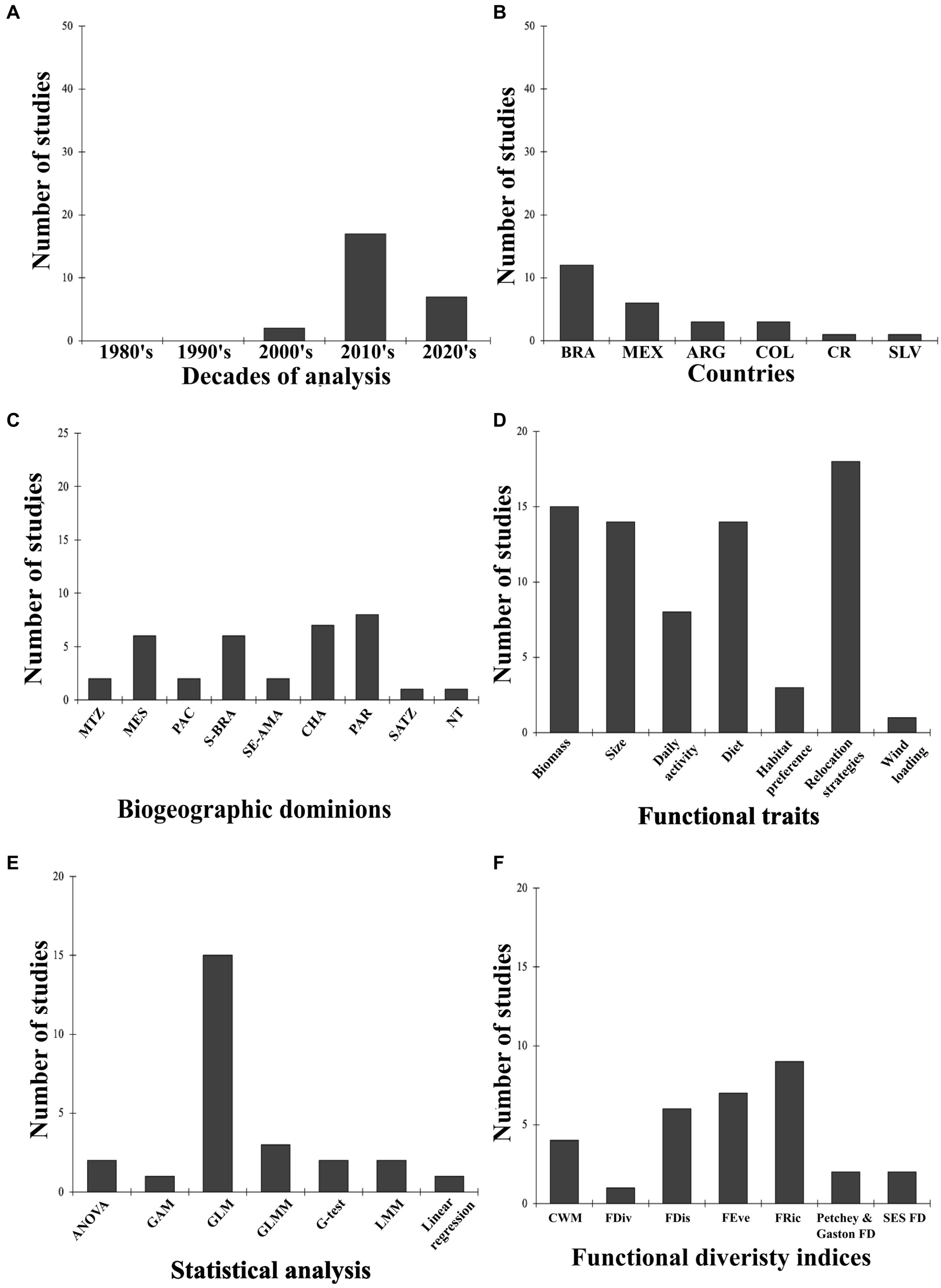

FIGURE 3
Number of functional diversity studies. **(A)** Over time (decades). **(B)** Per country. Brazil=BRA, Mexico=MEX, Colombia=COL, Costa Rica=CR, El Salvador=SLV, Argentina=ARG. **(C)** Per biogeographic dominion. Mexican Tranzition Zone=MTZ, Mesoamerican=MES, Pacific=PAC, Boreal Brazilian=B-BRA, SATZ=South American Transition Zone, South Eastern Amazonian=SE-AMA, Chacoan=CHA, Parana=PAR, Not tropical=NT. **(D)** Per functional trait. **(E)** Per statistical analysis. **(F)** Per functional diversity index.

references mainly cattle density, the total number of cattle, and livestock breed description (Supplementary Table S5). Information about water use is general (Supplementary Table S5). Approximately 19.23% of the reviewed manuscripts do not include livestock management information. Livestock practice data were scarce (68.42% of the studies without information), and the only mentioned practice was agrochemical use (Supplementary Table S5).

Most papers evaluated in this section used functional effect traits to perform functional analyses because of their relationship with the ecosystem functions and dung beetle performance in livestock systems

(Supplementary Table S1B). Food relocation strategies were commonly used functions in most studies (*n* = 18, 69.23%), while wing loading and habitat preference were the least used (*n* = 1, 3.85%; Figure 3D). In addition, a trend in the selection of four functional traits was observed: biomass, body size, diet, and relocation strategies (Figure 3D). According to the authors, biomass and body size were selected because those traits are related to the amount of organic matter manipulated and buried in the soil. Relocation behavior determined spatial distribution of resources (vertically and horizontally), and diet preference inferred the type of resource that dung beetles manipulated.

The reviewed studies used various statistical methods to model the observed functional diversity with environmental or biological parameters. These ranged from one-way ANOVAs to general linear mixed models. However, over half of the studies used general linear models (n = 11, 57.70%), followed by general linear mixed models (*n* = 2, 11.5%; Figure 3E). The remaining analytical methods were represented by one study each. Eleven studies (61%) used the FD statistical package to analyze functional diversity, and four (22.22%) used the dbFD function. The other functions from FD and the Picante package were used only by one or two studies. Functional diversity was evaluated using two approaches: functional groups and indices. Most reviewed studies grouped the selected traits into functional groups, with counts and proportions of these traits the most used approaches. In the second approach, three indices were the most used: functional richness (*n* = 9, 29.03%), evenness (*n* = 7, 22.58%), and dispersion (*n* = 6, 19.35%), respectively (Figure 3F).

Twenty-four of the reviewed functional diversity studies (92%) employed a local spatial approach, and the remaining studies used a regional system (*n* = 2, 7.7%). It should be noted, that of those 24 local-based articles, eight (33%) considered more than three habitats in addition to the grassland environment (with which they tried to understand the role of grasslands in the landscapes studied), and 16 studies (67%) only considered grasslands, generally comparing them with fragments of preserved vegetation. The two studies with a regional spatial approach only make a comparison between grasslands and preserved forests. Finally, two works (7.7%) made temporal comparisons.

3.3. Biodiversity and ecosystem functions and services in grazing lands

The total number of papers in our literature search that evaluated at least one function provided by dung beetles was 18 (Supplementary Table S1C). There has been an increasing trend in the number of studies dealing with grazing lands and functions in the dung beetle literature over the last five decades (Figure 4A). This result matches the general taxonomic and functional diversity sections. Before the 1990's we found no papers working on this subject. The pick of studies on this subject was in the 2010s with 10 papers, and the number of articles will probably be higher at the end of the 2020s. In terms of the countries supporting these papers, we found studies for six countries, with Mexico (*n* = 8, 44.44%) and Brazil (*n* = 6, 33.33%) as the main contributors, and several other countries with only one study (Figure 4B). This pattern is slightly different from the trend we found with the other topics, with Brazil being the dominant country. We did not find any article from several countries in Latin America (e.g., Bolivia, Chile, Ecuador, Guatemala, Honduras, Nicaragua, Panama, Venezuela, and all the Antilles) regarding work on grazing lands with a functional perspective. Biogeographically, we found studies in the principal dominions of Latin America, showing that there is no notable dominance of any dominion (Figure 4C). Mesoamerican (*n* = 6), Mexican Transition Zone (MTZ; *n* = 5), South Brazilian (*n* = 3), and Chacoan (*n* = 3) were the most studied regions. No papers were registered for functional studies in the Boreal or Parana dominions.

The trends observed in our review of articles on ecological functions and ecosystem services in grazing lands were like those we have found in our analysis of taxonomic and functional diversity. Most articles described grazing lands as grassland (76.92% of the 20 sampling sites), woodlands in only 3.85% (*n* = 1), and agroforestry systems described in 19.23% (*n* = 5). The proportions of each type of grassland, woodland, and agroforestry system in the reviewed articles are shown in Supplementary Table S4. Pasture lands included exotic pastures and treeless pastures. The most common species mentioned belonged to African grasses (Supplementary Table S4). The woodland systems belonged to South America grazing lands (Savanna; Supplementary Table S3). The principal mentioned agroforestry systems included a mix of pastures and banks of protein-rich legumes, such as *Leucaena leucocephala* (Lam.) de Wit (Fabaceae), and silvopastoral systems with commercial and native trees. Forest grazing included grazed primary and secondary vegetation and grazable forest land comprising small patches of grasses and ferns, predominantly covered by pine (*Pinus oocarpa* Schiede ex Schltdl.) with small numbers of *Callitropsis lusitanica* (Mill.) D.P. Little (formerly *Cupressus lusitanica* Mill.) and with little undergrowth vegetation (Supplementary Table S3). The information about livestock management in ecological functions and ecosystem services was similar to the authors' topics (Supplementary Table S5). However, other elements are integrated into the management description, such as land ownership, type of livestock operation, and technological aspects (Supplementary Table S5). Approximately 22.22% of the revised manuscripts do not include livestock management aspects. In articles reviewed for ecological functions and ecosystem services, the information about livestock management practices was scarce; in 96.15% of the documents, there was no information. Only the use of veterinary medical products for cattle is mentioned in the few studies where information on livestock management practices is available (Supplementary Table S5).

Taking into consideration the wide range of functions that dung beetles provide in different ecosystems, in this literature review for pastures we only found studies evaluating four functions: (i) dung removal, (ii) seed dispersal, (iii) soil bioturbation, and (iv) parasite control (Figure 4D). The primary function was dung removal in 18 studies, followed by soil bioturbation (*n* = 5, 27.78%). Other functions like reducing greenhouse gas emissions, nutrient cycling, soil structure (e.g., aeration, permeability, porosity), pollination, or food supply, were not mentioned in any published papers in our literature review for grazing lands in Latin America. Thus, it seems easy to study and design experimental studies that quantify some of these functions instead of others. Regarding the statistical analyses used in the studies, we found that the most common methods were GLM, ANOVA, linear

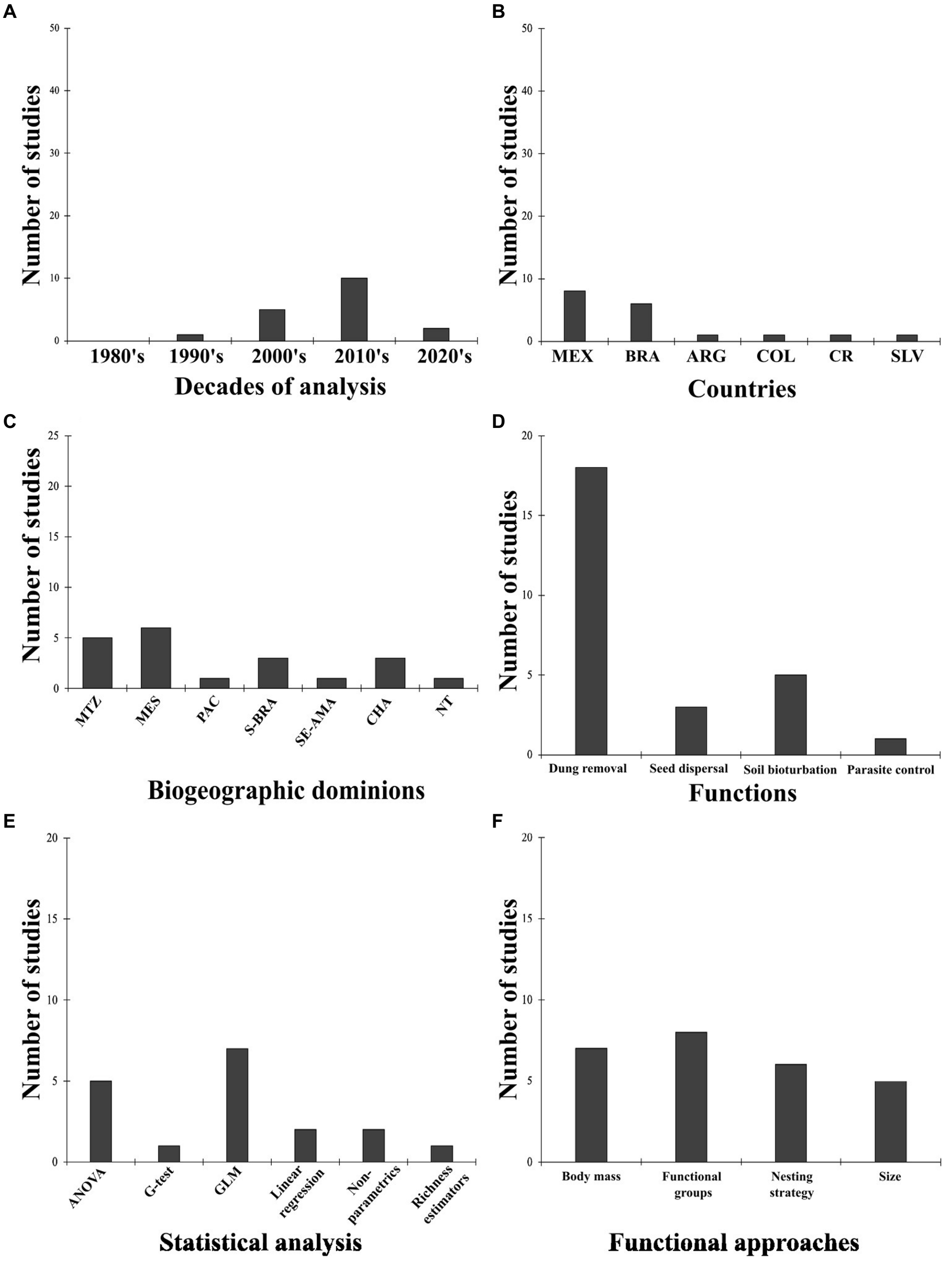

FIGURE 4
Number of ecological functions studies. **(A)** Over time (decades). **(B)** Per country. Brazil=BRA, Mexico=MEX, Colombia=COL, Costa Rica=CR, El Salvador=SLV, Argentina=ARG. **(C)** Per biogeographic dominion. Mexican Tranzition Zone=MTZ, Mesoamerican=MES, Pacific=PAC, Boreal Brazilian=B-BRA, SATZ=South American Transition Zone, South Eastern Amazonian=SE-AMA, Chacoan=CHA, Parana=PAR, Not tropical=NT. **(D)** Per function. **(E)** Per statistical analysis. **(F)** Per functional approach.

regressions, and non-parametric approaches (Figure 4E). Finally, in terms of function, we found four main variables: body mass, functional groups, nesting strategy, and size (Figure 4F). The most used were functional groups ($n = 8$, 44.44%), followed by body mass ($n = 7$, 38.89%). The conceptual separation between these approaches is not clear enough because some studies use size, body mass, or nesting strategy to build different functional groups.

4. Discussion

4.1. Taxonomic dung beetle diversity studies in grazing lands

The most common goal was evaluating the effects of “land use changes.” Indeed, land-use change has been one of the major causes of natural ecosystem transformation, causing global biodiversity declines (Newbold et al., 2015). Currently, livestock farming is the most significant land-use sector on Earth, occupying more than 30% of the planet's continental surface as grazing lands (FAO, 2017). Therefore, it is understandable that dung beetle researchers have driven their studies to understand the impacts of the conversion of natural vegetation to grazing lands, because that theme is urgent to preserve biodiversity and associated ecosystem functions and services.

Among studies, we found two approaches explaining the changes in species diversity in grazing lands. First, in the articles conducted in tropical rain forest is observed a high number of total and exclusive species, and they become locally extinct with the loss of trees or canopy cover in humid tropical landscapes. A loss of species is observed as vegetation fragments become smaller due to changes in land use and increased distance among the remnants. These small fragments serve as refuges for some forest species (Favila, 2005), and the diversity depends on nearby species pools, possibly primary forests, and host a greater spatial heterogeneity in species composition. Forest cover is the best predictor of dung beetle assemblages, positively related to species diversity and biomass across multiple spatial scales (Alvarado et al., 2018). Yet, landscape homogenization resulting from increased extension of grazing lands leads to changes in resource food selection related to the preference in the attraction of dung beetles to exotic omnivores and livestock (Alvarado et al., 2021).

In articles conducted more frequently in fragmented landscapes of tropical dry forest we found a the second approach: the authors found there has been no net reduction in regional species richness, although local species richness in natural ecosystems has declined (Halffter and Arellano, 2002). A change in species composition is observed as grassland species invade vegetation fragments. However, forest remnants, wooded systems, living fences, and silvopastoral systems generate new assemblages (species with different habitat requirements) within species-rich landscapes with greater connectivity (Reyes-Novelo et al., 2007; Arellano et al., 2008, 2013; de Farias et al., 2015); therefore, changes in species composition and species turnover becomes important. There are clear signs that tree structure and microclimatic conditions like forests, as found in agroforestry, can help preserve biodiversity by creating a propitious habitat for native species (Righi et al., 2018). Silvopastoral systems can buffer the adverse effects of rapid expansion of open areas and the consequent reduction of tropical dry forest area generated by conventional technified systems (Arellano et al., 2013). Although richness remains relatively constant in landscapes with intermediate degrees of disturbance (such as those that have been partially modified for human use), richness at the local level changes notably over short lapses of time, and the assemblage composition is very fluid (Halffter et al., 2007).

Finally, because dung beetles were proposed as indicator groups in taxonomic diversity studies, the integration of functional groups such as habitat preferences (Favila, 2005; Díaz et al., 2010; Bourg et al., 2016), daily activity (Navarrete and Halffter, 2008); relocation strategies (Escobar and Chacón de Ulloa, 2000; Horgan, 2008; Basto-Estrella et al., 2012; Noriega et al., 2012; Gómez-Cifuentes et al., 2019; Correa et al., 2019a, 2020a; Cajaiba et al., 2020; Salomão et al., 2020); body size (Escobar and Chacón de Ulloa, 2000; Halffter and Arellano, 2002; Navarrete and Halffter, 2008; Korasaki et al., 2013), food preferences (Favila, 2005; da Silva et al., 2008; Horgan, 2008; da Silva and Audino, 2011; Correa et al., 2013; Cajaiba et al., 2020) and their representativeness under different conditions or land uses continue to be considered, as well as the use of biomass as an essential value (e.g., Noriega et al., 2012; Costa et al., 2017; Alvarado et al., 2021), forming the basis for subsequent studies of functional diversity with precise and statistically more robust methods.

4.2. Dung beetle functional diversity studies in grazing lands

Functional diversity has been evaluated by its importance to ecology and biological conservation studies since it is a component of biodiversity that contributes to the understanding of the structure and functioning of ecosystems, including information on the identity of species through the description of their functional traits (Moore, 2001; Tilman, 2001). A first approach to functional diversity is the formation of functional groups, which are defined as a set of species that have a similar life history, such that they use a resource similarly in a given space and time (Moore, 2001; Steneck, 2001; Tilman, 2001), or that are related to some activity in ecosystems (Naeem et al., 2009). Species with similar functional traits are commonly assigned to functional groups (Moore, 2001; Steneck, 2001; Tilman, 2001). In Neotropic grazing lands, we found that in the reviewed articles, both analyses of functional groups and functional traits are carried out. However, most studies analyze each trait independently because counts and proportions are the most commonly used methods. Also, with this approach, it is necessary to consider the use of relevant terminology regarding dung beetle nesting behavior since it is one of the most widely used functional traits for categorizing functional groups (Tonelli, 2021).

In general, the studies reviewed on functional diversity showed how different traits, both ecological and morphological, have been considered over time (e.g., Halffter et al., 2007; Barretto et al., 2020; Davies et al., 2020, 2021; Souza et al., 2020; Correa et al., 2020b, 2021b; Whitworth et al., 2021; Guerra-Alonso et al., 2022). Beetle size (large, medium, and small species) has been the most frequently used qualitative functional trait (Barretto et al., 2020; Davies et al., 2020, 2021; Noriega et al., 2021b), although they also highlight the feeding pattern of relocation (telecoprid-rollers, paracoprid-tunnelers, and endocoprid-dwellers), daily activity (nocturnal, diurnal, and continuous or mixed activity), and diet (coprophagous, necrophagous, and generalist species). Biomass (dry weight) has been quantitatively estimated as an important trait (i.e., Correa et al., 2018; Gómez-Cifuentes et al., 2019, 2020), although it has also been used frequently in taxonomic diversity analyses, as a surrogate for abundance. A work that stands out in this review is Guerra-Alonso et al. (2022) because the authors measured different morphological response traits of dung beetles: (i) body area, (ii) biomass, (iii) total length, (iv) sphericity, (v) area of the head, (vi) width of the pronotum, (vii) length of the anterior tibia, (viii) area of the anterior tibia, (ix) area of the anterior femur, and (x) tooth width. Wing loading and color pattern (metallic, uniform, and patterned colors) also have recently been used as indicators of change in functional diversity (Whitworth et al., 2021).

Of the total number of articles reviewed, seven articles (27%) analyzed functional diversity as a complement to the taxonomic approach, applying these two methodological approaches to understand how grasslands modulate the function and diversity of beetles in the Neotropics (Correa et al., 2018, 2019b, 2020b, 2021a,b;

Gómez-Cifuentes et al., 2019; Cajaiba et al., 2020). Likewise, we were able to visualize key conclusions revealing the context of the landscape and type of management needed to generate alterations in the role of beetles, for example: (i) the most disturbed ecosystems are related to significant reductions in functional redundancy, which can have detrimental effects on the future resilience of the landscape (Cajaiba et al., 2020); (ii) for cattle grazing rotation to be effective, in introduced Brazilian pastures it has been seen that an extended period of time (at least 1 month) is required for cattle removal; this strategy can be helpful to conserve the diversity of grasses, dung beetles and, consequently, ecological functions (Correa et al., 2021a); and (iii) some authors such as Carvalho et al. (2021) have indicated that the responses of dung beetle assemblages and their ecological functions to subtle changes within a type of land cover are uncoupled, idiosyncratic and depend on the context, making it difficult to make predictions and generalizations in grasslands. Likewise, Guerra-Alonso et al. (2022) have shown that native forests and forests with cattle maintain functional diversity in all regions. In the case of open pastures, the authors argue that the answer depends on the regional context because the substitution of the native forest for open pastures strongly affects functional diversity.

4.3. Biodiversity and ecosystem functions and services in grazing lands

The low number of papers ($n = 18$) that include and evaluate at least one function provided by dung beetles in grazing lands, compared to the number of articles working with taxonomic ($n = 76$) or functional diversity ($n = 26$) in our review, is troubling. Even though there has been an increasing trend over the last five decades, it is indeed a new topic regarding grazing lands (e.g., Ortega-Martínez et al., 2016; Alvarado et al., 2019; Carvalho et al., 2021). There is a clear thematic dominance in terms of the countries that carry out this type of study (i.e., Mexico - Basto-Estrella et al., 2016; Ortega-Martínez et al., 2016; Huerta et al., 2018; Alvarado et al., 2019 and Brazil - Braga et al., 2013; Correa et al., 2019a; Carvalho et al., 2021). Most Latin American countries lack studies on ecosystem functions in grazing systems (see section 3.3). As well, there are few studies that analyze and study functions at the level of a single species (e.g., Miranda et al., 2000; Anduaga and Huerta, 2007; Martínez et al., 2018), and few studies that use mesocosms (e.g., Anduaga, 2004; Ortega-Martínez et al., 2016; Alvarado et al., 2019), or that carry out studies under laboratory conditions (e.g., Horgan, 2001; Mariategui et al., 2001; Ortega-Martínez et al., 2016), aspects to be explored in future studies.

Regarding ecosystem functions, there was a tendency to evaluate dung removal as the main activity of dung beetles (e.g., Miranda et al., 2000; Mariategui et al., 2001; Anduaga, 2004; Cruz et al., 2012; Alvarado et al., 2019). The main reason for this trend is the importance of this function as the basis for many ecosystem services and the methodological ease of evaluating it. However, it is important to mention that when comparing different studies, some experimental variations in the use of controls and units would need to be verified and standardized. The other ecosystem functions we reported were seed dispersal, soil bioturbation, and parasite control (see Giraldo et al., 2011; Braga et al., 2013; Martínez et al., 2018; Correa et al., 2019a; Carvalho et al., 2020, 2021). Other essential functions like greenhouse gas emissions control, nutrient cycling, soil aeration, permeability, porosity, pollination, or food supply (Nichols et al., 2008; Slade et al., 2016) were not registered in this review. It is possible that some services, such as seed dispersal, are more relevant in forest systems than in grasslands (e.g., Andresen, 2002), which would explain the absence of studies on this function. Likewise, the study of some services that may be important in livestock systems, such as the control of greenhouse gases, may be limited by the technical requirements and costs of this type of evaluation (Slade et al., 2016). This should undoubtedly be a priority for future studies in this type of system in the region.

Another critical aspect that needs to be standardized are the variables used in functional approaches. We found four main variables: (i) body mass (e.g., Anduaga, 2004; Braga et al., 2013; Alvarado et al., 2019), (ii) functional groups (e.g., Basto-Estrella et al., 2016; Correa et al., 2019b; Carvalho et al., 2021), (iii) nesting strategy (e.g., Braga et al., 2013; Alvarado et al., 2019; Correa et al., 2019b), and (iv) size (e.g., Mariategui et al., 2001; Anduaga, 2004; Carvalho et al., 2021). Most studies mix these concepts indistinctly, especially in the case of biomass, which is almost always assumed by utilizing the weight of individuals as a proxy. In many of these papers, the conceptual separation between these approaches, the way they are measured, or the categorization is not clear enough. The construction of functional groups using the combination between food resource relocation guilds (i.e., paracoprids, telecoprids, endocoprids, and kleptocoprids) and individual size (i.e., small, medium, large) seems to be a helpful strategy (see Noriega et al., 2021b). However, the construction and categorization of functional groups require an in-depth theoretical review and experimental studies that allow us to understand their separation at an operational level.

As well, we registered for taxonomic and functional diversity, a lack of information on livestock systems, type of management, use of anthelmintics, characteristics of pastures and soils, cattle species, grass species, and climatic conditions. The absence of this information in most of the papers is not only a severe methodological problem that constrains replicability, but also prevents large-scale comparisons or meta-analyses. This is one of the main reasons we propose a standard data collection format (Supplementary Box I) for work in these environments.

4.4. Grazing lands

In articles regarding the effects of grazing lands on dung beetle diversity, functions, and ecosystem services, we must start by recognizing that there is no clear standardization or unification of the criteria for "grazing lands." Over time, the approach and concept of pastures and the effect of the transformation of natural ecosystems to treeless and/or grazing lands on the taxonomic and functional diversity of dung beetles and their ecosystem functions and services have been evolving and transforming. Grazing land studies have long been focused on the presence/absence of tree cover (decreasing species diversity from forest to pastures: e.g., Navarrete and Halffter, 2008; da Silva and Hernández, 2014, 2016; Bourg et al., 2016; Silva et al., 2017; Salomão et al., 2020), and in most reviewed articles (using taxonomic and functional diversity and functions) they were described as open areas dominated by grasses and herbs (e.g., Halffter et al., 1992; Horgan, 2008; Navarrete and Halffter, 2008; Bourg et al., 2016; Salomão et al., 2020).

Currently, there are multiple studies describing declining species diversity over vegetation gradients (e.g., Halffter et al., 1992; Escobar and Chacón de Ulloa, 2000; Andresen, 2008; Almeida de and Louzada, 2009; Cajaiba et al., 2020; Rivera et al., 2020; Alvarado et al., 2021), or management gradients (e.g., Arellano et al., 2013; Korasaki et al., 2013; Montoya-Molina et al., 2016; Costa et al., 2017; de Farias and Hernández, 2017; Righi et al., 2018). Recent approximations compare species diversity between grazed rangelands and pasturelands (exotic pastures; e.g., Almeida et al., 2011; Correa et al., 2016a,b; Macedo et al., 2020). As the description of grazing lands becomes more precise, a better understanding of these spaces is permitted.

Approaches have been changed gradually, and other aspects have begun to be analyzed, such as the effect of boundaries between natural ecosystems and pastures (e.g., Silva et al., 2017; Martínez-Falcón et al., 2018), the relative importance of the presence of exotic food (cattle excrement), the loss of cover in managed secondary vegetation (Halffter and Arellano, 2002) and the spatial distribution of pastures in the landscape, their adjacent areas, and boundaries with other land uses (Arellano et al., 2008), or the species within pastures present in the areas. Since the 2010s, silvopastoral systems and managed secondary vegetation and their benefits for biodiversity conservation have begun to be incorporated into grazing lands. The variety, or the species of grass (e.g., Abot et al., 2012; Flota-Bañuelos et al., 2012; Correa et al., 2013, 2016a; Righi et al., 2018), the composition and density of tree species in pastures, the surrounding matrix, and local knowledge are being mentioned in dung beetle studies. Meanwhile, silvopastoral systems will increase in the coming decades due to the growing global population, with an estimated 30–70% increase in demand for timber, cellulose, oils, and food (Solorio et al., 2017). Further studies are needed to clearly understand how different silvopastoral systems (with different plant density, composition, and management) may affect dung beetle biodiversity in the Neotropics. There is little information regarding the impact of silvopastoral systems on Neotropical dung beetles (Colombia, see Montoya-Molina et al., 2016; Argentina, see Gómez-Cifuentes et al., 2019; Mexico, see Arellano et al., 2013, de Farias et al., 2015).

We need to understand the effect of vegetation structure of grazing lands (Agrosilvopastoral systems: ASPS, Voisin silvopastoral and pastoral grazing, biodiverse grasslands, monoculture pastures without trees) on Neotropical dung beetle assemblages. ASPS is a viable strategy for extensive livestock farming based on the principles of agroecology, agroforestry, and animal production. The objective of these systems is to optimize the positive interactions between agriculture, forestry, livestock, and the physical environment, and to maximize land productivity through spatial or sequential spatial arrangements or in temporal sequences (Murgueitio and Solorio, 2008; Nahed-Toral et al., 2013). However, afforestation often involves the creation of fast-growing tree plantations or SASP on non-forest lands. What will be the possible impacts of afforestation on the biodiversity of local species (e.g., Ueda et al., 2015)? Although grazing lands represent a large area in most terrestrial landscapes, management decisions within these systems that can affect the conservation of the dung beetle biodiversity are still poorly understood (Correa et al., 2021a).

4.5. Livestock management

Currently, livestock is the most prominent land-use sector on Earth, occupying more than 30% of the global continental land area (FAO, 2017). To understand the impact of livestock activities on dung beetle diversity over the last 20 years, analyses are increasingly investigating livestock practices and management. Some past studies have assessed the effects of shaded fields (Horgan, 2002, 2005), site complexity, soil quality, and management (de Farias et al., 2015); ivermectin use (Flota-Bañuelos et al., 2012; Tovar et al., 2016), fire use (Rangel-Acosta et al., 2020); cattle grazing abandonment time (Correa et al., 2019a, 2020b), animal consortium (e.g., horse and cattle, Louzada and Carvalho e Silva, 2009; sheep and cattle; Correa et al., 2020c), rotational pasture management (Correa et al., 2021a) and livestock intensification (Alvarado et al., 2018).

Research interest is growing in the Neotropics regarding the effect of agrochemicals, mainly anthelmintics (doramectin, eprinomectin, ivermectin, or moxidectin) and herbicides on dung beetles (Souza et al., 2018; Villada-Bedoya et al., 2019; Carvalho et al., 2020; Correa et al., 2022). The spatial and temporal impact of the macrocyclic lactone parasiticide treatments, which result in insecticide residues in cattle feces, will depend on a range of farm management factors, such as the frequency of anthelmintic use, the number of animals treated, and the choice of active ingredient, as well as a range of insect-related factors, such as abundance, population dynamics, and dispersal rates. More studies are needed to understand dung beetle assemblage responses to impacts from livestock activities on taxonomic and functional diversity, and in their ecological functions in the Neotropics. Equally important is how herd management, grazing intensity, area size, grazing time, and local history contribute to understanding how dung beetle species respond to pasture management in grazing lands and how this can help cattle farmers in decision-making to improve conservation strategies on their properties.

4.6. Context and history of land-uses

In the Neotropics, we also find differences in cattle raising protocols and their effects among countries and biogeographic regions. The greatest differences are found in the Pantanal, where the size of the herds is much larger than in other Neotropical areas, with no inputs used, and the animals are moved so that the land is left to rest for a sufficient time. The problems encountered have more to do with the introduction of exotic grasses. In the Brazilian Pantanal, the vast natural grassland plains, allied with a favorable climate, promoted extensive cattle ranching in this ecosystem in often pervasive areas (10,000 ha; Seidl et al., 2001; Eaton et al., 2011). Thus, in many Pantanal sites using cattle, there are private lands with livestock histories of at least 100 years using native grasses resistant to the seasonal flooding that occurs in this biome. These practices occur without intensive management (no use of fertilizers, herbicides, and veterinary drugs in cattle), with stocking rates between 0.5 and 1.0 animal unit ha^{-1}. Therefore, cattle breeding in natural grasslands of the Brazilian Pantanal can integrate livestock production with the conservation of dung beetles and their ecological functions (Correa et al., 2019a).

In Mesoamerica and other regions of South America, such as Mexico and Colombia, areas previously occupied by tropical forests were deforested, and monoculture pastures were implemented, which were gradually dominated by introduced African grasses. In the Mexican High Plateau, where extensive cattle ranching is common, grazing lands include open areas for crops, semi-open areas for cattle, and closed areas with native shrubby vegetation, which during the dry season are used for cattle foraging. Those grazing practices have transformed the natural arid environment into landscapes dominated by semi-open grazing areas, maintaining several species of domestic livestock associated with the original vegetation (Mellink and Riojas-López, 2020). The responses of dung beetle assemblages are modulated by the ecological conditions resulting from the transformation of native vegetation into grazing areas and the history of the species inhabiting different biogeographical provinces. The impact of grazing on dung beetle diversity is dependent to a considerable degree on the local ecological conditions and the biogeographical context that has shaped the composition of assemblages over time (Barragán et al., 2014).

Agricultural production systems are dynamic and complex because they have non-linear properties and experience imbalances over time by new interactions among their unique components. Therefore, the current status and response potential of livestock systems results from a complex historical process of interactions between physical, biological, and socioeconomic factors, adaptive tensions between society and nature, and production and ecosystem services. The changes in local grazing land conditions are driven by human management practices (Hutton and Giller, 2003; Alvarado et al., 2019; Gómez-Cifuentes et al., 2022). The knowledge of the historical trajectory of livestock farming in the Neotropics facilitates identification of the essential stages of the process to recognize the causes of biodiversity loss (Rodríguez-Moreno et al., 2020). Livestock management history in the Neotropics is a theme touched upon by some, not as a variable for analysis, but as a theme to involve the reader in the context of land use changes. How livestock management affects dung beetles in Neotropical grazing lands remains to be investigated in different biogeographical and social contexts.

4.7. New research frontiers, gaps, and future questions for grazing lands

4.7.1. Countries, regions, local vs. regional, and specific grazing habitats

As presented, a high proportion of reports on changes in dung beetle species diversity come from Brazil, Mexico, and Colombia. The latest research trends reported by UNESCO (2021), show that Brazil, Mexico, and Argentina have the highest rates of public investment in overall research and scientific production, as well as Ph.D. students in Latin America. Moreover, such productivity should also be reflected in environmental research with dung beetles. However, lack of investment creates a critical information gap, resulting in poor understanding of each country's identity, diversity, ecology, and species distribution. In addition, considering the publication trend over the last three decades, a geographical transition of publications from Mexico to Brazil can be seen due to a generational change in researchers.

4.7.2. Spatial and temporal comparisons

This review shows that the number of articles on the temporal changes in species diversity has been declining (e.g., Reyes-Novelo et al., 2007; Silva et al., 2010; Lopes et al., 2011; Flota-Bañuelos et al., 2012; Correa et al., 2016a, 2018, 2021b; Salomão et al., 2020). Although it is important to know monthly or seasonal variations in species diversity, long-term studies on the impact of land management on dung beetle assemblage dynamics are needed to understand the processes involved and suggest better management strategies. Overall, we found a lack of studies that include extensive time windows (more than 1 year of sampling) or analyses at broad spatial scales (landscape or between countries or regions). This produces an explicit spatio-temporal limitation of the patterns described and makes the results extremely local and punctual. Absence of this form of study is due to the non-existence of projects and funding sources covering more than 1 year, and the reduced interaction between scientists throughout Latin America. In this sense, it is necessary to expand these windows of time and space to compare studies among years and decades, as well as among countries and biogeographical regions, and create a more robust network of researchers in Latin America.

4.7.3. Livestock management studies

As we mentioned, there is a growing interest among researchers in the Neotropics regarding the effect of agrochemicals on dung beetle species. Most studies have been carried out using small, short-cycle species [e.g., Aphodiinae, *Euoniticellus intermedius* (Reiche)], which perform efficiently in the laboratory. However, it also is necessary to know the effect of these agrochemicals on large burrowing species (e.g., Iwasa et al., 2007), which are more sensitive to land use and management changes. Large bodies are often associated with lower fecundity and longer generation times (Halffter and Edmonds, 1982; Chown and Gaston, 2010), so a reduction in the ability of populations to compensate for increased mortality under anthropogenic pressures would be expected (Chown and Klok, 2011; Nichols et al., 2013). Species' abundances or the occurrence of specific sensitive species should be investigated concerning habitat and landscape factors before management and conservation plans of semi-natural pastures are made (Söderström et al., 2001). Performing more studies on the effect of herbicides, insecticides (e.g., Kryger et al., 2006; Sands and Wall, 2018), hormones, and vaccines on dung beetles would be highly beneficial. Thus, many field studies are currently being initiated (Villada-Bedoya et al., 2019).

Grazing management strategies are not carried out exclusively in space or time, so we must analyze the effect of grazing synergistically with other management practices (fire, agrochemical use, artificial fertilization, soil management practice, tillage, type of livestock) on dung beetle assemblages. This will facilitate the design of conservation and management strategies that favor the diversity of dung beetle species. Also, the importance of landscape composition for mobile organisms entails that management activities should focus on broader scales. Finally, studies evaluating dung beetle economic contributions to cattle production in tropical grazing lands are required (see Lopez-Collado et al., 2017). Information on the monetary value of dung beetle services may stimulate and encourage farmers to develop management plans for livestock production to conserve dung beetle diversity and their ecological benefits.

4.7.4. Management history

According to our review, the impact of animal livestock grazing and management on the environment has been of increasing interest over time, although the approach in each paper provides contrasts between the Old World and the New World due to the different contexts and histories of animal livestock maintenance. Livestock farming is an ancient human activity, which began with the domestication of cattle (sheep, goats) in the Neolithic (e.g., hieroglyphics in the Middle East, in Egypt dating from 4,500 years BC). In Europe, there are traditional management systems such as grazing of small herds of small livestock and the "dehesa" ecosystem, which, according to the legal context of the European Union (Habitat Directive), are considered Cultural Landscapes or semi-natural ecosystems and serve as model ecosystems in ecological restoration (Gann et al., 2019). The perpetuation of this type of landscape (since prehistoric times) is an example showing anthropic intervention in ecosystems can be sustainable, ensuring productive benefits while conserving biodiversity and climate regulation (Ferraz-de-Oliveira et al., 2016; Garrido et al., 2017).

To understand the reasons for the grazing and management practices used according to a particular context and management history also is important in order to suggest possible management strategies (e.g., Europe: Bokdam and Gleichman, 2000; Verdú et al., 2000; Lobo et al., 2006; Macagno and Palestrini, 2009; Rosa-García et al., 2013; Tocco et al., 2013). For example, we must consider that the tree species used in livestock systems, management practices, and the objectives in silvopastoral systems (SPS) are not the same. In Central America and Mexico, the tree species most used in SPS are forage and fruit trees, and in South America, timber species. The impact of the use of introduced grasses in pastures concerning native grasses is very different in Mesoamerica and South America.

Within agricultural management regimes, management history is important because of its implications for soil conditions, seed deposition and seedling propagation, existing diversity, and ecosystem resilience. Yet, in the articles we reviewed, less than 50% of the studies considered taxonomic diversity (46%), functional diversity (46.15%), or ecological functions (38.88%), nor included the history of land use (only as a descriptive explanation in the methods section or the introduction) to facilitate the understanding of the context in which the work takes place, mainly regarding the changes in land use over time, or the age of establishment of land uses. In the remaining studies, there is no information about land use history. This element is often not considered a variable in diversity analyses.

4.7.5. Ecosystem services less studied

Dung removal and burial is a crucial ecological function of dung beetles because it generates ecosystem services such as soil improvement, pasture cleaning and increased grazing area, control of cattle flies, greenhouse gas reduction, and secondary seed dispersal (Nichols et al., 2008). There have been multiple studies related to soil improvement, seed dispersal, and the identification of dung beetle species efficient in the control of cattle flies. However, there are no studies in the Neotropics related to the activity of Neotropical beetles and the emission of greenhouse gasses or fecal helminth transmission. More studies are needed that involve multiple functions and ecosystem services in grazing lands to have a more comprehensive assessment of the individual functional contributions of particular species and/or the mixture of species that drive ecosystem functioning (Manning et al., 2016; Slade et al., 2017; Piccini et al., 2018). We must identify changes in the function of manure burial and removal in response to traces of agrochemicals (e.g., Manning et al., 2017), hormones, vitamins, and other substances used in livestock management of manure, which change its quality. More economic valuations at local or regional scales on the ecosystem services of dung beetles are needed to communicate the importance of this group of insects and their roles to decision-makers. In terms of laboratory studies with one or several species or experimental designs in the field, we also found very few works showing alternative empty niches of possible analyses in livestock systems where physiological, behavioral, and ecological aspects of the assemblage could be evaluated.

4.7.6. Traits and multiple functions

Studies using functional trait approaches increase the understanding of ecological processes and inform conservation and restoration of ecosystems since traits are morphological, biochemical, physiological, structural, phenological, or behavioral characteristics that influence species' fitness (Nock et al., 2016). In future work, it is essential to include a variety of traits that represent species ecology and physiology to have a complete overview of functional diversity and the consequences of human disturbance on ecosystem functioning (Giménez-Gómez et al., 2022). In addition, it is necessary to assess the relationship between dung beetle traits and ecosystem functions delivered by them (deCastro-Arrazola et al., 2020), and distinguish dung beetle trait clusters that reflect assemblage adaptations to land use changes since they may better allow for generalizations of adaptive responses in ecosystems (Bui et al., 2020).

4.7.7. Conservation status

Most studies on dung beetle ecology are related to individual anthropogenic drivers of decline in richness, abundance, and biomass, changes in composition, increases of generalist species, and homogenization of assemblages. Further studies are required to analyze the synergic effects of the identified drivers (fragmentation, deforestation, agricultural management, defaunation, hunting, fire, invasive species, urbanization, global environmental change). Especially in Neotropical livestock systems, the presence of the invasive species *Digitonthophagus gazella* (Fabricius; see Noriega et al., 2020) can have a negative effect on the structure, diversity, and function of assemblages, which has not been experimentally quantified in the field.

There is a need for Neotropical research, mainly in population dynamics and natural history of dung beetle species and in monitoring any recent declines in population size or geographical range of some species in response to livestock activities. Comparisons between past and present population and range sizes over long periods are few. Most of these studies are carried out in Europe, Asia, and Africa. Adding information on geographic areas of dung beetles, where there are often significant knowledge gaps, contributes to the international conservation of species by deepening our understanding of their distribution, spatial niches, and phylogeographic barriers. The dung beetle species most vulnerable to isolation and local extinction are those with naturally low population levels, restricted niches, high biomass, and are forest specialists, which may require forest tracts greater than 200 ha to maintain the evolutionary variability of their communities (Larsen et al., 2008; Rivera et al., 2022). The main threat affecting these species is the destruction of their natural habitats due to anthropogenic activities. Many forest-dependent species, such as those native to the Atlantic Forest of Brazil, are at high risk due to accelerated deforestation resulting from expanding agricultural and livestock activities (Rezende et al., 2018). Species depending on highly specialized habitats, such as the burrows of small mammals (e.g., rats, gophers), caves, snail droppings, or species that have monetary value because of their size or beauty should be considered candidates for conservation and/or protection using legal coverage. For some Red List species, their scarcity may not signal danger, as they have not been assessed adequately (low collection effort, insufficient biological study), which is very likely to occur for some dung beetle species.

In the other hand, using a meta-analytical approach with dung beetles, Rivera et al. (2023) evaluated how anthropogenic habitat disturbances influence taxonomic, functional, and phylogenetic diversity to conserved forest sites in the Neotropics, and they found that heavy disturbances erode and homogenized all diversity dimensions of dung beetles with close dependence on forest habitats species. Moreover, they promote the protection of disturbed off-reserve forests (e.g., second-growth forests and agroforestry systems) in management schemes, since favoring the coexistence between functional and phylogenetically distant species and maintaining assemblages similar to those in conserved forests.

Therefore, safeguarding ecosystem functions and services that insects perform in the Neotropics required to add efforts in new public policies in protected areas including Indigenous and Community Ecological Reserves as well as species-specific action policies to prevent further declines and ensure their continuity in the ecosystems. In addition, it is required to potentiate the study of insect distribution modeling to identify areas of priority conservation habitat (Duffus et al., 2023), considering an integral vision of the study of biodiversity (i.e., taxonomic, and functional diversity) in the tropics (Moreno et al., 2018); since global warming is a growing threat, and its synergies are potentially far-reaching with other causes of anthropogenic origin (Laurance et al., 2011).

4.7.8. Methodological bias

Most of the studies included in this analysis more commonly comprise the Scarabaeinae subfamily, with few investigations incorporating the subfamily Aphodiinae. If this subfamily is included, their taxonomic identification is often deficient. This shows a lack of taxonomic tools (i.e., keys and academic proficiency) to identify this group, but at the same time, a lack of ecological, physiological, and behavioral information on this group, which is extremely relevant and essential in grassland areas. This should be a priority for future studies in this region.

We recommend following a framework trait-based, since it is recognized the multi-functionality of traits of the dung beetle, considering characteristics of their morphology, feeding, reproduction, physiology, activity, and movement which involve traits with response to the environment and affect ecosystem processes in different spatial, temporal, and biological scales (for more details deCastro-Arrazola et al., 2023). Also, is therefore required to address the trophic complexity of ecosystems, since traits also influence interactions within trophic levels. For example, via competitive interactions between dung beetle species with similar ecological niches (Schleuning et al., 2023).

5. Conclusion

Forest cover is the best predictor of dung beetle assemblages, being positively related to species diversity and biomass across multiple spatial scales (Alvarado et al., 2018). Landscape homogenization resulting from increases in the extension of open grasslands reduces species diversity and composition. The most disturbed ecosystems are related to significant reductions in functional redundancy, which can have detrimental effects on the future resilience of a landscape (Cajaiba et al., 2020). In the case of open pastures, the answer depends on the regional context because the substitution of native forest for open pastures strongly affects functional diversity (Guerra-Alonso et al., 2022).

Native forests and forests with cattle maintain functional diversity in all regions. Biodiverse grazing lands with tree species are an option for not reducing regional species richness in fragmented landscapes. There are clear signs that tree structure and microclimatic conditions provided by forests, as found in agroforestry, can help preserve biodiversity by creating productive habitats for native species (Righi et al., 2018). Silvopastoral systems can buffer the adverse effects of rapid expansion of open areas and the consequent reduction of tropical dry forest area generated by technified conventional systems (Arellano et al., 2013). Forest remnants, wooded systems, living fences, and silvopastoral systems favor new assemblages (species with different habitat requirements) within species-rich landscapes with greater connectivity (Reyes-Novelo et al., 2007; Arellano et al., 2008, 2013; de Farias et al., 2015).

Species with similar functional traits are commonly assigned to functional groups (Moore, 2001; Steneck, 2001; Tilman, 2001). However, the construction and categorization of functional groups requires an in-depth theoretical review and experimental studies that permit a better understanding of their separation at an operational level. As well, the variables used in functional approaches must be standardized.

Most Latin American countries lack studies on ecosystem functions in grazing systems. In our review, there are few papers that include and evaluate at least one function provided by dung beetles in grazing lands (mainly dung removal) compared to the number of articles working with taxonomic or functional diversity. The responses of dung beetle assemblages and their ecological functions to subtle changes within a type of land cover are uncoupled, idiosyncratic and depend on the context, making it difficult to make predictions and generalizations in grasslands (Carvalho et al., 2021). Considering the importance of the data to be included in future work, we propose a collection format to unify the information collected in the field when conducting ecological studies in grazing lands. We recorded a lack of information on livestock systems, type of management, use of anthelmintics, characteristics of pastures and soils, cattle species, grass species, and climatic conditions. The absence of this information in most of the papers is not only a severe methodological problem that constrains replicability, but also prevents large-scale comparisons or meta-analyses. This is one of the main reasons we propose a standard data collection format (Supplementary Box I) for work in these environments. Moreover, we define a classification system to homogenize the features that distinguish the multiple tropical grazing lands found in the literature. Preserving dung beetle diversity and associated ecological functions is urgent for maintaining ecosystem services in grazing lands.

Author contributions

LA, JN, and IO-M contributed to the conception and approach of the text and coordinated the progress of each of the main sections of the document. JN, JR, CC, AG-C, FB, and AR-H were responsible for the design of the final figures and methods. All authors participated with content of the manuscript, review of papers,

synthesis of ideas, results, Supplementary material, and general redaction and writing of the document.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

Supplementary material

The Supplementary material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2023.1084009/full#supplementary-material

SUPPLEMENTARY FIGURE S1
Juliana Kuchenbecker (picture B and E), J. León and A. Armida (picture D), Pedro H. Ribeiro (picture G) and S. López (picture J).

SUPPLEMENTARY TABLE S1
Sources for analysis of taxonomic diversity, functional diversity, and dung beetle ecological functions in grazing lands.

SUPPLEMENTARY TABLE S2
Taxonomic, Functional and Ecological Functions and ecosystem services synthesis of Neotropical dung beetles from pasture habitats.
At the end of the Table, please insert: In most of the revised publications, the authors considered more than one category of this table, therefore, the percentage described in results vary and include more of 26 studies in count of functional synthesis

SUPPLEMENTARY TABLE S3
Information about grazing lands in the reviewed articles.
At the end of the Table, please insert: In most of the reviewed publications the authors considered more than one type of grazing land for sampling sites. Then, in the row type of grazing land, we included the percentage of sites by each type of grazing land and in parentheses the number of sites for each main category (grassland, woodland, agroforestry and others) included in all articles according to the type of analysis. In the row Particular grazing lands are mentioned grazing lands in particular. See levels of grazing lands in Methods. SPS= silvopastoral systems. TDF= Tropical Deciduous Forest.

SUPPLEMENTARY TABLE S4
Species of grasses mentioned as a part of grazing lands in the reviewed articles according to the topic analyzed.

SUPPLEMENTARY TABLE S5
(A) Percentage of studies with information on livestock management.
(B) Percentage of studies with information on management practices.

SUPPLEMENTARY BOX I
Data collection format for ecological pasture studies.

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The relationships between dung beetles and monkeys in the Neotropical region

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The relationship between dung beetles and arboreal mammals has been scarcely studied, and many of the reports refer to observations without a standardized methodology. The accelerated loss of tropical forests urges us to understand this mutualistic association. Using our studies on arboreal dung beetles in the Palenque Archaeological Zone-National Park, Mexico, as a baseline, we analyzed the information on arboreal dung beetles in Neotropical forests in Mexico and around the world. *Canthon euryscelis* Bates, 1867, *Canthon angustatus* Harold, 1867, *Canthon subhyalinus* Harold, 1867, and *Canthon femoralis* (Chevrolat, 1834) are the main species collected in trees of Palenque, *Onthophagus maya* Zunino, 1981 and other non-Scarabaeinae species were occasionally collected from trees in Palenque. The small *Canthon* species are skilled fliers strongly relationship with monkeys in Palenque and other tropical regions of Mexico and Central America. In South America, arboreal dung beetles are more diverse and include these and other dung beetle species associated with monkeys. Several dung beetle species of the genus *Onthophagus* have been reported in association with African monkeys. In India, several studies report a wide variety of dung beetle species associated with monkeys. In Australia and New Guinea, only some species of Macropocopris are described as being associated with arboreal marsupials, but in Borneo, several dung beetle species have been observed associated with arboreal marsupials, mostly in managed forests. In Madagascar, *Arachnoides gandi* is the only beetle species reported in trees. We need to formulate a systematic and comparative methodology to understand better how arboreal beetles search for food, where the food is located, and how brood balls are made, how male-female pairs meet and nest, and how they contribute to arboreal dung recycling.

KEYWORDS

Scarabaeinae, arboreal, trees, tropical forests, dung

Introduction

The dung beetles of the subfamily Scarabaeinae are essentially a terrestrial group, considered part of the soil fauna (Hanski and Cambefort, 1991). However, aspects of the ecology and behavior of Scarabaeinae species that spend much time of their life in canopy of trees in different tropical forests have been described worldwide (Davis et al., 1997; Rivera-Cervantes and Halffter, 1999; Larsen et al., 2006; Vulinec et al., 2007; Noriega, 2015). Studies addressing this line of research have been discontinuous, and much of the current information has been reported as anecdotic or incidental observations, sometimes recorded during studies on mammal behavior (Tirado-Herrera et al., 2002; Jacobs et al., 2008). Recirculating the dung of monkeys living on trees by "aerial" dung beetles is not a marginal but an essential aspect for tropical forests to survive (Halffter and Halffter, 2009). Systematic studies focused on the eco-ethology of this group of canopy beetles are scarce. Compiling and categorizing the data available in the literature and elsewhere will allow us to assess the current state of knowledge, the topics investigated, the aspects that remain unknown, and the methodological approaches used to study Scarabaeinae species inhabiting the canopy in tropical forests.

In tropical rainforests, many vertebrates live in the upper forest canopy and some dung beetle species have been observed foraging or perching in the upper canopy and different vegetation layers of forests (Davis et al., 1997). The number of species and the species that forage or perch on plants or tree branches of tropical forests differ between the Neotropical region and other regions of the world (Cambefort and Walter, 1991; Gill, 1991). However, the association between dung beetles and the vertebrate fauna that lives in the forest canopy has not been studied to the same extent as the one between ground dung beetles and vertebrates that live in this stratum.

We aimed to evaluate the current knowledge of the relationship between monkeys and dung beetles and propose a systematic methodology for studying these relationships in the Neotropical region and other tropical forests of the world. In addition to the Scarabaeinae, other coleopterans and insects are associated with monkey dung.

Our research questions were the following:

1. What has been investigated about the Scarabaeinae species inhabiting the arboreal layer of tropical forests, and what questions do they suggest? Why do the prevailing species in the forest canopy belong to the genus *Canthon* in America but to the genus *Onthophagus* in Africa? What are the methodological approaches for studying beetles living in the canopy, and how can they be improved to obtain comparable results?
2. What are the foraging and perching behaviors of arboreal dung beetles? Is there evidence of Scarabaeinae species being closely associated with certain species of arboreal mammals? How does the resource relocation behavior take place in the canopy? How do beetles of different sexes meet? How do they make the ball? How do they roll it?
3. What is the vertical distribution of Scarabaeinae species in tropical forests of southern Mexico and other tropical regions? Do the observed patterns match the vertical temperature and humidity gradients or the behavior of monkeys and other arboreal mammals?

Materials and methods

Field work

Palenque, Chiapas (Mexico)

The Palenque Archaeological Zone-National Park stretches across 1771 hectares. It is located in the northern limit of the Lacandona forest in Chiapas. Palenque was one of the great Mayan cities during the classic period (250-900 BC). It reached peak development between 600 BC and 800 BC. After different conflicts and invasions, this and other Mayan towns declined and were almost completely abandoned (Mathews, 2007). Nearly 600 hectares of high evergreen forest still remain, altered but maintaining its ecological structure thanks to the local authorities in charge of preserving the archaeological zone. The monkeys thriving in the area that are a food source for dung beetles are the black howler or howler monkey, *Alouatta pigra* Lawrence, 1933, which is relatively abundant, and the spider monkey, *Ateles geoffroyi* (Kuhl, 1820).

We collected dung beetles for 24 h on 21 June 1993. Traps were set at 5 m, 10 m, 15 m, and 20 m high onto six large trees separated by almost two hundred meters between them in the forest, far from the archaeological zone. Each trap consisted of a 9 cm × 9 cm × 8 cm plastic box with a triangular opening in the lid, filled with a 2 cm-thick layer of soil and baited with 4 g of human feces or carrion (fish) (for further details, refer to Halffter and Favila, 1993). The baits remained active for 24 hours. The results reflect the total number of beetles collected in 25 traps, six baited with fish carrion and 19 with human feces (Table 1).

Literature search strategy

We constructed a database conducting a systematized search of peer-reviewed papers on the Web of Science (WoS) to collect the studies about the species of dung beetles associated with monkeys in the Neotropical region and other regions of the world. The search was conducted during the first semester of 2023, including articles published from 1980 to 2023. We search the next terms in the title, abstract, and keywords for each paper: "arboreal dung beetle*" AND "arboreal carrion beetles" AND "monkeys and dung beetles" OR "vertical stratification dung beetles" OR "perching dung beetles" OR "dung beetles and trees". In addition, we used other search strategies to broaden the scope of the review, such as directly contacting some authors.

TABLE 1 Dung beetle species caught in 18 copro traps (3 per tree)/and 6 necro traps (one per tree) affixed to 6 trees separated by at least 100 m between them in the tropical forest of the Archaeological zone in Palenque, Chiapas, Mexico.

Species/Height	5 m	10 m	15 m	20 m
Canthon euryscelis	210/23	47	151/50	10
Canthon angustatus	161	6	110/20	30
Canthon subhyalinus	161/9	129/2	90/3	7
Canthon femoralis	84	6/2	6/2	2
Onthophagus maya	1	—	—	—

Inclusion criteria and screening protocol

The WoS search retrieved 277 articles, of which we included only those meeting the following criteria: the study should analyze arboreal, perching, and/or flying behaviors of dung beetles associated with monkeys, food location, or search of mates in tropical forests. After reviewing the titles and abstracts of the full WoS search results, we selected 12 articles for a full review, which were those related to the monkeys and arboreal dung beetles, perching behavior, and dung beetles in trees. As the systematic search did not capture articles or chapters that were published before 1980 or the journal or book lacked a digital repository, we used other search strategies to broaden the scope of the review such as directly contacting some authors and including articles from the personal library of the authors.

Data extraction

We extracted the following data from the selected literature: a) the taxonomic identity of each dung beetles species studied (current names of species were used in case of synonyms or new combinations; b) study location, including locality and country; the environment and known food resources of each species c) flying behavior observed in different dung beetle species, including duration, location of the food or mate; d) average duration of flying behavior observed in different dung beetle species; f) nest characteristics in the trees (structure, complexity, and location relative to the base of the tree); g) male/female nesting behavior h) male/female searching behavior, perching heights.

Results

The studies conducted to analyze the vertical distribution patterns of the species of the subfamily Scarabaeinae in Neotropical and other tropical forests have used arboreal pitfall traps with different baits (human feces, fruits, and carrion) and positioned at different heights; only a single article mentions having conducted direct observations (Howden and Young, 1981). There is a comprehensive review by Noriega and Vulinec (2021) about dung beetle perching and their vertical stratification in the understory, which does not include canopy beetles.

Tropical America

The most frequent species collected on trees was *Canthon euryscelis* Bates, 1867 (418 individuals), followed by *Canthon subhyalinus* Harold, 1867 (387 individuals), *Canthon angustatus* Harold, 1867 (307 individuals), and *Canthon femoralis* (Chevrolat, 1834) (102 individuals) (Table 1). All these *Canthon* species are small and skilled fliers, suggesting a strong relationship with monkeys, but maybe also with other mammals and reptiles living on trees. *Canthon euryscelis* and *Canthon angustatus* were mostly collected at 5 m high (50.23% and 52.4%, respectively, of individuals collected in aerial traps) and 15 m high (36.12% and 35.8% respectively); however, *C. euryscelis* was collected more frequently at 10 m than at 20 m (11.2% and 2.4%, respectively), and the opposite occurred for *C. angustatus* (1.9% and 9.7%, respectively). More *Canthon subhyallinus* individuals were collected a 5 m (41.6%), then at 10 m (33.3%) and 15 m (23.3%) high, but were rarely caught at 20 m high (1.8%). Only a single individual of *Onthophagus maya* Zunino, 1981, was collected at 5 m high (Table 1).

Mexico

This section outlines the information gathered about arboreal dung beetles inhabiting the tropical forests of México. This information shows that the association of a certain beetle species with monkey dung is common in a given location but varies significantly between sites. The relationship between beetles and monkey dung is strong and determines the abundance of some species in the canopy, being substantially reduced at ground level. In the tropical forests of southern Mexico, four species of Scarabaeinae (*Canthon* spp.) show this relationship with the monkeys *Alouatta palliata* (Gray, 1849), *A. pigra* Lawrence, 1933, and probably with *Ateles geoffroyi* Gray, 1866.

Canthon angustatus Harold, 1867

In Mexico *Canthon angustatus* is the most abundant species associated with monkeys in Mexico and shows the strongest and most constant relationship. It is distributed from the ground level up to 30 m high (with up to 50 specimens caught per trap, Halffter personal observations). In the state of Chiapas, *C. angustatus* has been collected in the Montes Azules Biosphere Reserve (Howden and Young, 1981; Solís and Kohlmann, 2002; Chamé-Vázquez and

Gómez-Gómez, 2005; Navarrete and Halffter, 2008) and Palenque (this work). In Veracruz, *C. angustatus* has been collected in Las Choapas (Sánchez-Huerta et al., 2019). This species is also found in Campeche, Quintana Roo, and Tabasco (Sánchez-Huerta et al., 2019). Besides, it has been described from Nicaragua and cited from Belize, Costa Rica, El Salvador, Honduras, Nicaragua, Guatemala, Panama, Colombia, Ecuador, and Peru (Sánchez-Huerta et al., 2019), always strongly associated with dung of *Alouatta palliata* and *Allouatta pigra*. Howden and Young (1981) pointed out that *C. angustulus* inhabiting Barro Colorado Island is a diurnal species with two peaks of activity, one from 06:00 to 10:00 hours and the other from 15:00 to 18:00 hours, coinciding with the periods of monkey defecation. Food balls are made on the foliage of trees. *Canthon angustatus* and *Canthon subhyalinus* have been observed at more than 20 m high in the forest canopy (Howden and Young, 1981). These beetles first separate a fragment of dung that then falls to the ground with the beetles clinging to it, resembling a rain of dung balls and beetles (personal observations). Once on the ground, the beetle reshapes the ball and rolls it like other roller beetles. In Panama, *C. angustatus* is only associated with howler monkeys in lowland moist forests. It probably does not compete with *C. subhyalinus*, which prefers high-canopy areas with a flat terrain where *C. angustatus* is uncommon (Howden and Young, 1981). However, this observation remains to be confirmed in future research on Neotropical arboreal dung beetles.

Canthon (Glaphyrocanthon) subhyalinus Harold, 1867

Canthon subhyalinus is the second arboreal dung beetle species associated with monkeys in Mexico and Central America. Like the other *Canthon* species, it is small and an excellent flyer. Halffter and collaborators conducted an intense collection of dung beetles in the Palenque forest in 1965 using pitfall traps placed on the ground. Only a single individual of *C. subhyalinus* was caught in these traps, among other species; in contrast, in traps set at 15 m high, they caught over 222 individuals (see Rivera-Cervantes and Halffter, 1999). These authors reported that in 1993 (this study) in the same zone, no *C. subhyalinus* specimens were caught in any of 22 traps placed at ground level; by contrast, many specimens were captured in three traps affixed at 5 m, 10 m, 15 m, and 20 m high (Table 1). These observations suggest that *C. subhyalinus* spends more time in the forest canopy, closely related to *Alouatta* monkeys. The abundant catches of *C. subhyalinus* in trees of other tropical forests of Chiapas (Boca de Chajul) and Los Tuxtlas, Veracruz, confirm the above (Estrada et al., 1993; Navarrete and Halffter, 2008).

The dispersal center of *C. subhyalinus* appears to be the intermontane valleys of Colombia (Rivera-Cervantes and Halffter, 1999; Figure 1A). It is located on the Pacific slope of Ecuador and expands southward to Peru and Bolivia. Along the Caribbean coast, it reaches Venezuela and French Guiana. To the north, *C. subhyalinus* has been found in Panama, Costa Rica, and in some tropical forest areas of southern Mexico (Lacandona forest, Chiapas, and Quintana Roo). The known northernmost distribution limit is Los Tuxtlas, Veracruz (Rivera-Cervantes and Halffter, 1999).

Canthon (Glaphyrocanthon) euryscelis Bates, 1887

Canthon euryscelis is also commonly associated with monkeys. This species thrives in evergreen forests and is highly abundant in sites inhabited by *Alouatta* monkeys, although, unlike the species described above, it can be captured in partially cleared patches (Rivera-Cervantes and Halffter, 1999). The behavior of *C. euryscelis* is similar to that of *C.* (*Gl.*) *subhyalinus.* In 1993, an average of 2.2 specimens per trap were caught in traps placed on the ground (Rivera-Cervantes and Halffter, 1999), but was quite abundant at 5 m and 15 m high (Table 1). *Canthon euryscelis* has been caught in tropical forests of southeastern Mexico (Campeche, Chiapas, Quintana Roo, Oaxaca, Tabasco, and Veracruz). In Central America, it has been observed in Belize, Guatemala, Honduras, Costa Rica, and Panama (Rivera-Cervantes and Halffter, 1999, Figure 1B).

Canthon (Glaphyrocanthon) femoralis (Chevrolat, 1834)

Canthon femoralis is also a species commonly associated with monkeys in tropical forests of southeastern Mexico. It is widespread in tropical Mexico, Central America and northwestern South America (Figure 1C). *Canthon femoralis* has a strong predilection for monkey dung in tropical rainforests. However, this species can be considered the least obligatory height specialist of the four dung-beetle *Canthon* species since it is also found in cow dung on the ground in partially cleared forest patches (Rivera-Cervantes and Halffter, 1999; Amézquita and Favila, 2010). At the Tropical Biological Station in Los Tuxtlas, Mexico, *C. femoralis* has been abundantly collected on the ground (Favila and Díaz, 1997), although more than 25 individuals per trap have been caught in traps affixed at 20 m and 27 m high (Estrada et al., 1993). In other tropical forests, this species has been observed flying between 5 m and 15 m or higher (height not specified by the authors) and perching on leaves between 0.3 m and 1.5 m high (Morón, 1979; Rivera-Cervantes and Halffter, 1999). In Palenque, Chiapas, *C. femoralis* was observed by the first author in 1965 rolling small fragments of monkey dung on leaves.

In Palenque, Chiapas, traps placed at ground level caught 1 to 9 specimens of *C. femoralis* per trap. This species has also been captured at ground level and 6 m high in Jalcomulco, Veracruz, in a disturbed tropical deciduous forest at an altitude of 400 m asl (Rivera-Cervantes and Halffter, 1999). The presence, and especially the abundance, of *C. femoralis* is highly variable geographically. It may be the most abundant dung roller beetle associated with monkeys in a given location, while being rare in other similar places. This species probably also uses the dung of other arboreal mammals, like the coati (*Nasua narica*, Estrada et al., 1993). *Canthon femoralis* has been caught at elevations ranging from sea level to 1600 m asl (Rivera-Cervantes and Halffter, 1999).

Canthon femoralis makes unique brood balls (Figure 2), which are left abandoned on the ground after being finalized. For its

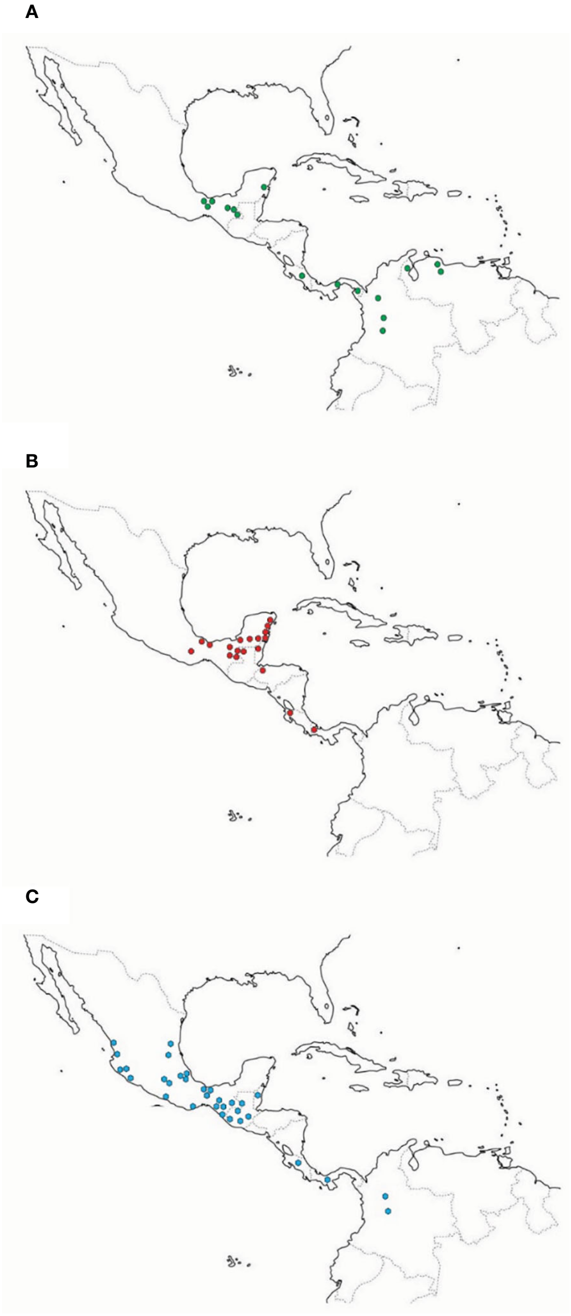

FIGURE 1
(A) Distribution of *Canthon subhyalinus*; **(B)** Distribution of *Canthon euryscelis*, **(C)** Distribution of *Canthon femoralis*.

elaboration, the ball is first separated from the upper center or upper surface of a dung mass; the male, the female, or a bisexual pair initiates this operation. Afterward, the male pushes the food ball forward, with the female traveling on top of it. As a result, the ball is gradually coated with a layer of soil (4 mm thick). It has an opening and a "neck" that ends in a well-defined aeration channel (Figure 2). The egg chamber is located at the base of the channel. Nest balls are abandoned on the ground or in a slightly excavated crater (Rivera-Cervantes and Halffter, 1999).

Central America

The relationship between dung beetles and monkeys observed in Mexico also occurs in Central America. In Panama, Howden and Young (1981) reported *Canthon angustatus* Harold and *Canthon subyhalinus* Harold caught in traps at more than 20 m high within forested areas. *Canthon subyhalinus*, was found on the leaves among fresh monkey dung masses. The *Canthon* species fall to the ground clinging to the ball, where the usual rolling process

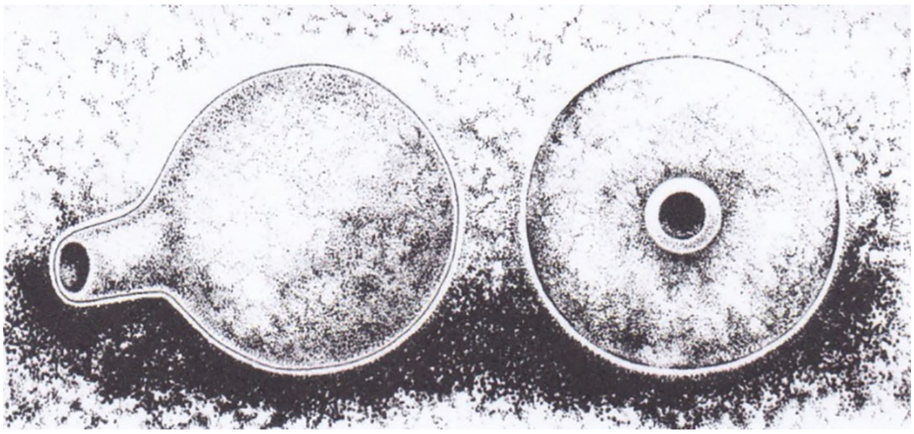

FIGURE 2
Brood balls of *Canthon femoralis*.

continues. For its part, Gill (1991) observed *Canthon aequinoctiale* Harold, 1869, at 8 m high eating monkey dung deposited on the leaves but has not been seen building food balls. This author reports highly abundant *Canthon* (*Glaphyrocanthon*) sp. associated with *Callicebus* monkey dung at 10 m high, along with some individuals of *Sylvicanthon foveivenre* (Schmit, 1920) plus a few specimens of other two Scarabaeinae species. Gill (1991) reported *Canthon angustatus* in a tropical forest of Panama making balls of monkey dung in the forest canopy.

South America

For reasons not yet explained, there is a remarkable change in the dung beetle-monkey relationship in forests of southwestern Mexico, Central America, and South America. In the tropical forests of Mexico and Central America, there is a clear relationship of *Canthon* species with monkeys, mostly of the genus *Alouatta*, with differences in abundances between sites. The perching behavior is common in these *Canthon* species. According to Gill (1991), the two foraging behaviors observed in dung beetles in the Neotropical region are perching and flying, and differences in both behaviors may influence the dispersal ability of the species. Fast fliers are also widely distributed across South America and Central America. Comparing the geographic range of perching versus flying species during foraging will help to determine whether these two foraging behavior strategies are related.

Noriega (2011) collected *Canthon smaragdulus* (Fabricius, 1781) in Colombia using a new model of elevated pitfall traps baited with *Alouatta seniculus* dung. Later, in a study carried out in the same locality, Noriega (2012) compared the assemblages of dung beetles that reached the feces of *A. seniculus* and *Lagothrix lagotricha* (Humboldt, 1812), finding 32 species and marked differences in the species composition of beetles attracted by each dung type. Subsequently, Noriega et al. (2020) collected 369 specimens of 21 dung beetle species perching on plants. These included three species of *Onthophagus*, seven *Canthidium*, two *Dichotomius*, two *Eurysternus*, two Phanaeini (*Oxyternon conscipillatum* (Weber, 1801) and *Phanaeus chalcomelas* (Perty, 1830) and five Deltochilini, including *Sylvicanthon aequinoctialis* (Harold, 1869). Undoubtedly, this assemblage of beetles associated with monkeys is markedly different from the ones collected in Mexico and Central America. Finally, Noriega and Vulinec (2021) summarized the information on dung beetles perching on leaves worldwide.

In the tropical forests of Peru, the relationship of dung beetles with tamarin monkeys (*Seguinus myxtrax* Spix and *Seguinus fuscicollis* Spix) was studied by Culot et al. (2011). They followed a tamarin group and collected their feces immediately after defecation. Traps baited with this dung were buried in the ground for 24 hours. These authors collected 330 beetles of 25 species of Scarabaeinae. The medium-sized-to-large species included two Canthidium, two Dichotomius, and numerous species of rollers (Deltochilini). Also in Peru, Larsen et al. (2006) captured *Canthon brunneus*, *C. femoralis bimaculatus*, *C.* sp., and *C. subyhalinus* in the canopy of a primary terra firma or a floodplain forest. In the French Guiana, Feer (2000; 2015) noted that a severe reduction of the arboreal mammal fauna may also reduce the Scarabaeinae fauna (refer to Nichols et al., 2009).

Vulinec (2002) examined beetles associated with monkeys in Peru, the Amazonas, and Rondonia (Brazil). She estimated that primates eat between 25% and 40% of the biomass produced by the forest, being they an essential element in the food chain. When a part of the forest is cleared, the populations of Scarabaeinae beetles also decrease. *Alouatta palliata* is a diurnal monkey frequently observed on fig trees (Gill, 1991). Its feces attract multiple species, including hundreds of individuals of *C. angustatus*, which form a dense cloud that covers the area where monkeys thrive. The stinking, greenish-yellow dung is defecated in the forest canopy, falling onto the vegetation as a cascade. This excrement is transported by beetles as firm balls that are rolled in the canopy until they fall to the ground with the beetles clinging to them. Once on the ground, beetles form male-female pairs that keep rolling the food ball.

Halffter and Matthews (1966) published the first review on the ecology and behavior of the Scarabaeinae, including several of the first publications addressing the relationship between dung beetles and monkeys (or, where appropriate, other mammals). Thus, according these authors Luederwaldt (1922) reported individuals of *Canthon* (*Glaphyroncanthon*) *quadrigutatus* (Olivier) in Tapajos, Brazil, on both monkey feces and a recently hunted monkey, with about ten specimens around the anus. The monkey was reported as corresponding to *Alouatta* sp by Pereira and Martínez (1956). According to these authors, *C. subhyalinus* was collected from another monkey, *Callicebus brunnens* Wager, in Guapó, Brazil.

Vaz de Mello and Louzada (1997) reported the capture in Viçosa, Minas Gerais, Brazil, of 22 specimens of *Sylvicanthon foveiventris* (Schmidt) (a Canthonina beetle) in traps baited with human feces at 10 m high in the forest, in addition to *Canthon* (*Glaphyrocanthon*) sp., *Parahyboma furcatum* (Laporte, 1840), and *Canthidum* sp. The forest is home to a rich fauna of Scarabaeinae, including the beetles that thrive on the ground. Although illustrative, the publications reviewed for South America are punctual and in quantity and quality. Some of the beetle species associated with monkeys in Mexico are also found in South America, but other arboreal beetle species in this region are larger than *Canthon* species (Vaz de Mello and Louzada, 1997).

Africa

Published works on African dung beetles are scarce. Walter (1983) studied the beetle-monkey relationship in Gabon, specifically in the Mpassa forest. This was the first study addressing the Scarabaeinae in the canopy of African forests. Traps were placed at 3 m, 5 m, 10 m, and 21 m high in dense, humid, evergreen forests. The traps were wooden squares (50 cm × 50 cm) affixed horizontally at the heights indicated. The lid had a central orifice, which attracted the specimens into the baited trap. Walter collected five species at different heights (Table 2). Similar to our sampling in Mexico, he observed few abundant species. The three most common species were collected mainly at 5 m and 10 m high. All the beetle species caught are small. *Sisyphus* does not exceed 5 mm in length and *Onthophagus* is 3.5 *mm* in length; the exception was *O. mpassa*, which is 7.2 mm in length. *Onthophagus ahenominas* (4 specimens) and *O. mppasa* were the rarest species. The other three beetle species were abundant. Arboreal *Sisyphus* species make the ball in the canopy, and before leaving it, the ball remains attached to a leaf or a branch, not falling to the ground. *Onthophagus* species cannot bury their eggs in trees. Thus, eggs are scattered among the dung in the canopy. The association of these beetle species with monkeys and the canopy has made them lose the nesting habit throughout evolution, returning to a highly primitive form, similar to the most primitive Scarabaeinae. Walter (1981) described that *Sisyphus arboreus* makes balls and rolls them in the canopy of forest trees. In addition, four species of *Onthophagus* use dung excreted *in situ*. These fascinating data from Walter are the first to report an *Onthophagus* species as a roller of an elaborate ball.

The comments by Hanski and Cambefort (1991) on the Scarabaeinae-monkey relationship in Africa do not fully coincide with those by Walter (1985). The information reported by Hanski and Cambefort (1991) was recorded from the Makukon forests and referred to three species collected between 10 m and 20 m high. A *Sisyphus* individual was observed rolling a dung ball in the canopy. They also reported that *Onthophagus*, unable to dig in the canopy, accumulates dung and litter to form a mass that protects the eggs.

The relationship between beetles and monkeys in Africa mentioned above is consistent with our observations in Mexico: very few important beetle species are highly abundant at different heights in forest trees. These findings contrast markedly with the reports for South America and the cases mentioned below, where multiple species are associated with monkey dung.

Madagascar

In the Madagascar forest, the small roller beetle *Arachnodes gandi* was observed making nests at ground level and 50 cm high (Vadon, 1947). According to Vadon (1947), *A. gandi* makes a dung ball in the canopy, which falls to the ground, and the beetle continues rolling it as described for other rollers.

India

This region hosts multiple species of dung beetles, some of which are very large, associated with monkeys of many different taxa. By contrast, in Mexico and Central America this role is played by the Canthonini, which are also abundant in other areas of the Neotropics.

In the Western Ghats, a global biodiversity hotspot in southwestern India, Sabu and Nithya (2016) collected *Caccobius*

TABLE 2 Dung beetle species caught by Walter (1983) in the Mpassa forest.

Height	Ground	3 m	5 m	10 m	21 m
Total sampling duration (hours)	120	36	60	48	60
Onthophagus laeviceps	1/0	4/0	12/0	8/37	0/1
Onthophagus possoi	—	—	1/0	7/1	21/13
Onthophagus ahenomicans	—	1/0	—	2/1	—
Onthophagus mpassa	—	—	0/1	—	—
Sisyphus arboreus	—	—	3/1	30/6	10/3

The first and second figures refer to diurnal and nocturnal catches, respectively (from Walter, 1983).

gallinus Arrow, *Caccobius meridionalis* Boucomont, *Onthophagus vladimiri* Frey, *Onthophagus furcillifer* Bates, and *Onthophagus centricornis* (Fabricius) in pitfall traps set at approximate 15 m height attached to a rope. These authors consider that the lower abundance of arboreal primates in this region explains the low abundance of arboreal dung beetles. However, the abundance and diversity of arboreal dung beetles are higher in dry forests because the rainy season is very short and, as a consequence, dung is available in the canopy for longer periods than in the wet forest (Sabu and Nithya, 2016). These authors also proposed that arboreal dung beetles are a more recent group than beetles that forage and reproduce on the ground. Phylogenetic studies are necessary to test this hypothesis.

Borneo

We have relatively abundant information from the tropical forests of Borneo, which are home to populations of 10 primate species, including colobins, orangutans, gibbons, and two macaque species. Davis et al. (1997) reported having collected 2378 beetles in traps at 5 m and 10 m high. A curious phenomenon has been observed in Borneo, contrasting with observations in other tropical forests: arboreal beetles have not been mostly collected in the primary (undisturbed) forest. Instead, they are collected in high abundances in managed forests or plantations (refer to Davis and Sutton, 1998). According to these authors, the percentage of beetle species caught is distributed as follows: 1.72% in primary forests, 22.32% in managed forests, and 75.96% in forest plantations. According to Davis and Sutton (1998), arboreal beetles are absent on the ground but abundant at 5 m and up to 20 meters high, with some individuals being spotted at 25 m high. This unusual importance of managed forests and plantations was again mentioned by Davis et al. (2000) for Sabah-Borneo. The beetles considered “forest specialists” are primarily found in plantations. In fact, 14 of the 40 species of dung beetles found in plantations are endemic to Borneo.

The importance of the edge of tropical forests in Borneo is the opposite of their role in other tropical forests. Borneo is relatively well studied, and the beetles that dominate in its forests and plantations are taxonomically different from those in other areas. In Borneo, Deltochilini species are not rollers; instead, dung beetle assemblages are dominated by groups that are typically diggers. Davis et al. (2000) highlighted this remarkable shift in behavior.

Davis (1993) pointed out that the use of dung excreted by monkeys (or other arboreal mammals) and carrion by the Scarabaeinae is possible when these food types are available in the canopy in sufficient amounts and with continued supply. This, along with the existence of tall trees, favors the presence of arboreal dung beetles. Given the competitive nature between species that is common in tropical forests, the existence of arboreal beetles highlights the competition for one of their main resources: monkey feces. Borneo is characterized by the diversity of the resources exploited by beetles (Abdul Rahman et al., 2021). The genus *Onthophagus*, which comprises most beetle species (632) in Sabah Malasyan, Borneo, includes six fruit-eating species, among them one that consumes fruits while these still are hanging from tree branches (the other fruit-eating beetles consume fruits that have fallen to the ground) (Davis and Sutton, 1997). Perching, which occurs in many species, is a food-searching strategy and a thermoregulation mechanism (Davis, 1993). *Onthophagus* displays the same type of association described by Walter in Africa. When Andrew J. David worked on the subject from 1990 to 1993, he shared with one of us (Halffter) original information (notes and drawings) on the Scarabaeinae inhabiting trees in Borneo from a collecting campaign in Sabah (Borneo, Malay) in 1990. He found three arboreal *Onthophagus* species associated with primates. *Onthophagus nanus* was described as the most abundant arboreal beetle species, and it was observed rolling — a truly exceptional behavior for a burrower like *Onthophagus*. A pair of beetles roll a “ball” (a piece of dung) in the way typically reported for many rollers, such as *Canthon* species: the male pushes the “ball” forward with his hind legs while the female remains on top of it, serving as a counterweight and favoring the rolling of the food ball.

Two articles Tregidgo et al. (2010), from Malaysia, and Rahman et al. (2021), from Singapore), confirm several of the findings just mentioned: the importance of *Onthophagus* and *Caccobius* as arboreal beetles (especially in secondary forests). Both species show the morphological adaptations mentioned above: very long metatarsals, spurs on the metatarsals, and tarsi of the hind legs adapted to hold the foliage better. Among *Onthophagus*, *O. deliencis* is particularly abundant, making and rolling dung balls in the forest canopy.

Australia, New Guinea

Several species of *Macropocopris* Arrow (an Onthophagini genus from Australia) have modified tarsal nails that allow them to attach to hair, especially in the anal region (cited by Halffter and Matthews, 1966: 43-44; Hanski and Cambefort, 1991). When a feces pellet is defecated, the beetle falls with it to the ground, where it is used to build the nest.

Discussion

At the beginning of our systematic information gathering on the Scarabaeinae-monkey relationships in tropical forests around the world, we expected significant differences between regions. The plant composition of these forests differs according to the region, and the arboreal Scarabaeinae fauna is also different (Davis et al., 1997). However, we did not expect to find functional differences as important as those observed. In this chapter, we have examined the most important differences and the questions that arise from them.

In the tropical forest of southern Mexico, arboreal Scarabaeinae species are scarce: four almost permanent and abundant species and one that is rarely observed. The frequent species are small

Canthonina, which are excellent rollers. These species can make nest balls in the canopy, then drop the ball while clinging to it, continue rolling it on the ground, and ultimately bury the ball in the usual way described by Halffter and Matthews (1966). The structure and composition of arboreal dung beetle assemblages are similar in Central America, although there may be some additional distinctive species.

In South America, there are far more species of monkeys and beetles. Their number, but also their taxonomic diversity, is much greater. The species are much more taxonomically varied, although the type of association remains relatively unchanged. Interesting, some arboreal species in South America are large species, not yet found in tropical forest of México and Central America.

Information about this relationship obtained in Africa is scarce, but the data available suggest that it differs markedly from the relationship observed in South America. In Africa, the Scarabaeinae associated with monkeys are mostly from genus *Sisyphus* and *Onthophagus.* An exceptional feature is that these beetles nest in the canopy. In the case of *Sisyphus*, the ball made in the tree canopy remains attached to a branch. For its part, the case of *Onthophagus* is extraordinary. This abundant genus of burrowing species that make a nest on the ground displays a unique behavior in its relationship with the African monkeys: it builds its nests in the canopy using the dung that accumulates between the leaves.

In India, the Scarabaeinae-monkey association comprises numerous species of beetles from different taxonomic groups, including several large species. Further studies in this region will broaden our understanding of arboreal dung beetle habits.

In Borneo, the relationship is radically different. There are multiple arboreal species, but they are mainly found in forest edges and plantations not in undisturbed forests. The opposite of Mexico and Central America, where very few arboreal dung beetle species thrive under these conditions.

An essential aspect detected from comparing all the works focusing on arboreal beetles and their association with primates is the lack of a standardized sampling methodology. There are many types of traps, and no single model is used consistently in different study areas. Different types of traps may yield different results and attract or capture other species (see Bacc et al., 2023).

In 1993 we propose a methodology for the studies of dung beetles as an insect focal group for analyzing the effects of human activity on the biodiversity (Halffter and Favila, 1993). Here we suggest using a standardized methodology to compare the arboreal diversity found at different heights or layers of the tropical forest. We suggest selecting a fixed number of trees, 20 or much better 30, each one separated approach 100 m longtwo, a distance that has been considered adequate to ensure independence between samples. However, we have to investigate which is the minimal distance between traps to this goal. In each tree, we suggest putting two traps hung at 5, 10, 15, 20 and 25 meters high if it is possible. We suggest using the arboreal dung traps proposed by Noriega (2011). The same number of traps must be placed in each selected tree. To avoid bait interference between types of baits, we suggest using a type of bait in each tree (dung, carrion, or fruits). The review of the traps must be made every hour or two hours. If that it is not possible, one in the morning, the other at noon, and the last in the afternoon. We can rebait at the afternoon the traps to collect nocturnal arboreal dung beetles and pick up the traps in the morning (6:00 AM). In an extreme case, we can hang the traps in the trees in the morning until the afternoon (6:00 PM), rebait the traps, and leave them the night picking up them in the morning. We can repeat our sampling protocol for five days. In all cases, the traps must be protected with a cover (a plastic plate) to prevent the traps from flooding, if rains.

We suggest conducting comparative studies on arboreal dung beetles in different regions using the same methodology according to the research objectives. This review opens new areas of research into the role and dynamics of arboreal dung betel in the tropical region.

Data availability statement

The original contributions presented in the study are included in the article/Supplementary Material. Further inquiries can be directed to the corresponding author.

Author contributions

All authors listed have made a substantial, direct, and intellectual contribution to the work and approved it for publication.

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In memoriam

During the period of the elaboration of the Research Topic “Neotropical Dung Beetle Diversity: Ecological, Historical, and Anthropogenic Perspectives,” I received the draft of this contribution written by Dr. Halffter, but unfortunately, he passed away. I took the Halffter draft and, with the approval of his family, I finished this paper.

Hereby I wish to express my deepest gratitude to Prof. Gonzalo Halffter, who was my dear teacher, a great friend, and a colleague.

Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

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The Taxonomic Revolution of New World dung beetles (Coleoptera: Scarabaeidae: Scarabaeinae)

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After almost two decades of stagnation, the taxonomy of the New World Scarabaeinae dung beetles has since 1988 been going through a period of great effervescence. In the last 35 years, 81 complete revisions and 69 supplements have been produced by 86 authors based in 15 countries, addressing the taxonomic status of 950 species. This is what we christen as the Taxonomic Revolution of New World dung beetles. We review the history and products of this revolution, explore its causes and its apparent exceptionalism among most other New World Coleoptera groups, and point to the many great challenges that still face the scarabaeine taxonomists. An aspect of interest to ecologists is the coevolution of the Taxonomic Revolution with what we call the Ecological Revolution of dung beetles, i.e., the similar expansion in ecological studies about these organisms. We argue that it has been the continuous feedback between these two simultaneous processes that has enabled each of them to exist and flourish: without the Ecological Revolution, the Taxonomic Revolution could not have existed, and vice-versa. Ecologists and taxonomists are partners in the scientific enterprise, symbionts one may say.

KEYWORDS

systematics, Neotropical, Nearctic, scarabs, catalogue, taxonomic revision, taxonomic monograph, phylogenetics

An ongoing revolution

Anyone familiar with the taxonomic literature on the New World Scarabaeinae must have realized that we live in a rather special period. Since 1988, no less than 81 complete revisions have been published, and these were later updated by 69 supplements. Combined, these works address the systematics of 950 species in the Western Hemisphere (Tables 1, 2; Figure 1). This is not to say that, previously, the taxonomic knowledge of the fauna had been static. Rather the contrary, ever since Linnaeus (1758), the number of new taxa

TABLE 1 List of the taxonomic revisions, monographs, and their supplements published during the Taxonomic Revolution of New World dung beetles.

Tribe	Genus	Subgenus or species group	Last major revisions or monographs and supplements	Number of species currently recognised
Ateuchini			Montreuil, 1998; Vaz-de-Mello, 2008	Macrotaxonomic only (tribal, subtribal and generic levels)
	Agamopus Bates, 1887		Costa-Silva et al., 2022	5
	Aphengium Harold, 1868		Silva and Vaz-de-Mello, 2015	4
	Ateuchus Weber, 1801	*Lobidion* Génier, 2010	Génier, 2010; Génier and Cupello, 2018; Montoya-Molina et al., 2021	2
	Deltorhinum Harold, 1867		Génier, 2010; Montoya-Molina and Vaz-de-Mello, 2019a	7
	Feeridium Vaz-de-Mello, 2008		Vaz-de-Mello, 2008	1
	Genieridium Vaz-de-Mello, 2008		Vaz-de-Mello, 2008	7
	Nunoidium Vaz-de-Mello, 2008		Vaz-de-Mello, 2008	1
	Pedaridium Harold, 1868		Ferreira and Galileo, 1993; Vaz-de-Mello, 2008	22 (in Ferreira and Galileo, 1993), 1 described plus 1 undescribed (in Vaz-de-Mello, 2008)
	Pereiraidium Vaz-de-Mello, 2008		Vaz-de-Mello, 2008	1
	Scatimus Erichson, 1847		Génier and Kohlmann, 2003; see also Martínez-Revelo et al., 2020a	13
	Scatrichus Génier and Kohlmann, 2003		Génier and Kohlmann, 2003	3
	Silvinha Vaz-de-Mello, 2008		Vaz-de-Mello, 2008	1
Coprini			Montreuil, 1998; Tarasov and Dimitrov, 2016	Macrotaxonomic only (tribal level)
	Copris Geoffroy, 1862	*Copris s. str.*: incertus group: incertus and laeviceps complexes	Darling and Génier, 2018	9
Deltochilini			Tarasov and Dimitrov, 2016	Macrotaxonomic only (tribal level)
	Anomiopus Westwood, 1842		Canhedo, 2004a, b, 2006; see also Vaz-de-Mello et al., 2011; Edmonds and Figueroa, 2013; Figueroa and Edmonds, 2015; Cano, 2018a, b; Valois et al., 2020	63
	Atlantemolanum González-Alvarado et al., 2019		González-Alvarado et al., 2019	2
	Boreocanthon Halffter, 1958		Edmonds, 2022	13

(Continued)

TABLE 1 Continued

Tribe	Genus	Subgenus or species group	Last major revisions or monographs and supplements	Number of species currently recognised
	Canthon Hoffmannsegg, 1817	*Bajacanthon* Halffter, 2022	Halffter et al., 2022a	1
		Canthon s. str.: humectus group	Halffter et al., 2015	4
		Goniocanthon Pereira & Martínez, 1956	Nunes et al., 2018	3
		Peltecanthon Pereira, 1953	Nunes et al., 2020	4
		Pseudepilissus Martínez, 1954	Vieira et al., 2019	14
	Deltochilum Eschscholtz, 1822	*Deltochilum* s. str.	Génier, 2012	7
		Aganhyboma Kolbe, 1893	Silva et al., 2015, 2018	27
		Deltohyboma Lane, 1946	González-Alvarado and Vaz-de-Mello, 2021a	Macrotaxonomic only (species-group level)
		Deltohyboma Lane, 1946: gilli group	González-Alvarado and Vaz-de-Mello, 2021b	5
		Euhyboma Kolbe, 1893	Nazaré-Silva and Silva, 2021a	1
		Hybomidium Shipp, 1897	González-Alvarado and Vaz-de-Mello, 2014	13
		Parahyboma Paulian, 1938	Nazaré-Silva and Silva, 2021a	2
		Rubrohyboma Paulian, 1939	Nazaré-Silva and Silva, 2021a	1
	Deltepilissus Pereira, 1949		Silva et al., 2022	2
	Hansreia Halffter and Martínez, 1977		Valois et al., 2015, 2017b	6
	Holocanthon Martínez and Pereira, 1956		Sawaris et al., 2019	2
	Scatonomus Erichson, 1835		Valois et al., 2020	11
	Scybalocanthon Martínez, 1948		Silva and Valois, 2019; see also Silva and Génier, 2019	24
	Scybalophagus Martínez, 1953		Ocampo and Molano, 2011	5
	Sylvicanthon Halffter and Martínez, 1977		Cupello and Vaz-de-Mello, 2018	15
	Tetraechma Blanchard, 1841		Nunes and Vaz-de-Mello, 2022	5

(Continued)

TABLE 1 Continued

Tribe	Genus	Subgenus or species group	Last major revisions or monographs and supplements	Number of species currently recognised
Dichotomiini			Montreuil, 1998; Tarasov and Dimitrov, 2016	Macrotaxonomic only (tribal level)
	Chalcocopris Burmeister, 1846		Rossini and Vaz-de-Mello, 2015; see also Cupello et al., 2016, 2023b	2
	Holocephalus Hope, 1838		Smith and Génier, 2001; see also Nunes and Vaz-de-Mello, 2016b	6
	Dichotomius Hope, 1838	*Cephagonus* Luederwaldt, 1929	Nunes and Vaz-de-Mello, 2019	40
		Dichotomius s. str.: buqueti group	Arias-Buriticá and Vaz-de-Mello, 2019	3
		Dichotomius s. str.: mamillatus group	Rossini and Vaz-de-Mello, 2020	4
		Dichotomius s. str.: reclinatus group	Arias-Buriticá and Vaz-de-Mello, 2023	4
		Homocanthonides Luederwaldt, 1929	Maldaner et al., 2018a	1
		Selenocopris Burmeister, 1846: agenor group	Montoya-Molina and Vaz-de-Mello, 2021; see also Solís and Kohlmann, 2022	17
		Selenocopris: assifer group	Nunes et al., 2016	5
		Selenocopris: batesi group	Valois et al., 2023	5
		Selenocopris: globulus group	Valois et al., 2022	10
		Selenocopris: nisus group	Cassenote et al., 2020	1
		Selenocopris: sericeus group	Valois et al., 2017a; see also Silva et al., 2020	9
		Selenocopris: speciosus group	Maldaner et al., 2015; see also Maldaner and Vaz-de-Mello, 2022	5
		Selenocopris: superbus group	Cassenote et al., 2020	1
	Isocopris Pereira and Martínez, 1960		Rossini and Vaz-de-Mello, 2017	7
Eucraniini			Philips et al., 2002; Ocampo and Hawks, 2006	Macrotaxonomic only (tribal level)
	Anomiopsoides Blackwelder, 1944		Ocampo, 2005, 2007	4
	Ennearabdus Van Lansberge, 1874		Ocampo, 2010a	1
	Eucranium Brullé, 1838		Ocampo, 2010b	6
	Glyphoderus Westwood, 1838		Ocampo, 2004	3

(Continued)

TABLE 1 Continued

Tribe	Genus	Subgenus or species group	Last major revisions or monographs and supplements	Number of species currently recognised
Eurysternini	*Eurysternus* Dalman, 1824		Génier, 2009	53
Oniticellini			Philips, 2016	Macrotaxonomic only (tribal and subtribal levels)
	Attavicinus Philips and Bell, 2008		Philips and Bell, 2008	1
Onthophagini	*Digitonthophagus* Balthasar, 1959		Génier and Krell, 2017; Génier and Moretto, 2017	16 (one introduced species in the New World)
	Hamonthophagus Roggero et al., 2016		Roggero et al., 2016	5 (two introduced species in the New World)
	Onthophagus Latreille, 1802		Zunino and Halffter, 1988a, 1997	Macrotaxonomic (species-group level)
		Onthophagus s. str.: chevrolati group	Zunino and Halffter, 1988a, 1988b; Delgado and Capistan, 1996; Delgado, 1999; Delgado and Howden, 2000; Zunino and Halffter, 2005; Arriaga-Jiménez et al., 2016; Moctezuma et al., 2016; Gasca-Álvarez et al., 2018; Sánchez-Huerta et al., 2018; Halffter et al., 2019; Joaqui et al., 2019; Moctezuma and Halffter, 2019a, 2020b, 2020c; Moctezuma et al., 2021b	58
		Onthophagus s. str.: dicranius group: dicranius complex	Howden and Gill, 1993; Génier and Howden, 1999; Kohlmann and Solís, 2001; Solís and Kohlmann, 2003; Génier, 2017; Delgado and Mora-Aguilar, 2019; Moctezuma and Halffter, 2019b	12 plus one undescribed
		Onthophagus s. str.: dicranius group: mirabilis complex	Howden and Gill, 1993; Génier and Howden, 1999; Génier and Medina, 2004; Génier, 2017; Moctezuma et al., 2023b	9
		Onthophaguss. str.: mexicanus group	Moctezuma and Halffter, 2021b; Moctezuma et al., 2023a	20
		Onthophagus s. str.: lecontei-subopacus complex	Howden and Génier, 2004	5
		Onthophagus s. str.: hircus group	Rossini et al., 2018a	Macrotaxonomic only (species-group level)
		Onthophagus s. str.: hircus group: osculatii complex	Rossini et al., 2018b	8
Phanaeini			Arnaud, 2002b (phanaeines sensu Edmonds, 1972 only – i.e., modern Phanaeina less *Bolbites* – except for *Dendropaemon*)	117
	Bolbites Harold, 1868		Cupello et al., 2021a	1
	Coprophanaeus d'Olsoufieff, 1924		Edmonds and Zídek, 2010; see also Kohlmann and Solís, 2012; Cupello and Vaz-de-Mello, 2013a, 2014b; Maldaner et al., 2017; Arnaud, 2018; Maldaner et al., 2018b, 2019	44 (plus six *species inquirenda*)
	Dendropaemon Perty, 1830		Génier and Arnaud, 2016; see also Cupello and Génier, 2017	41

(Continued)

TABLE 1 Continued

Tribe	Genus	Subgenus or species group	Last major revisions or monographs and supplements	Number of species currently recognised
	Diabroctis Gistel, 1857		Valois et al., 2018	5
	Gromphas Brullé, 1838		Cupello and Vaz-de-Mello, 2013b, 2014a, 2015	6
	Megatharsis Waterhouse, 1891		Gillett et al., 2009	1
	Oxysternon Castelnau, 1840		Edmonds and Zídek, 2004; see also Arnaud, 2004; Hielkema, 2017	11
	Phanaeus MacLeay, 1819		Edmonds, 1994; Edmonds and Zídek, 2012; Zunino, 2013; Arnaud, 2018; Moctezuma and Halffter, 2021a; Moctezuma et al., 2021c; Halffter et al., 2022b; Solís and Kohlmann, 2023	83
	Sulcophanaeus d'Olsoufieff, 1924		Edmonds, 2000; Arnaud, 2002a	15
Incertae sedis	*Bdelyrus* Harold, 1869		Cook, 1998, 2000	27
	Canthidium Erichson, 1847	*Neocanthidium* Martínez et al., 1964: gigas group	Carvalho-de-Santana et al., 2019	6
	Cryptocanthon Balthasar, 1942		Cook, 2002; see also Arias-Buriticá and Medina, 2014; Mora-Aguilar and Delgado, 2018; Martínez-Revelo et al., 2020b; Giraldo-Mendoza, 2022	43
	Isacanthon Pacheco and Vaz-de-Mello, 2019		Pacheco and Vaz-de-Mello, 2019a	1
	Ontherus Erichson, 1847		Génier, 1996, 1998; see also González-Alvarado and Medina, 2015	60
	Paracanthon Balthasar, 1938		Pacheco and Vaz-de-Mello, 2019b	15
	Paracryptocanthon Howden and Cook, 2002		Pacheco and Vaz-de-Mello, 2017	2
	Streblopus Van Lansberge, 1874		Cupello et al., 2020	2
	Tesserodoniella Vaz-de-Mello and Halffter, 2006		Vaz-de-Mello and Halffter, 2006	2
	Zonocopris Arrow, 1932		Vaz-de-Mello, 2007a	2

Most revisions are complete revisions, i.e., they reassess the taxonomic status of all taxa included in the group revised, both micro-and macrotaxonomic ones, and propose a classification (even if an unaltered one). A few works, however, are devoted exclusively to macrotaxonomic revisions at the tribal, subtribal, or species-group levels. Faunistic revisions, species descriptions published not in the context of a revision, and purely phylogenetic works without taxonomic decisions (either new or confirmatory ones) are not listed.

described from the New World has been growing steadily (Figure 2). Before the current period – which we name the Taxonomic Revolution of New World dung beetles – there had been two other moments when the fauna was systematically revised: the first, during the late 1860s, was led by Edgar von Harold, who, among other works, monographed four of the most diverse genera on the continent, *Ateuchus*, *Canthidium*, *Dichotomius*, and *Canthon* (Table 3; Figure 3). In this short three-year period between 1867 and 1869, 205 new species-group taxa (i.e., taxa now considered valid species and subspecies) were described, an impressive 70% increase in the known diversity of the subfamily (Figure 2). Thereafter, a 69-year period of revisionary stasis would follow, punctuated in the middle almost solely by d'Olsoufieff's (1924) magnificent phanaeine revision.

Then, in 1938, a second period of revisionary activity started with the publication of the first part of Paulian's (1938) "canthonine" monograph. This second period would eventually be much longer than the Haroldian one. Over the next 33 years, 12 authors writing from 10 countries would produce 29 complete revisions and address the systematics of 266 species (Tables 3, 4; Figure 3). In addition, 12

TABLE 2 Glossary with our definitions of terms used in the text and whose meaning may be confusing, unknown, or disputed among systematists.

Term	Definition
Systematics	The discipline of evolutionary biology concerned with building a general reference inventory of the diversity of life (a system of life). Modern systematics comprises two major subfields: phylogenetics (cf.) and taxonomy (cf.). The end product of systematics is a monographic revision (cf.). Microsystematics is the combination of microphylogenetics and microtaxonomy, whereas macrosystematics is the combination of macrophylogenetics and macrotaxonomy.
Phylogenetics	The subdiscipline of systematics dealing with the reconstruction of the phylogeny, i.e., the pattern of genealogical change and diversification between living beings, from clades, to populations, to organisms, to genes. Phylogeny is the combination of the processes of reproduction, gene flow, hybridization, introgression, lateral gene transfer, population expansion and contraction, cladogenesis, lineage fusion, convergent, divergent, and parallel anagenesis, stasigenesis, and extinction. Microphylogenetics deals with the delimitation of (meta)population lineages and the relationships existing within them, whereas macrophylogenetics deals with the relationships between such lineages, including their organization into clades.
Taxonomy	The subfield of systematics dealing with the classification of organisms, i.e., the delimitation and categorization of taxa, as well as with the naming and identification of these taxa. In modern taxonomy, taxa are delimited based on the phylogenetic relationships of organisms, which are investigated by the other subfield of systematics, phylogenetics (cf.). In a few words, phylogenetics investigates the genealogical diversification of genes, populations, and clades and so constructs a phylogenetic tree; taxonomy, based on a set of principles (metataxonomy), divides this tree into taxonomic units, taxa, which are then named and usually ranked in the Linnean Hierarchy, giving rise to a classification. Finally, diagnoses, descriptions, dichotomous keys, genetic profiles, and other such tools are provided to allow the identification of organisms belonging to each taxon.
Microtaxonomy	The taxonomy of taxa at the level of species and subspecies (coined by Mayr, 1982).
Macrotaxonomy	The taxonomy of taxa at the supraspecific levels (coined by Mayr, 1969).
Taxonomic revision	A study that reevaluates the taxonomic status of a particular taxon or of taxa subordinated to a more comprehensive taxon. This reevaluation may encompass a taxon and all of its subordinated taxa across all ranks and geographical regions (a complete revision), or just the taxon and/or its subordinated taxa in a particular geographical region (a faunistic revision), or only subordinated taxa at a particular taxonomic rank or group of ranks (e.g., tribal-level-only revision, or species-level-only revision). A taxonomic revision implies, as far as existing material allows, an attempt to give equal treatment to all taxa revised and presents a fully comparative analysis between them. Works including comparable descriptions or diagnoses for all the taxa revised, for example, qualify as revisions. The result of a taxonomic revision is a revised classification.
Complete taxonomic revision	A revision that reevaluates the taxonomic status of a taxon and all of its subordinated taxa in all regions of the globe. For example, the revision of a genus that reevaluates the status of this genus and all the species included in it, or the revision of a species that reevaluates the status of this species and all of its known populations and/or subspecies. The result of a complete revision is a fully revised classification.
Faunistic taxonomic revision	A revision that reevaluates the taxonomic status of a taxon and its subordinated taxa in a particular geographical area, not in its full geographical range. For example, the revision of the species of a genus in a given country, state, biogeographic region, or ecosystem to which the genus is not endemic.
Taxonomic review	A study without a particular geographical focus that reevaluates the taxonomic status of some, but not all, the subordinated taxa at a particular taxonomic rank of a more comprehensive taxon, and whose presentation does not allow a fully comparative analysis between these subordinated taxa. For example, the description of a new species accompanied by an identification key to the congeneric species is a review, not a revision, because an identification key does not allow a full comparison between taxa, nor does it imply reevaluation of their taxonomic statuses.
Taxonomic synopsis	A summary of the taxonomic knowledge of a taxon without reevaluating itself the status of the taxonomy addressed (modified from Mayr, 1969).
Taxonomic monograph	A fully revised encyclopedic classification of organisms. It is a work that combines the characteristics of a taxonomic revision with the attempt to compile in a synthetic way the entire knowledge about the concerned taxa. For example, a work that, besides reevaluating the taxonomic status of taxa, also presents sections on their ecology, biogeography, evolution, complete taxonomic history, list of references, and whatever other aspect worthy of mention qualifies as a taxonomic monograph.
Taxonomic character	Characters that present different states between different taxa. Whether a character is a taxonomic character depends on the level of universality of the analysis. For instance, if one is addressing beetles, whether the forewings are modified into elytra or not is not a taxonomic character, for the forewings of all beetles are modified into elytra. But if one is talking about insects as a whole, whether the forewings are modified into elytra or not becomes a taxonomic character, for there are insects with elytra (beetles) and others without them (the other insects). Definition modified from Mayr (1969).

reviews also appeared in this period, as well as some faunistic revisions (e.g., Howden and Cartwright, 1963; Matthews, 1966; Vulcano and Pereira, 1966). This second period of taxonomic revisions eventually ended in the 1970s, microtaxonomically with Howden's (1971) revision of *Bdelyropsis* and macrotaxonomically with the final part of Halffter and Martínez's (1966, 1967, 1968, 1977) "Canthonina" monograph. In comparison with the Haroldian period, this mid-20th-century phase was much less prolific in the description of new species-group taxa: over 33 years, a "mere" 268 new such taxa were discovered, raising by 28% the number for the year preceding the start of the period, 1937. A special trend of this period, however, and one which reaches maximum expression today, was the geographical transition of the taxonomic center of investigation from its cradle in Europe in the late 1930s (with authors like Balthasar, Paulian, and Blut) to the New World countries in the mid-1940s onwards (especially Howden, Matthews, Halffter, Martínez, Pereira, and Vulcano) (Figures 4–6). Likewise, the role of Maria Aparecida Vulcano (or d'Andretta, her married name used to sign her debuting scarabaeinae papers in 1955) and Violeta Halffter (Gonzalo Halffter's wife) as the first women to participate in the description of new species-group taxa is yet another relevant social change initiated in this period (Figure 7).

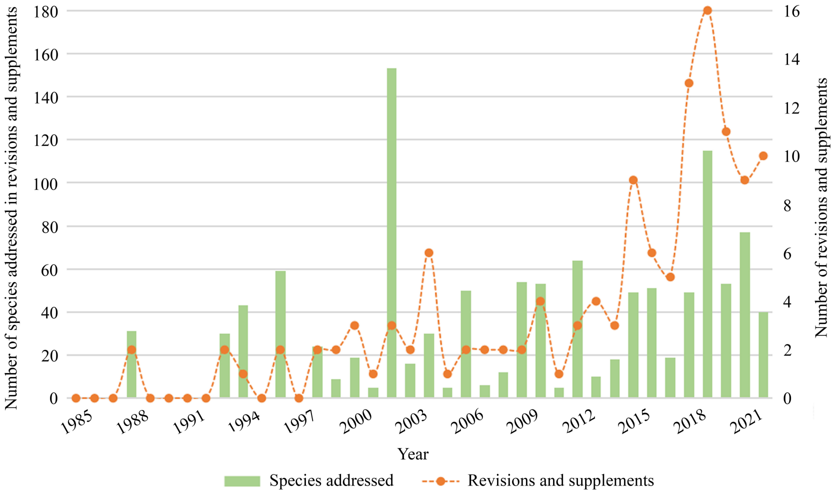

FIGURE 1
Taxonomic progress during the New World Scarabaeinae Revolution. Note that the number of revisions and monographs published each year has been growing since the start of the Revolution in 1988 (see also Table 1). The last year that saw no published work was 26 years ago, in 1997.

The late 1980s would then mark the beginning of a new era. Starting with Zunino and Halffter's 1988 revision of the *Onthophagus chevrolati* species group, the last 35 years have witnessed both a quantitative and a qualitative transformation in the systematics of the New World Scarabaeinae, one without parallel in the history of the discipline. The frequency of new revisions being published has exploded and continues to grow (Figures 1, 2, 8). As said, 150 complete revisions and supplements have appeared and 950 species, revised. The authors of these works are no longer a few researchers based in separate countries as in the mid-20th-century period. There are now instead active research groups widespread in the Americas based in countries like Canada, the US, Costa Rica, Mexico, Colombia, and Brazil, at least the latter three vibrantly composed of both established researchers and numerous students (Table 5). The Brazilian case illustrates the scale of change: in the entire pre-1990s history of the country's entomology, there had been merely eight people who published on the taxonomy of scarabaeines (Vaz-de-Mello, 2000; see Table 6). In contrast, during the 35 years of the Scarabaeinae Taxonomic Revolution, no less than 34 people living in the country have authored at least one taxonomic paper on the group, an almost fourfold increase. In Colombia, there had been none, but the Taxonomic Revolution has seen the work from 21 researchers based in the country so far. The same phenomenon is observed throughout the continent (Table 5). In all, 147 people have contributed with at least one work in the last 35 years, 63 of whom have authored at least one revision.

Qualitatively, the revisions composing this new age are characterized by seven features. First, most of them follow a phylogenetic rather than a faunistic approach. That is, instead of revising the species from a certain area in the Americas (e.g., Halffter, 1961; Howden and Cartwright, 1963; Howden, 1966; Matthews, 1966; Howden and Young, 1981; Kohlmann, 1984), they seek to study the entire diversity of whole taxa, usually genera, but sometimes focused on particular subgenera or species groups. A second characteristic is that they are no longer limited to the holdings of a few collections most easily accessible in their home countries, but are now based on an exhaustive search for specimens in as many collections as possible, including the nomenclaturally pivotal type specimens in European museums. Thirdly, these new revisions are lavishly illustrated, showing the most important taxonomic characters through either drawings or high-resolution photographs. The compilation of published data, usually with a catalog for each species and a section on ecological knowledge, is the fourth characteristic of the new phase. Fifthly, a detailed list of material examined is given for each species. Not only does it provide readers with the information necessary to locate the specimens and re-evaluate the observations noted in the revisions, but they also present additional data such as the date of collection that may prove useful to workers researching other questions about the taxa. Sixthly, modern taxonomists have much richer material available for their studies. Large local and geographical series, with detailed collection data, caught usually by the taxonomists themselves or by ecologists doing large-scale fieldwork, provide much richer data on intra- and interspecific variation than the small, geographically scattered series used by earlier workers. Lastly, the seventh characteristic is the increasing attention paid to the male genitalia, not only to the tegmen, as often done before, but also to the endophallus.

Of course, each of these characteristics can be found in works published before 1988. The study of the male genitalia for taxonomic studies on New World dung beetles was already present in d'Olsoufieff's (1924) revision of the Phanaeini, whereas comprehensive museum studies, including of the type specimens, were certainly a preoccupation of as early authors as Harold. But, generally speaking, works published before the current revolution lacked one or more of the characteristics listed above. Perhaps the closest pre-1988 examples are Kohlmann's (1984) revision of the North American *Ateuchus*, Matthews' (1966) revision of the

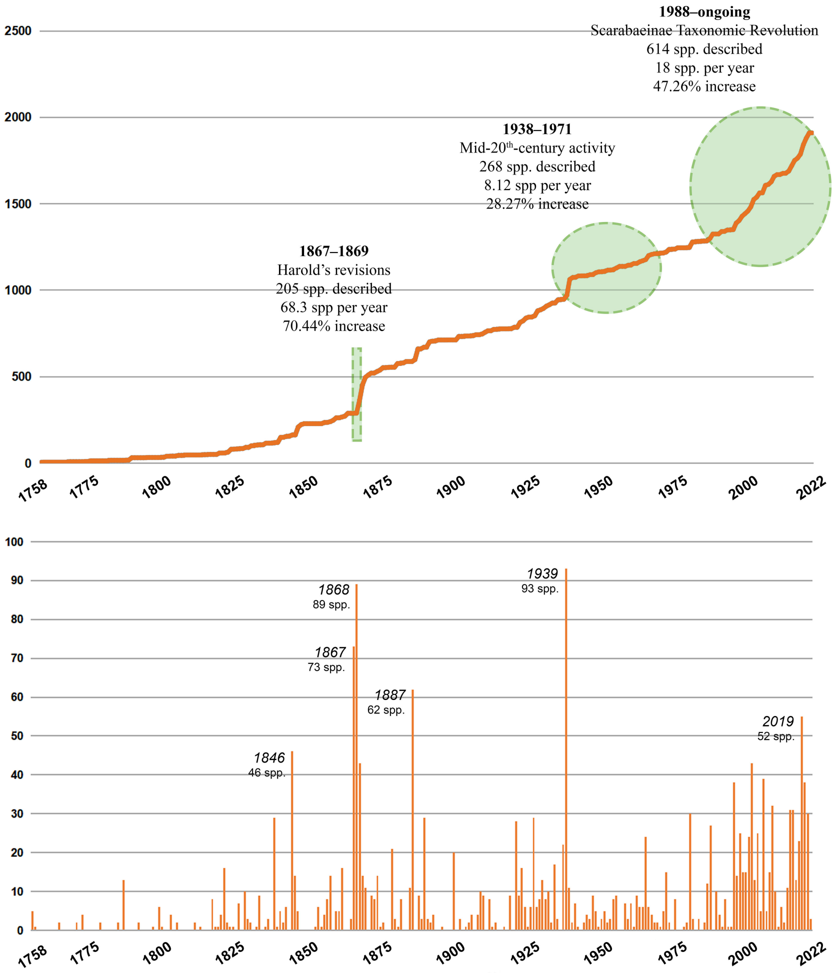

FIGURE 2
Progress in the discovery of new species-group taxa (i.e., species and subspecies) of New World Scarabaeinae since Linnaeus (1758). The upper graph shows the species-group taxa accumulation curve for the continent. Note that, although the number of known species and subspecies has never been truly static, the current Revolution is the longest period of consistent increase. The lower graph shows the number of species-group taxa discovered by year; the years highlighted are the six with the highest figures. Note that two of these years belong to the Haroldian period, one to the mid-20th-century period, and one to the current Revolution. In both graphs as well as in the rest of the paper, we consider the year of the discovery of a species-group taxon as the year of publication of its valid name, even if this name was originally used to denote a taxon whose circumscription matches only partially that of the currently denoted taxon (e.g., a name originally coined for a species taxon encompassing populations that are now considered heterospecific; therefore, the taxon which the name currently denotes – the one including solely the population of the name-bearing type(s) – does not correspond to the original taxon – the one including this and other populations). Data compiled from Schoolmeesters (2022).

TABLE 3 **Taxonomic revisions and reviews published for the New World Scarabaeinae in the period preceding the Revolution (1860–1987).**

Taxa revised	Revision	Number of species recognised
Eucraniini	Burmeister (1861)	12
Canthidium	Harold, (1867a, b)	61
Uroxys, *Trichillum*	Harold (1868a)	11
Ateuchus (as *Choeridium*)	Harold (1868b)	30
Canthon	Harold (1868c)	97
Dichotomius (as *Pinotus*)	Harold (1869)	39

(Continued)

TABLE 3 Continued

Taxa revised	Revision	Number of species recognised
Holocephalus (as *Atrichius* Gillet, 1907)	Gillet (1907); see also Gillet (1909)	3
Phanaeini	d'Olsoufieff (1924)	136
Eudinopus, *Deltochilum* [in part]	Paulian (1938)	40
Canthonidia, *Canthotrypes*, *Deltochilum* [in part], *Glauconia* (*Megathoposoma*), *Ipsepilissus* (= *Canthochilum*), *Megathopa*, *Paracanthon*, *Sinapisoma*, *Streblopus*	Paulian (1939)	24
Dendropaemon	Blut (1939)	28
Dichotomius: bitiensis section (as *Pinotus*)	Pereira (1942a)	4
Dichotomius: semianeus section (as *Pinotus*)	Pereira (1942b)	11
Anomiopsoides	Martínez, (1945a, b)	8
Zonocopris	Pereira (1946)	1
Dichotomius: batesi section (as *Pinotus*)	Pereira (1947)	7
Phanaeus (*Metallophanaeus*) (currently, a subgenus of *Coprophanaeus*)	Pereira (1949a)	3
Deltorhinum	Pereira (1949b)	1
Oniticellini	Janssens (1953)	7
Dichotomius: speciosus section	Pereira (1953)	3
Scatonomus	Pereira (1954)	7
Canthonella, *Xenocanthon*	Martínez (1954)	2
Deltochilum (*Calhyboma*)	Pereira and d'Andretta (1955b)	12
Anisocanthon, *Holocanthon*	Martínez and Pereira (1956)	4
Paracanthon	d'Andretta and Martínez (1957)	4
Canthomoechus (= *Canthon*), *Francmonrosia* (currently, a subgenus of *Canthon*), *Trichocanthon* (currently, a subgenus of *Canthon*)	Pereira and Martínez (1959)	4
Bdelyropsis, *Bdelyrus*	Pereira et al. (1960)	3
Vulcanocanthon (= *Canthon* (*Pseudepilissus*))	Pereira and Martínez (1960)	1
Gromphas	Barattini and Sáenz (1961)	4
Copris	Matthews (1961)	23
Sisyphus	Howden (1965)	2
Eudinopus, *Megathopa*, *Megathoposoma*, *Malagoniella*, *Streblopus*	Halffter and Martínez (1966)	16
Antillacanthon (= *Canthochilum*), *Canthochilum*, *Canthonella*, *Chapincanthon* (= *Canthochilum*), *Nesocanthon* (currently, a subgenus of *Canthon*)	Vulcano and Pereira (1966)	10
Oniticellus (species now in *Euonicitellus*), *Drepanocerus* (species now in *Anoplodrepanus*), *Canthochilum*, *Canthonella*	Matthews (1966)	19
Canthonella, *Ipselissus* (= *Canthochilum*), *Peltecanthon* (currently, a subgenus of *Canthon*)	Halffter and Martínez (1967)	10
Agamopus, *Canthon* (*Pseudepilissus*), *Canthotrypes*, *Ipselissus* (= *Canthochilum*), *Scybalophagus*, *Sinapisoma*	Halffter and Martínez (1968)	16
Bdelyropsis	Howden (1971)	2
"Phanaeines" (i.e., Phanaeini less Gromphadina and *Bolbites*)	Edmonds (1972)	Macrotaxonomic (genus and subgenus levels)

(Continued)

TABLE 3 Continued

Taxa revised	Revision	Number of species recognised
"Canthonina" (part of Deltochilini)	Halffter and Martínez (1977)	Macrotaxonomic (genus and subgenus levels)
Eurysternus	Jessop (1985)	20
Taxa reviewed	**Review**	**Number of species recognised**
Canthon	Schmidt (1922)	144
Ontherus	Luederwaldt (1931)	31
Uroxys	Arrow (1933)	29
Diabroctis (as *Taurocopris*)	Pessôa (1935)	4
Scatimus	Balthasar (1938)	8
Ateuchus (as *Choeridium*)	Balthasar (1939a)	69
Canthon	Balthasar (1939b)	162
Trichillum	Balthasar (1939c)	13
Scybalophagus	Martínez (1954)	5
Geocanthon [= *Canthon* (*Glaphyrocanthon*)], *Glaphyrocanthon* (currently, a subgenus of *Canthon*), *Goniocanthon* (currently, a subgenus of *Canthon*), *Ipselissus* (= *Canthochilum*), *Nesocanthon* (currently, a subgenus of *Canthon*), *Scybalocanthon*	Pereira and Martínez (1956)	49
Boreocanthon, *Melanocanthon*	Halffter (1958)	14
Isocopris, *Vulcanocanthon* [= *Canthon* (*Pseudepilissus*)]	Pereira and Martínez (1960)	3
Ipselissus (= *Canthochilum*)	Pereira and Martínez (1963)	4
Glaphyrocanthon (currently, a subgenus of *Canthon*)	Martínez et al. (1964)	27
Trichillum s. str.	Martínez (1967)	7

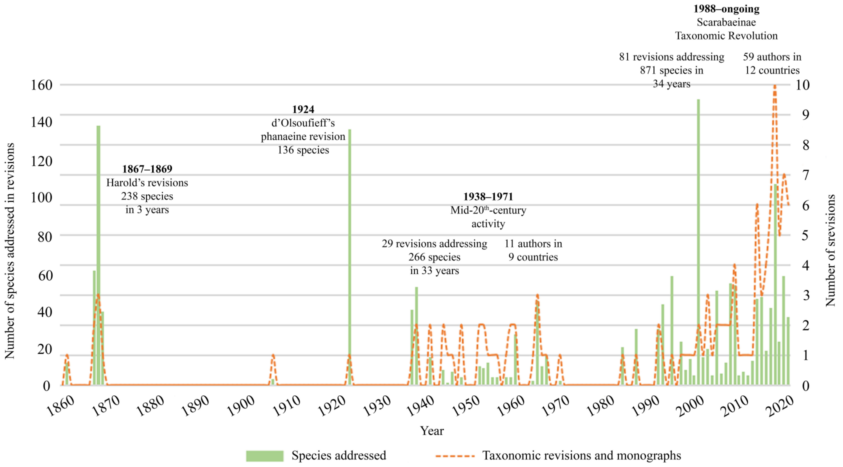

FIGURE 3
Revisionary activity over the history of the New World Scarabaeinae taxonomy. It is possible to see that there have been three well-delimited periods of revisionary effervescence: the first one, in the late 1860s, was the work of a single author, Edgar von Harold. The second, during the mid-20th century, was much longer and carried out by a larger number of people, but never reached the intensity and scale of the current period, the Taxonomic Revolution started in 1988.

TABLE 4 Authors who published taxonomic revisions and reviews of New World Scarabaeinae prior to the Taxonomic Revolution.

Country (current borders)	Authors
Slovakia	V. Balthasar (1938)
Czechia	V. Balthasar (1939)
Germany	**H. Blut** (1939), **H. Burmeister** (1861), **E. von Harold** (1867–1869), A. Schmidt (1922)
Belgium	**J.-J.E. Gillet** (1907), **A. Janssens** (1953)
France	**R. Paulian** (1938–1939), **G. d'Olsoufieff** (1924; or Madagascar? See Vinson, 1946: 89)
United Kingdom	**L. Jessop** (1985)
Canada	**H.F. Howden** (1965–1971)
United States	**W.D. Edmonds** (1972)
Mexico	**G. Halffter** (1958–1977)
Puerto Rico	**E.G. Matthews** (1961–1966)
Brazil	H. Luederwaldt (1931), **F.S. Pereira** (1942–1966), S.B. Pessôa (1935), **M.A. Vulcano** (D'Andretta) (1955–1966)
Argentina	**A. Martínez** (1945–1977)
Uruguay	**L.P. Barattini** (1961), **A. Sáenz** (1961)

In bold are the authors of at least one taxonomic revision, whether complete or only macrotaxonomic (see Table 3). Authors are classified by country of affiliation at the moment of publication (modern boundaries considered, though); this information is usually present on the first page of their works, but in a few cases (e.g., d'Olsoufieff) it is inferred from other sources. Years in parentheses following each author's name indicate their first and last work published in the period.

Antillean scarabaeines, and Halffter and Martínez's (1966, 1967, 1968, 1977) canthonine series. But while they can certainly be seen as legitimate precursors of the current phase – see, e.g., Kohlmann's pioneering usage of the endophallus for species delimitation – they still differ from the typical work of the Revolution for having a faunistic rather than a phylogenetic perspective, in the first two cases, and for the rather small series available for examination in the case of Halffter and Martínez.

A milestone in this Scarabaeinae Taxonomic Revolution has been the publication of Vaz-de-Mello et al.'s (2011) identification key to the New World genera. Until then, the information available for identifying these taxa was dispersed across the taxonomic literature, there existing no comprehensive and reliable tool allowing ecologists, conservationists, systematists, museum curators, and other specialists and amateurs to identify the specimens of their studies. Eighty-eight genera and 42 subgenera were included in the key, as well as a list of the most relevant publications for species-level identification. The relevance of Vaz-de-Mello et al.'s work cannot be overstated: as we write these lines, Google Scholar lists no less than 333 citations of the key in the scientific literature, whilst Research Gate counts 3,158 reads. However, as inevitably happens to any publication in an active field of scientific inquiry, the work is, at some points, already outdated. Four new genera have since been described (Génier, 2010; Roggero et al., 2016; González-Alvarado et al., 2019; Pacheco and Vaz-de-Mello 2019a) (one of them, *Lobidion* Génier, 2010, not included in the key, has since been lowered to a subgenus of *Ateuchus*; Génier and Cupello, 2018), a subgenus has been re-elevated to genus, *Boreocanthon* (Edmonds, 2022), a new subgenus has been described, *Canthon* (*Bajacanthon*) (Halffter et al., 2022a), the subgeneric classification of *Dendropaemon* has been completely modified, including the recognition of 12 subgenera in contrast to the previous three (Génier and Arnaud, 2016; Cupello and Génier, 2017), some names used as valid in the key have now been invalidated (*viz.*, *Eucanthidium* Martínez and Halffter, 1986, *Luederwaldtinia* Martínez, 1951, *Telhyboma* Kolbe, 1893, *Tetramereia* Klages, 1907, and *Vulcanocanthon* Pereira and Martínez, 1960) (Génier, 2012; Génier and Arnaud, 2016; Cupello, 2018; Nunes and Vaz-de-Mello, 2019; Vieira et al., 2019), some genera have been re-delimited and the key is no longer adequate to identify them completely (e.g., *Sylvicanthon* and *Tetraechma*) (Cupello and Vaz-de-Mello, 2018; Nunes and Vaz-de-Mello, 2022), and some names, due to nomenclatural problems discovered since 2011, have changed their allocation and denote different taxa in the key than they now do (e.g., *Selenocopris* and *Canthidium s. str.*) (Cupello, 2018; Nunes and Vaz-de-Mello, 2019). Moreover, some later works have found errors in the key that need correction (e.g., the supposed lack of a margin between the pygidium and the propygidium in all of the species of *Gromphas*, or an excavated hypomera in all the *Ateuchus*) (Cupello and Vaz-de-Mello, 2013b; Cupello, 2022). Despite all this, Vaz-de-Mello et al.'s key continues to be the main identification tool used by New World scarabaeine specialists and will likely remain so until a revised version is published.

Progress has also been made on other fronts. Catalogs have been published for almost every South American country since the 2000s, as well as for Panama, Costa Rica, Nicaragua, El Salvador, Mexico, Canada, and several of the Antilles (Table 7; Figures 9, 10). Like for the key, many of these catalogs are already outdated as new species are discovered every year and dozens of new country records (as well as refutations of previous records) appear in the taxonomic revisions. Rather than something to regret, the short time these catalogs are superseded is a sign of the vigor of the field. The only country that has had its catalog first published and then updated

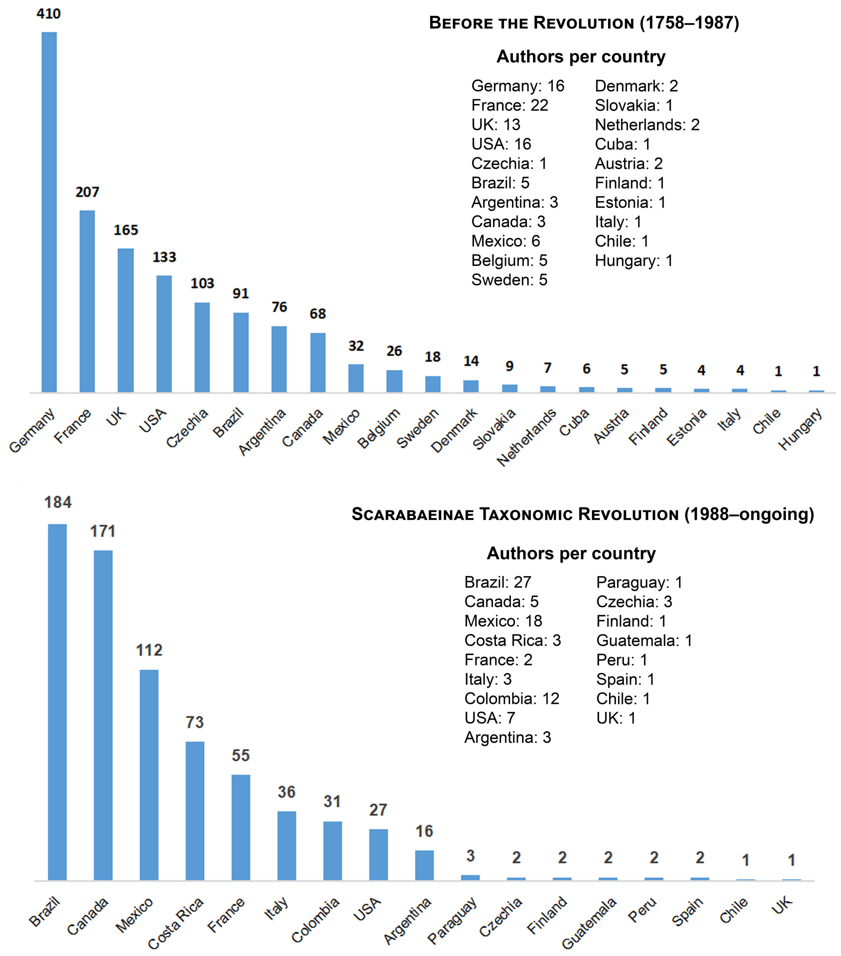

FIGURE 4
Number of new species-group taxa of New World Scarabaeinae described by authors based in each country before (above) and during (below) the Revolution. Countries are treated by their modern borders and names, even though they may not have been the same at the author's time. While new taxa were usually discovered by authors based in European countries during the first 229 years of the taxonomic history of the group, the last 35 years have seen a shift to authors based in the Americas. As noted in the text, the start of this trend actually dates back to the mid-20th-century period. Note that, if a taxon was described in a work whose authors are based in different countries, the species is counted again for each of these countries; therefore, the summed numbers will be greater than the total number of known species-group taxa from the continent. Data compiled from Schoolmeesters (2022).

during the Revolution, Brazil, epitomizes the period: whereas at the turn of the millennium 617 species were known from the country (Vaz-de-Mello, 2000), this figure has now risen to 784 (Vaz-de-Mello, 2023), a ~20% increase. This should be no different for the other South American countries. The Brazilian catalog also points to the direction that others should follow: openly available online, it allows additions and corrections in real-time, with the inclusion of newly discovered species, corrections associated with nomenclatural novelties, and updates in geographical distribution, among others. Currently, only the valid name, invalid synonyms, and the distribution of each species among the Brazilian states are available. In the future, further data such as type material, life habits, and habitat occupied will be added. We envision a future where the same tool will be available for each of the New World countries.

Much of the Revolution's success has been due to the great expansion that our Scarabaeinae museum collections have been experiencing since the second half of the 20th century, particularly during this millennium in South America. Until then, specimens were usually caught fortuitously by general entomologists who, by not being particularly interested in dung beetles, applied collection methods not properly suited to find them (e.g., active search with insect nets, light traps, Malaise traps). Now, the scarabaeine taxonomists themselves and, most importantly, a host of ecologists using the group as bioindicators are going regularly to the field in their search. They have designed and continuously perfected methods to collect ever more efficiently the highest richness and abundance of dung beetles as possible, including pitfall traps baited with as diverse materials as dung, carrion, mushrooms, decaying fruits, and dead millipedes (see, e.g., Lobo et al., 1988; Kryger, 2009; Araújo et al., 2022), as well as flight interception traps for both generalist species and those not regularly attracted to baits (e.g., Puker et al., 2020) (see Mora-Aguilar et al., 2023 for a review).

And field collections have not only become more frequent and efficient, but also more geographically encompassing. Though it is

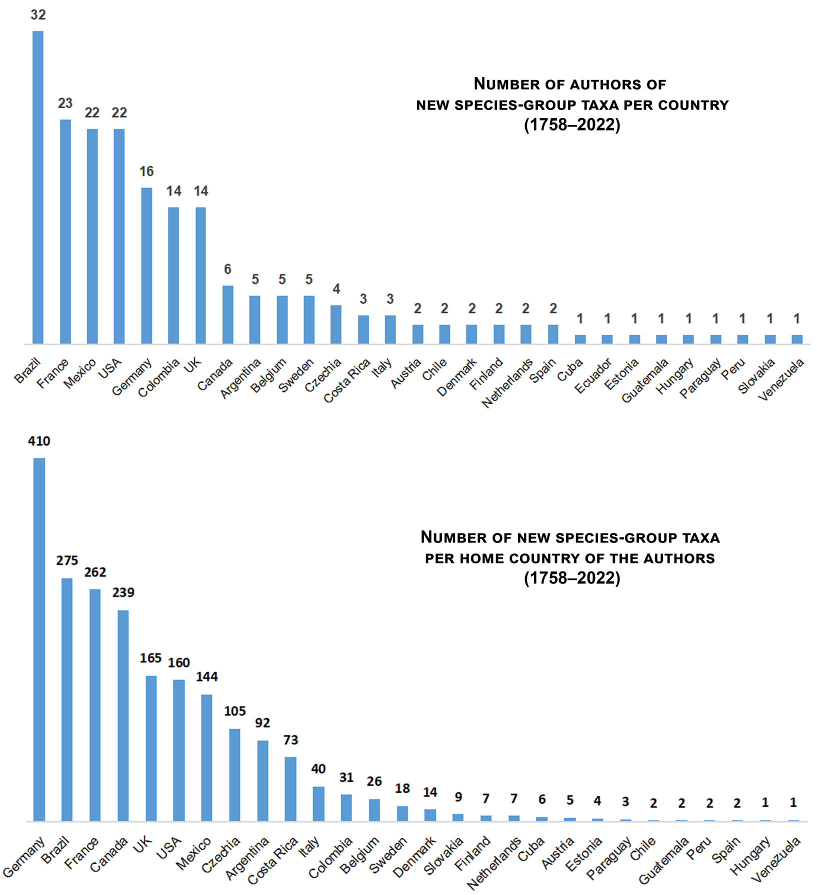

FIGURE 5
Species-group taxa, authors, and home countries across the taxonomic history of the New World Scarabaeinae. Like in Figure 5, countries are treated by their modern borders and names. The upper graph shows for each country the number of authors who have over the past 265 years discovered at least one New World species-group taxon of dung beetles. The graph below, in turn, shows the number of such taxa discovered by authors based in each of the countries. As in Figure 4, if a taxon was discovered by two or more authors based in different countries, it was counted again for each of those countries. Note that, although the last Germany-based author to discover a new species-group taxon was Blut (1939), the country still leads the number of discovered species by a wide margin. This is primarily due to the amazing efforts of Edgar von Harold in the latter half of the 19th century, who alone was responsible for the discovery of 275 species-group taxa, or ~69% of the German share and ~15% of the entire fauna (see Figure 6). Data compiled from Schoolmeesters (2022).

true that more intrepid naturalists have been exploring the most isolated corners of the New World since the 18th century in search of insects (see Papavero, 1971, 1973), most of the dung beetle specimens accumulated in collections until the 1950s–1970s came from more easily accessible localities, usually closer to the coast and larger urban centers, including the temperate forests of the eastern United States, localities in Mexico and Central America explored by the *Biologia Centrali-Americana* naturalists and, later, by US biologists, the West Indies, the southern Brazilian Atlantic Forest, and the Pampas grasslands of southern Brazil, Argentina, and Uruguay. Over the past decades, however, vast areas that, for centuries, had been seldom visited by naturalists have now turned into the ground of frequent fieldwork. These locations include the southern, eastern, and western Amazon rainforest in Ecuador, Peru and the Brazilian states of Rondônia, Mato Grosso and Pará, as well as the forests around Manaus and in French Guiana; the savannas, shrublands, and dry forests of the Cerrado in central Brazil; the tropical rainforests and cloud forests of southern Central America, particularly those of Costa Rica; the montane tropical forests of Los Chimalapas region of southern Mexico; the Pacific rainforests of Ecuador; the forests of the Magdalena Valley in Colombia; and the last remnants of Atlantic Forest in northeastern Brazil. The combination of adequate collecting techniques and broader geographical coverage, as well as the development of scientific institutions, including museums, in Latin America, have transformed the character of the material available for taxonomic investigation. It changed from being composed of scattered, usually poorly labeled specimens preserved in European museums until the mid-20th century to huge geographical and population series bearing precise collecting information housed in countries throughout the Americas.

The abundance of material available for study led, in turn, to a new character of the taxonomic revisions. If, before, little could be said about intraspecific variation, now work after work has been revealing how diverse the dung beetle species can be across their distribution, often showing complex patterns of population structure (e.g., Edmonds, 1994; Edmonds, 2000; Solís and Kohlmann, 2002; Génier and Kohlmann, 2003; Génier, 2009;

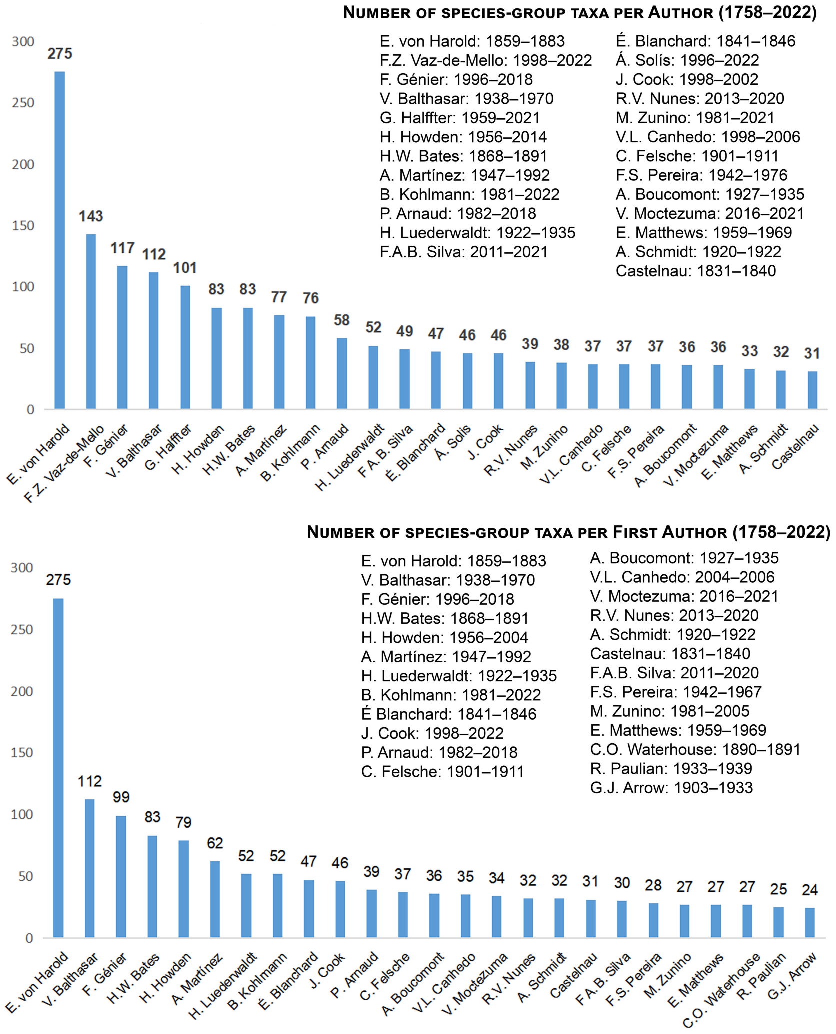

FIGURE 6
Number of new species-group taxa by the 25 most prolific authors over the taxonomic history of the New World Scarabaeinae. The upper graph shows all authors combined regardless of their position in the authorship of the name of the taxon. The lower graph shows only the figures as first authors. The years next to the name of the authors refer to the period in which they described new species-group taxa. Refer to Table 5 for more details. Data compiled from Schoolmeesters (2022).

Cupello and Vaz-de-Mello, 2018; Maldaner et al., 2019; Cupello et al., 2020, 2021a; Nazaré-Silva and Silva, 2021b; Costa-Silva et al., 2022; Solís and Kohlmann, 2023). Also, while the scarcity of material previously prevented the recognition of subtler interspecific taxonomic characters, now the abundance of specimens for comparison has led to the discovery of cryptic species among the continent's dung beetles (e.g., Cupello and Vaz-de-Mello, 2013b, 2018; Darling and Génier, 2018; Génier, 2019a). This discovery posed the necessity of exploring other character systems in addition to the ones traditionally used by the taxonomists, so leading to the revelation of the diversity and taxonomic informativeness of the endophallus (see Zunino, 2012 for part of this history) and the first attempts at species delimitation using genetic data (Solís and Kohlmann, 2012; Nolasco-Soto et al., 2017; Maldaner et al., 2019; Nolasco-Soto et al., 2020).

Another major result of the revolution in field collecting has been the re-discovery of long-disappeared species. These include, for instance, *Sulcophanaeus rhadamanthus* (Harold, 1875), a phanaeine species that had vanished before the 1950s and was re-found 60 years later in Rio Grande do Sul, Brazil, more than 1,000 km south of its previously known range in Rio de Janeiro state (da Silva et al., 2011, 2012, 2013). More recently, another new population was found in the state of Santa Catarina (Simões-Clivatti and Hernández 2022). These discoveries suggest that the presence of this species in the Argentinian province of Buenos Aires, as indicated by the label of a specimen in the Museu de Zoologia, São Paulo, and called into question by Pereira and d'Andretta (1955a), may, after all, be correct. Another example of a species that has recently reappeared is *Paracryptocanthon borgmeierei* (Vulcano et al., 1976). Until the last decade, it was known from just seven females, all collected in the 1960s and 1970s from a forest fragment in the heart of the city of Rio de Janeiro (Vulcano et al., 1976; Howden and Cook, 2002). It was then re-discovered, in 2013, through the collection of a larger series of

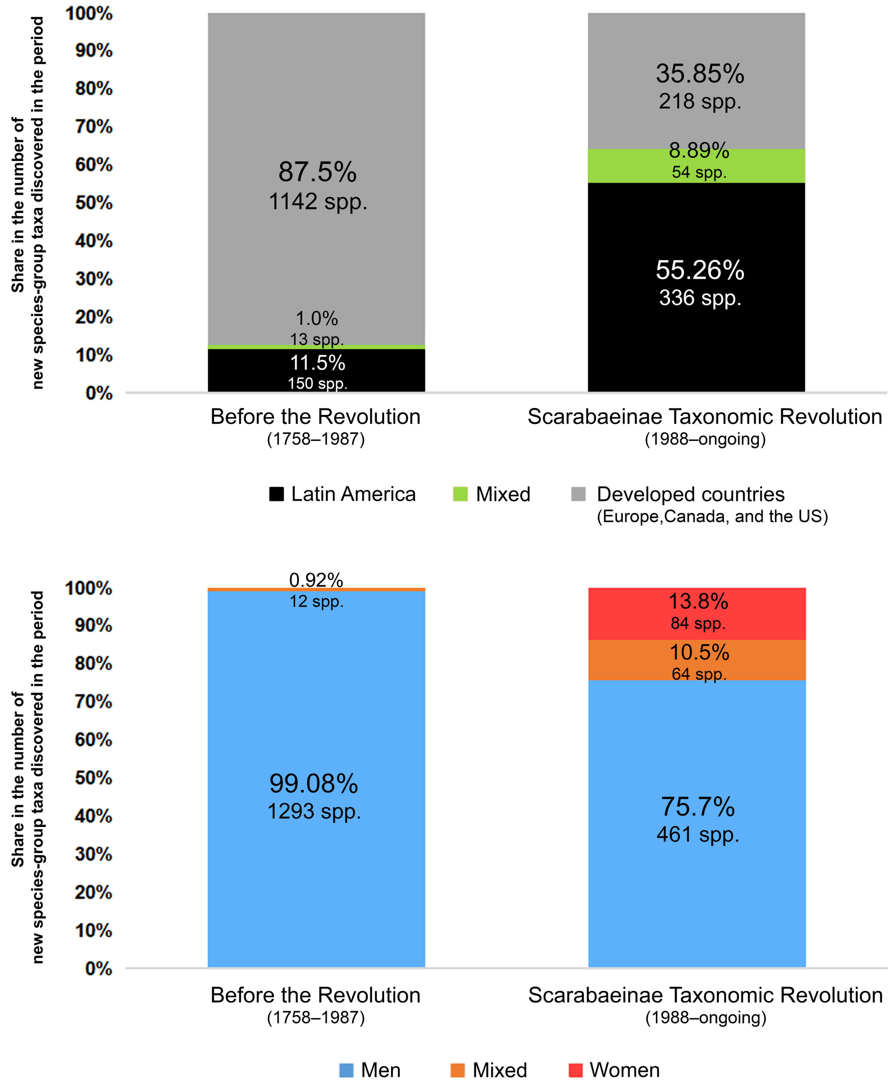

FIGURE 7
Social changes in the community of New World scarabaeine taxonomists. The upper bar chart shows the relative participation of authors based in Latin America and the developed world in the discovery of new species-group taxa before and during the Revolution; "mixed" refers to taxa described by pairs or groups of authors distributed across countries belonging to the two groups. Note that whereas before the Revolution authors based in Latin American countries participated in the description of less than 13% of new taxa, their share has grown to more than 60% over the past 35 years. As argued in the text, this was made possible at least partly by the expressive economic expansion experienced by these countries since the mid-20th century. The lower chart depicts the differential participation of men and women in the same process. "Men" and "women" refer to taxa described by either a single person or by a group of people of the same sex, whereas "mixed" refers to taxa discovered by composite groups of both men and women. Women's participation has greatly expanded in recent decades. Among the 112 authors who published new species-group taxa in the 230 years preceding the Revolution, only two, or 1.78%, were women, the Brazilian Maria Aparecida Vucano (d'Andretta) (starting in Pereira and d'Andretta 1955a) and the Mexican Violeta Halffter (idem in Martínez et al., 1964), and they were always co-authored by men. During the Revolution, this number has so far risen to 17, or 20% of all the 85 authors. The Revolution has also seen the first women to ever publish new species-group taxa without being co-authored by men, Ana Margarete Ferreira and Maria Helena Galileo, in their 1993 revision of *Pedaridium*; this was later followed by Joyce Cook (Cook, 1998, 2000, 2002) and Virgínia Canhedo (Canhedo, 2004a, b, 2006). Altogether, the percentage of new species-group taxa whose description had at least a woman involved has risen from less than 1% before the Revolution to ~24% in the last 35 years.

specimens of both sexes at the same locality from where it had been previously known (Pacheco and Vaz-de-Mello, 2017). A third example is *Dichotomius malyi* Maldaner et al., 2015, originally known from two old, possibly 19th-century specimens labeled simply as "São Paulo" and then re-discovered in 2014 living in Minas Gerais state (Maldaner and Vaz-de-Mello, 2022). Other groups, such as *Aphengium*, *Deltorhinum*, *Megatharsis*, *Coprophanaeus* (*Metallophanaeus*), *Dendropaemon*, *Paracanthon*, and *Streblopus*, that used to be among the rarest of the Scarabaeinae have now, thanks to the intensified collection efforts, become, if not common, at least more frequently found in the field and numerous in collections (Gillett et al., 2009; Edmonds and Zídek, 2010; Génier, 2010; Gillett et al., 2010; Silva and Vaz-de-Mello, 2015; Génier and Arnaud, 2016; Montoya-Molina and Vaz-de-Mello, 2019a; Pacheco and Vaz-de-Mello, 2019b; Cupello et al., 2020).

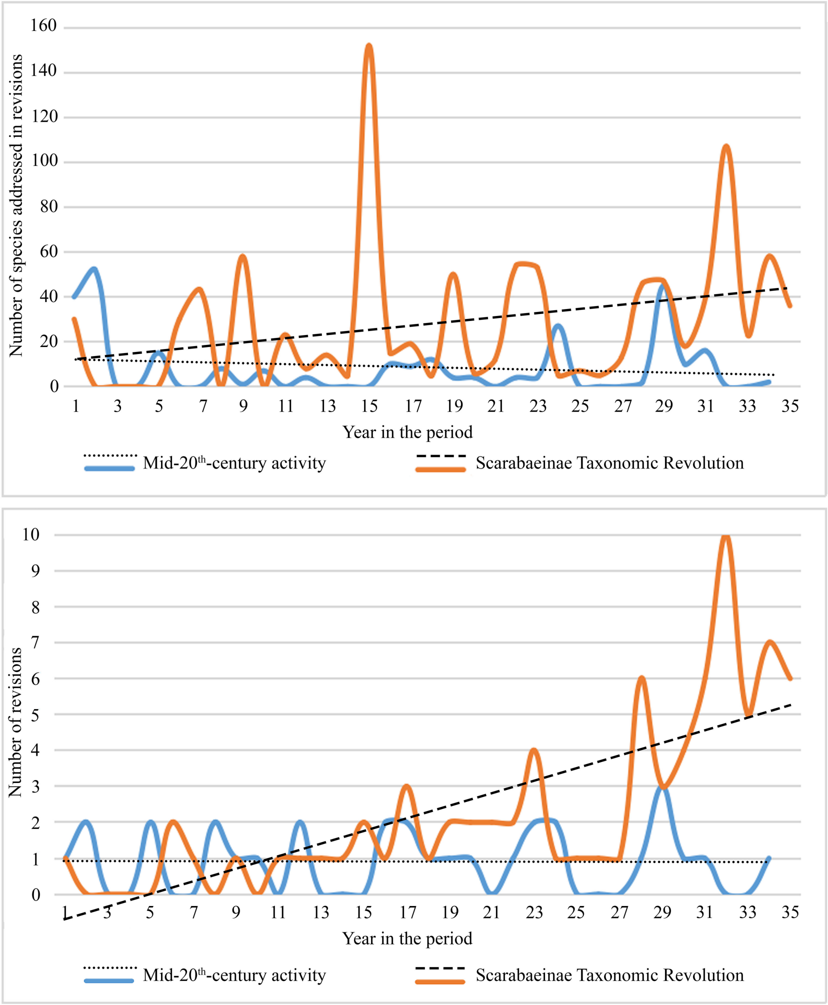

FIGURE 8
Comparisons between the 34 years of the mid-20th-century period (1938–1971, with macrotaxonomic extension to 1977) and the so far 35 years of the Taxonomic Revolution (1988–ongoing). Year 1 corresponds to 1938 and 1988, respectively, and so on. The upper graph compares the rhythm in the number of species addressed annually during each of the two periods. Dashed lines indicate the overall trend for each period. Note that, in the mid-20th-century period, the trend was of a slow decrease, whereas for the current Revolution, it is of consistent growth. The lower graph compares the rhythm of new revisions and monographs appearing in each year of the two periods. Note that the trend in the number of new works remained stagnated throughout the mid-20th-century period, whereas, in the Revolution, it has been in steep increase.

TABLE 5 Authors who have published systematic papers on Scarabaeinae during the Taxonomic Revolution (1988–ongoing).

Country	Authors
Canada	**J. Cook** (1998–2002), **J.D.G. Darling** (2018), **F. Génier** (1996–2021), **B.D. Gill** (1993–2003), **H.F. Howden**† (1993–2014)
United States	**K.L. Bell** (2008), **W.D. Edmonds** (1994–2022), **D.C. Hawks** (2006), M. Ivie (1990–2008), F.-T. Krell (2016–2017), S. McCleve (2005), **F.C. Ocampo** (2002–2004), **T.K. Philips** (1990–2016), D. Price (2007–2009), B.C. Ratcliffe (1998–1999), **A.B.T. Smith** (1999–2001), W.B. Warner (1990)
Mexico	**A. Arriaga-Jiménez** (2016–2022), J. Blackaller-Bages (1993), F. Capistan (1996), D.J. Curoe (2014), L. Delgado (1990–2019), C. Deloya (1990–2019), F. Escobar (2019), F. Escobar-Hernández (2019), M.E. Favila (2017–2020), H.J. Gasca-Álvarez (2018), J. González-Astorga (2017–2020), **G. Halffter**† (1988–2023), **V. Halffter**† (2003–2015), Ben. Hernández (2021–2023), T. Joaqui (2019), **V. Lizardo** (2021–2023), P.A. Martínez-Rodríguez (2021), **V. Moctezuma** (2016–2023), **A.E. de los Monteros** (2017–2022), E.F. Mora-Aguilar (2015–2023), J.L. Navarrete-Heredia (1993–2023), G. Nogueira† (2020–2022), **J. Nolasco-Soto** (2017–2022), M. Pensado (1998), L.N. Peraza (2006), G.A. Quiroz-Rocha (2023), **L.E. Rivera-Cervantes** (1999–2015), **S. Rivera-Gasperín** (2022), M. Rös (2018–2020), J.L. Sánchez-Huerta (2017–2023), J. Valdez-Carrasco (2020), F.Z. Vaz-de-Mello (2005–2006)
Guatemala	E.B. Cano† (2003–2018)
Nicaragua	Blas Hernández (2020), J.-M. Maes (2020)
Costa Rica	G.E. Alvarado (2019), **B. Kohlmann** (1996–2023), Á Solís (1996–2023)

(Continued)

TABLE 5 Continued

Country	Authors
Suriname	**C.P.T. Gillett** (2009), A.J. Hielkema (2017–2019)
Venezela	J. Clavijo (1990)
Colombia	G. Amat-García† (2014), **J.A. Arias-Buriticá** (2012–2019), J. Castillo-García (2014), W. Chamorro (2020–2021), **C. Giraldo-Echeverri** (2021), **A. González-Alvarado** (2009–2015, 2021), M.S. Herrera (2019), L.C.P. Locarno (2014), A. Lopera-Toro (2001–2021), D.E. Martínez-Revelo (2020), C.A. Medina (2001–2020), **F. Molano-Rendón** (2009–2019), J.C. Neita-Moreno (2020), J.A. Noriega (2020), C. Pardo-Diaz (2019), D.A. Parrales (2015), C. Salazar (2019), R. Sarmiento-Garcés (2014–2019), E. Torres (2020), S.A.P. Tovas (2019), A. Vítolo (2001)
Ecuador	W. Chamorro (2019), D. Marin-Armijos (2019), S. Villamarin (2009)
Peru	L. Figueroa (2012–2015), Giraldo-Mendoza (2022), F. Meza-Velez (2012)
Brazil	J.F. Araújo (2022), **J.A. Arias-Buriticá** (2023), A. Asenjo (2019), **V.L. Canhedo**† (1998–2006), **M.S.G. Carvalho** (2016), **E.C. Carvalho de Santana** (2019–2022), **S. Cassenote** (2020), W. Chamorro (2014), **V. Costa-Silva** (2020–2022), **M. Cupello** (2013–2022), **A.B.M. Ferreira** (2022), **A.M. Ferreira** (1993), **D.C. Ferreira** (2017–2019), **M.H. Galileo** (1993), M. Gavino (2001), **A. González-Alvarado** (2019–2021), **L. Harada** (2018), L. Iannuzzi (2022), **J. Louzada** (2001–2015), **M.E. Maldaner** (2015–2022), **S. Montoya-Molina** (2019–2021), A.B.G. Moura (2022), R.C. de Moura (2022), **E.E. Nazaré-Silva** (2021), **L.G.O.A. Nunes** (2018–2022), **R.V. Nunes** (2013–2020), **T.L. Pacheco** (2017–2019), **C.S. Ribeiro-Costa** (2020–2022), **L. Sawaris** (2019), **F.A.B. Silva** (2011–2023), **D.M. Takiya** (2018–2019), **M.C. Valois** (2015–2023), **F.Z. Vaz-de-Mello** (1998–2004, 2007–2023), **M.K. Vieira** (2019)
Bolivia	A.C. Hamel-Leigue (2006), S.K. Herzog (2006)
Paraguay	C. Aguilar (2001–2009)
Argentina	Adr. Martínez (1990), Ant. Martínez† (1990–1992), **F. Ocampo** (2007–2011)
Chile	M. Pino (2021), F. Tello (2021), J. Mondaca (2023)
Norway	**D. Dimitrov** (2016), **S. Tarasov** (2015–2016)
Finland	M. Rossini (2020–2021)
Czechia	V. Malý (2008), S. Pokorný† (2008), **J. Zídek**† (2004–2012)
Switzerland	E.F.A. Toussaint (2020)
Italy	**E. Barbero** (2016), P. Gandini (2009), **C. Palestrini** (2016), **A. Roggero** (2016), **M. Rossini** (2015–2020), **M. Zunino** (1988–2021)
France	**P. Arnaud** (1996–2018), **M. Dierkens** (2016), **O. Montreuil** (1998), **P. Moretto** (2016), O. Boilly (2021)
Belgium	P. Schoolmeesters (2011)
Netherlands	M.A. Hielkema† (2019)
United Kingdom	M.V.L. Barclay (2018), D.J. Mann (2006)
Spain	E. Galante (1997–2020), J.R. Verdú (1997–2021)
South Africa	E. Pretorius (2004), C.H. Scholtz (2002–2004)

In bold are the authors of at least one complete taxonomic revision (see Table 1). Authors are classified by country of affiliation as stated in each of their works; authors may be listed for different countries if they changed their affiliation over the years. Years in parentheses following each author's name indicate the year of publication of their first and so far last taxonomic work during the Revolution while based in the respective country. Dagger (†) indicates authors known to be deceased.

TABLE 6 Authors who have described New World dung beetle species-group taxa.

Author	Species described	As first author	Country	Author	Species described	As first author	Country
E. von Harold (1859–1883)	275	275	Germany	M.H. Galileo (1993)	3	3	Brazil
F..Z. Vaz-de-Mello (1998–2022)	143	16	Brazil/ Mexico	A. Lopera-Toro (2020–2021)	3	3	Colombia
F. Génier (1996–2018)	117	99	Canada	M.E. Maldaner (2015–2021)	3	3	Brazil
V. Balthasar (1938–1970)	112	112	Czechia/ Slovakia	E. Nazaré-Silva (2021)	3	3	Brazil

(Continued)

TABLE 6 Continued

Author	Species described	As first author	Country	Author	Species described	As first author	Country
G. Halffter (1959–2021)	101	12	Mexico	J. Neita-Moreno (2020)	3	3	Colombia
H.F. Howden (1956–2014)	83	79	Canada	L.W. Saylor (1935–1943)	3	3	USA
H.W. Bates (1868–1891)	83	83	UK	E.L. Taschenberg (1870)	3	3	Germany
A. Martínez (1947–1992)	77	62	Argentina	E. Torres (2020)	3	3	Colombia
B. Kohlmann (1981–2022)	76	52	Mexico/ Costa Rica	C. Aguilar-Julio (2001–2009)	2	2	Paraguay
P. Arnaud (1982–2018)	58	39	France	G.E. Alvarado (2019)	2	2	Costa Rica
H. Luederwaldt (1922–1935)	52	52	Brazil	J.G. Audinet-Serville (1828)	2	2	France
F.A.B. Silva (2011–2021)	49	30	Brazil	H. Blut (1939)	2	2	Germany
É. Blanchard (1841–1846)	47	47	France	J.B.L. Buquet (1844)	2	2	France
A. Solís (1996–2022)	46	12	Costa Rica	M. Carvalho (2016)	2	2	Brazil
J. Cook (1998–2002)	46	46	Canada	W. Chamorro (2020–2021)	2	2	Ecuador/ Colombia/ Brazil
R.V. Nunes (2013–2020)	39	32	Brazil	L.A.A. Chevrolat (1834–1844)	2	2	France
M. Zunino (1981–2021)	38	27	Italy	V. Costa-Silva (2020–2022)	2	2	Brazil
V. Canhedo (1998–2006)	37	35	Brazil	J. Curtis (1844)	2	2	UK
C. Felsche (1901–1911)	37	37	Germany	J.W. Dalman (1824)	2	2	Sweden
F.S. Pereira (1942–1976)	37	28	Brazil	P.A.J. Drapiez (1819–1820)	2	2	Belgium
A. Boucomont (1927–1935)	36	36	France	D. Drury (1773)	2	2	UK
V. Moctezuma (2016–2021)	36	34	Mexico	L. Figueroa (2013–2015)	2	2	Peru
E. Matthews (1959–1969)	33	27	USA	P. Gandini (2009)	2	2	Italy
A. Schmidt (1920–1922)	32	32	Germany	J. Gistel (1857)	2	2	Germany
Castelnau (Laporte) (1831–1840)	31	31	France	H.L. Gory (1831–1844)	2	2	France
C.O. Waterhouse (1890–1891)	27	27	UK	Ben. Hernández (2021)	2	2	Mexico
R. Paulian (1933–1939)	25	25	France	H.G. Hubbard (1894)	2	2	USA
G.J. Arrow (1903–1933)	24	24	UK	P.A. Latreille (1812)	2	2	France
O.P. Young (1981)	24	0	USA	A.L.M. Le Peletier de Saint-Fargeau (1828)	2	2	France
L. Delgado (1990–2019)	22	16	Mexico	F. Ocampo (2007–2010)	2	2	USA/ Argentina
M. Valois (2015–2020)	19	11	Brazil	G.W.F. Panzer (1794)	2	2	Germany
W.F. Erichson (1835–1848)	18	18	Germany	L.N. Peraza (2006)	2	2	Mexico
B. Gill (1987–2003)	18	3	Canada	M. Rös (2018)	2	0	Mexico
A. González-Alvarado (2010–2021)	17	15	Colombia/ Brazil	J. Sturm (1826–1843)	2	2	Germany
T.L. Pacheco (2017–2020)	17	14	Brazil	J.R. Verdú (1997–2021)	2	1	Spain
E.F. Germar (1813–1823)	16	16	Germany	W.B. Warner (1990)	2	2	USA

(Continued)

TABLE 6 Continued

Author	Species described	As first author	Country	Author	Species described	As first author	Country
J. Louzada (2001–2015)	16	0	Brazil	M. Weber (1801)	2	2	Denmark
G. d'Olsoufieff (1924)	16	16	France	G. Amat-Garcia (2014)	1	0	Colombia
H. Burmeister (1848–1874)	14	14	Germany/ Argentina	J.F. Araújo (2020)	1	0	Brazil
J.C. Fabricius (1775–1801)	12	12	Denmark	M. Barclay (2017)	1	0	UK
M. Ivie (1990–2008)	12	5	USA	G.J. Billberg (1815)	1	1	Sweden
A.G. Olivier (1789)	12	12	France	J. Blackaller-Bages (1993)	1	0	Mexico
T.K. Philips (1990–2008)	12	7	USA	O. Boilly (2021)	1	1	France
A. Preudhomme de Borre (1880–1886)	12	12	Belgium	C. Bruch (1925)	1	1	Argentina
M. Robinson (1940–2051)	12	12	USA	G.A. Brullé (1838)	1	1	France
O.L. Cartwright (1956–1970)	11	0	USA	F. Capistan (1996)	1	0	Mexico
J.L. LeConte (1847–1866)	11	11	USA	J. Clavijo (1990)	1	0	Venezuela
L.E. Rivera-Cervantes (1999–2015)	11	10	Mexico	D.J. Curoe (2014)	1	0	Mexico
J.J.E. Gillet (1907–1911)	10	10	Belgium	S. Endrödi (1962)	1	1	Hungary
M. Perty (1830)	10	10	Germany	F. Escobar-Hernández (2019)	1	0	Mexico
M. Rossini (2015–2021)	10	5	Italy/Finland	L. Fairmaire (1893)	1	1	France
J.L. Sánchez-Huerta (2017–2021)	10	2	Mexico	E. Fleutiaux (1889)	1	1	France
M. Cupello (2015–2020)	9	7	Brazil	C.J. Gahan (1894)	1	1	UK
V. Halffter (1964–2009)	9	0	Mexico	E. Galante (1997)	1	0	Spain
P.H. Lucas (1859)	9	9	France	H.J. Gasca-Álvarez (2018)	1	1	Colombia
W.J. Brown (1927–1946)	8	8	Canada	M. Gavino (2001)	1	0	Brazil
W.D. Edmonds (1979–2022)	8	7	USA	C. Giraldo-Echeverri (2021)	1	0	Colombia
F.E. Guérin-Méneville (1838–1855)	8	8	France	S.S. Haldeman (1843)	1	1	USA
T. Say (1823–1835)	8	8	USA	L. Harada (2018)	1	0	Brazil
M.A. Vulcano (d'Andretta) (1955–1976)	8	4	Brazil	J.F.W. Herbst (1789)	1	1	Germany
J.O. Westwood (1835–1842)	8	8	UK	J. Huijbregts (1984)	1	1	Netherlands
C.H. Boheman (1858)	7	7	Sweden	A. Janssens (1932)	1	1	Belgium
C. Linnaeus (1758–1767)	7	7	Sweden	T. Joaqui (2019)	1	0	Mexico
W.S. Macleay (1819)	7	7	UK	E.A. Klages (1906)	1	1	USA
B.G. Nevinson (1889–1892)	7	7	UK	H.J. Kolbe (1893)	1	1	Germany
T. Kirsch (1871–1873)	6	6	Germany	J.T. Lacordaire (1855)	1	1	Belgium
C. Medina (2010–2020)	6	0	Colombia	R.B. Lange (1945)	1	1	Brazil

(Continued)

TABLE 6 Continued

Author	Species described	As first author	Country	Author	Species described	As first author	Country
S. Montoya-Molina (2019–2021)	6	6	Brazil	S.I. Ljungh (1799)	1	1	Sweden
J.W. Van Lansberge (1874)	6	6	Netherlands	V. Malý (2008)	1	1	Czechia
de Zayas (1966)	6	6	Cuba	S. McCleve (2005)	1	1	USA
J. Darling (2018)	5	5	Canada	A.B.G. Moura (2020)	1	0	Brazil
C. Deloya (1990–2019)	5	5	Mexico	R.C. de Moura (2020)	1	0	Brazil
G.H. Horn (1875–1894)	5	5	USA	A. Murray (1856)	1	1	UK
C.G. de Mannerheim (1828)	5	5	Finland	J.L. Navarrete-Heredia (1993)	1	0	Mexico
E.F. Mora-Aguilar (2015–2019)	5	5	Mexico	G. Nogueira (2020)	1	0	Mexico
G. Nunes (2018–2020)	5	5	Brazil	H. d’Orbigny (1905)	1	1	France
B. Ratcliffe (1980–1999)	5	5	USA	D.A. Parrales (2015)	1	0	Colombia
E. Carvalho de Santana (2019–2022)	4	4	Brazil	M. Pensado (1998)	1	0	Mexico
E.A. Chapin (1930–1935)	4	4	USA	S.B. Pessôa (1934)	1	1	Brazil
J.F. Eschscholtz (1822)	4	4	Estonia	R.A. Philippi (1859)	1	1	Chile
Adr. Martínez (1982–1990)	4	4	Argentina	S. Pokorný (2008)	1	0	Czechia
D.E. Martínez-Revelo (2020)	4	4	Colombia	L.J. Reiche (1848)	1	1	France
F. Molano (2010–2015)	4	4	Colombia	A. Sallé (1889)	1	0	France
A.M.F.J. Palisot de Beauvois (1805)	4	4	France	R. Sarmiento-Garcés (2014)	1	1	Colombia
L. Redtenbacher (1868)	4	4	Austria	L. Sawaris (2019)	1	1	Brazil
C. Schaeffer (1906–1915)	4	4	USA	J.C.D. von Schreber (1759)	1	1	Germany
A.B.T. Smith (1999–2001)	4	4	USA	C. Schreibers (1802)	1	1	Austria
M. Vieira (2019)	4	4	Brazil	D. Sharp (1877)	1	1	UK
J. Arias-Buriticá (2014)	3	3	Colombia/ Brazil	J.W. Shipp (1897)	1	1	UK
A. Arriaga-Jiménez (2018–2019)	3	2	Mexico	F. Tello (2021)	1	1	Chile
W.S. Blatchley (1918–1928)	3	3	USA	N.A. Vigors (1825)	1	1	UK
E. Cano (2003–2018)	3	3	Guatemala	J. Zídek (2012)	1	0	Czechia
A.M. Ferreira (1993)	3	3	Brazil				

“Species described” and “As first author” refer to the number of new species-group taxa that each author described, respectively, regardless of his/her position in the authorship of the newly established species-group name and exclusively as its first (or sole) author. Data retrieved from Schoolmeesters (2022). “Country” refers to the country where the author was based when the new species description was published. Note, however, that we take into consideration modern borders and names, not necessarily those contemporary to the authors. The only exception – made in recognition of his pivotal role in the history of entomology – is the Dane J.C. Fabricius, who is listed for Denmark even though the city where he was based, Kiel, is now part of Germany; at Fabricius’s time, even though part of the Holy Roman Empire, Kiel was under Danish rule. Underline indicates authors who have published species-group taxa during the Taxonomic Revolution. Authors are ordered in decreasing order by the number of “Species described”.

Often treated as a minor, almost esoteric subject, important contributions have also been made toward the nomenclature of the American scarabaeines. The allocation of species-group names established by 19th- and early 20th-century workers was, most of the time, difficult to define with the paucity of information usually available in the original descriptions. This insufficiency of the majority of the old descriptions (but see Harold’s for exceptions) is something typical of a by-gone era when the emphasis was given

TABLE 7 Number of species of Scarabaeinae for each New World country and other major political units.

Country and other territories	Species recorded in the last catalog for the country	Species recorded in Schoolmeesters (2022)	Species per thousand km^2 of land surface	Endemic species according to Schoolmeesters (2022)	Endemic species per thousand km^2	Proportion of endemic species over total richness
Canada	14 (Bousquet et al., 2013)	14	0.001	0	0	0%
United States	58 (Leng, 1920)	99	0.010	38	0.004	38.38%
Mexico	228 (Morón, 2003)	344	0.176	186	0.095	54.06%
Belize	Never published	42	1.841	0	0	0%
Guatemala	Never published	94	0.877	2	0.018	2.12%
El Salvador	52 (Pablo-Cea et al., 2023)	35	2.509	1	0.048	1.92%
Honduras	Never published	42	0.373	0	0	0%
Nicaragua	87 (Maes et al., 2020)	78	0.725	1	0.008	1.28%
Costa Rica	185 (Solís and Kohlmann, 2012; Solís and Kohlmann, 2023)	202	3.623	40	0.783	19.80%
Panama	133 (Ratcliffe, 2002)	158	2.125	16	0.215	10.12%
Bahamas[1]	2 (Turnbow and Thomas, 2008)	1, correct figure 2	0.199	0	0	0%
Turks and Caicos Islands	Never published	0	0	0	0	0%
Cuba[2]	12 (Peck, 2005), 11 (Ivie and Philips, 2008)	13	0.118	10	0.091	76.92%
Cayman Islands	1 [introduced] (Thomas et al., 2013)	0, correct figure 1 [introduced] (Thomas et al., 2013)	3.787	0	0	0%
Jamaica	6 (Ivie and Philips, 2008)	6	0.553	4	0.369	66.66%
Haiti[3]	6 (Perez-Gelabert, 2008)	5, correct figure 7	0.253	2	0.072	28.57%
Dominican Republic[4]	11 (Perez-Gelabert, 2008)	23, correct figure 22	0.455	16	0.331	72.72%
Puerto Rico	7 (Ivie and Philips, 2008)	7	0.768	6	0.659	85.71%
British Virgin Islands[5]	1 (Valentine and Ivie, 2005; Ivie and Philips, 2008)	0, correct figure 1	6.622	0	0	0%
US Virgin Islands	2 (Ivie and Philips, 2008)	2	5.780	0	0	0%
Anguilla	1 [introduced] (Peck, 2016)	0, correct figure 1	10.989	0	0	0%
Sint Maarten[6]	1 [introduced] (Colijn et al., 2019)	0, correct figure 1	24.390	0	0	0%
Saba (Caribbean Netherlands)	0 (Colijn et al., 2019)	0	0	0	0	0%

(Continued)

TABLE 7 Continued

Country and other territories	Species recorded in the last catalog for the country	Species recorded in Schoolmeesters (2022)	Species per thousand km^2 of land surface	Endemic species according to Schoolmeesters (2022)	Endemic species per thousand km^2	Proportion of endemic species over total richness
Sint Eustatius (Caribbean Netherlands)[6]	1 [introduced] (Colijn et al., 2019)	0, correct figure 1	47.619	0	0	0%
Saint Kitts and Nevis[7]	2 (Peck, 2016)	0, correct figure 2	7.662	0	0	0%
Antigua and Barbuda[8]	1 [introduced] (Peck, 2016)	0, correct figure 1	2.262	0	0	0%
Montserrat[9]	2 (Peck, 2016)	1, correct figure 2	19.607	0	0	0%
Guadeloupe	5 (Peck, 2016)	5	3.071	2	1.228	40%
Dominica[4]	3 (Peck, 2016)	0, correct figure 3	3.994	1	1.331	33.33%
Martinique[4]	6 (Peck, 2016)	4, correct figure 6	5.514	0	0	0%
Saint Lucia[4]	3 (Peck, 2016)	3	4.950	2	3.300	66.66%
Barbados	0 (Peck, 2009a)	0	0	0	0	0%
Saint Vincent and the Grenadines[10]	6 (Peck, 2016)	4, correct figure 6	15.424	0	0	0%
Grenada[11]	7 (Peck, 2016)	5, correct figure 7	20.348	0	0	0%
Bonaire (Caribbean Netherlands)	0 (Colijn et al., 2019)	0	0	0	0	0
Curaçao[12]	1 (Colijn et al., 2019)	0, correct figure 1	2.252	0	0	0%
Aruba	0 (Colijn et al., 2019)	0	0	0	0	0%
Trinidad and Tobago	Never published (Peck et al., 2002 list 9 species from Tobago alone)	24	4.680	1	0.195	4.16%
French Guiana	130 (Hielkema and Hielkema, 2019)	160	1.915	8	0.095	5.00%
Suriname	117 (Hielkema and Hielkema, 2019)	120	0.750	1	0.006	0.83%
Guyana	79 (Hielkema and Hielkema, 2019)	83	0.401	4	0.020	4.81%
Venezuela	72 (Roze, 1955)	167	0.189	26	0.029	15.56%
Colombia	283 (Medina et al., 2001)	366	0.352	54	0.051	14.75%
Ecuador	223 (Chamorro et al., 2019)	245	0.955	46	0.179	18.77%
Peru	278 (Ratcliffe et al., 2015)	285	0.222	28	0.021	9.82%
Brazil	782 (Vaz-de-Mello, 2023)	800	0.094	344	0.040	43.00%
Bolivia	216 (Hamel-Leigue et al., 2006)	254	0.234	30	0.027	11.81%
Paraguay	Never published	161	0.405	15	0.037	9.31%

(Continued)

TABLE 7 Continued

Country and other territories	Species recorded in the last catalog for the country	Species recorded in Schoolmeesters (2022)	Species per thousand km^2 of land surface	Endemic species according to Schoolmeesters (2022)	Endemic species per thousand km^2	Proportion of endemic species over total richness
Chile	10 (Mondaca, 2023)	11, correct figure 10[13]	0.013	3	0.004	27.27%
Argentina	202 (Martínez, 1959)	247	0.090	41	0.016	16.59%
Uruguay	Never published	62	0.354	5	0.028	8.06%

[1] Schoolmeesters (2022), following Matthews (1966), listed *Euoniticellus cubiensis* (Castelnau, 1840) as the sole species present in the Bahamas. He overlooked, however, Ivie and Philips's (2008) more recent record of a second species for the country, *Pseudocanthon perplexus* (LeConte, 1847). For this reason, we use Ivie & Philips's number for our calculations.

[2] Ivie and Philips (2008) overlooked Peck's (2005) record of the presence in Cuba of the introduced African species *Digitonthophagus gazella* (Fabricius, 1787). This record was also overlooked by Schoolmeesters (2022), who, in turn, added two other species to Peck's list, *Onthophagus fragosus* Génier and Howden, 2014 and *O. marginicollis* Harold, 1880. While the first is certainly present in Cuba (Génier and Howden, 2014), why Schoolmeesters cites the latter for the country is unknown to us; as far as we know, *O. marginicollis* is restricted to the New World mainland. Putting everything together, we follow Peck (2005) while adding the confirmed *O. fragosus* to his 12-species list.

[3] Schoolmeesters (2022) overlooked literature records (Matthews, 1966; Vulcano and Pereira, 1966) of *Canthon violaceus* (Olivier, 1789) for Haiti, listing it solely from the Dominican Republic. Furthermore, the Haitian species recorded by Matthews (1969) as *Canthochilum* sp. was also not included in Schoolmeesters' catalog. Because of these two omissions, we use Perez-Gelabert's (2008) number for our calculations added by the taxonomic rearrangements of Ivie and Philips (2008). The two endemic species to Haiti are *Canthochilum* sp. (sensu Matthews, 1969) and *C. ciboney* Matthews, 1969. In contrast, all the species that Matthews (1966) had recorded as endemic to Haiti have since then been discovered living in the Dominican Republic: *Canthon callosus* (Harold, 1868) (Vulcano and Pereira, 1966), *C. signifer* (Harold, 1868) (Vulcano and Pereira, 1966), and *Onthophagus capitatus* (Castelnau, 1840) (Ivie and Philips, 2008). It is also worth mentioning that Perez-Gelabert (2008) listed *Digitonthophagus gazella* from Hispaniola without specifying in which of the two countries, Haiti or the Dominican Republic, the species was found; his record was explicitly based on Ivie and Philips' then-still unpublished data. In the latter's publication itself (Ivie and Philips, 2008), it is clarified that all the known records of this species concern the Dominican Republic. Though it is very likely that the species has also invaded Haiti by now, formal confirmation is still lacking. We thus do not include *D. gazella* in our numbers for the country.

[4] Schoolmeesters (2022) confused Dominica with the Dominican Republic and cited *Pseudocanthon caeranus* Matthews, 1966 and *P. sylvaticus* Matthews, 1966 as present exclusively in the latter country. In actuality, neither species occurs in the Dominican Republic; they are both endemic to the Lesser Antilles, the first occurring in Dominica and Martinique, the second only in Dominica (Matthews, 1966; Peck, 2006; Peck, 2016). A third and final Dominica species, *Onthophagus antillarum* Arrow, 1903, is widespread in the Lesser Antilles, but its presence in Dominica as recorded by Matthews (1966) and Peck (Peck, 2006; Peck, 2016) was omitted by Schoolmeesters. At the same time, Saint Lucia, an island that is not inhabited by the *O. antillarum* (Matthews, 1966; Peck, 2009b; Peck, 2016), is misreported for the species by Schoolmeesters. On the other hand, the presence of the invasive species *Digitonthophagus gazella* in St. Lucia, as first reported by Ivie (2009), has not been taken into account by Schoolmeesters. Finally, *Onthophagus albicornis* Palisot de Beauvois, 1805, whose presence in the Dominican Republic has been confirmed in the literature (Matthews, 1966; Ivie and Philips, 2008), is listed as occurring in "Santo Domingo, Hispaniola" by Schoolmeesters; though this is not technically incorrect, as Santo Domingo was indeed the colonial name of the current country, it is inconsistent with the other records from there given in his catalog under the modern name Dominican Republic. Due to all these errors, Dominica is not cited in the Schoolmeesters catalog, and the Dominican Republic is said to harbor one more species than it actually does; St. Lucia, in turn, has the number incidentally correct in Schoolmeesters, since, whilst one of its species is omitted (*D. gazella*), another is incorrectly assigned to it (*O. antillarum*). As for Martinique, Schoolmeesters also erred in not citing for it *O. antillarum* and the African introduced *Digitonthophagus gazella* (Fabricius, 1787) (see Peck, 2011b; Peck, 2016), resulting in the number of Martinique species in the catalog being two less than the correct figure. Given these errors, we decided to use the data provided by Matthews (1966) and Peck (Peck, 2006; Peck, 2009b; Peck, 2011; Peck, 2016) for these places in our calculations instead of Schoolmeesters'.

[5] Schoolmeesters (2022) overlooked Ivie and Philips's (2008) record of *Canthochilum taino* Matthews, 1966 from the island of Tortola, in the British Virgin Islands. The species is further known from two other islands, St. John, in the US Virgin Islands, and Puerto Rico.

[6] Schoolmeesters (2022) overlooked Colijn et al.'s (2019) record of *Digitonthophagus gazella* from the islands of Saint Martin and Sint Eustatius. Concerning the former, the original record is from Yokoyama's (2013) field guide to the wildlife of Saint Martin. This island is politically divided into two regions: the northern part is the Collectivity of Saint Martin, part of the French Republic, whereas the southern part is Sint Maarten, one of the four constituent countries of the Kingdom of the Netherlands. It is unclear in which part of the island the specimen shown by Yokoyama was found, but since the island is so small (87 km^2) and *D. gazella* is spreading so fast through the Caribbean (Ivie and Philips, 2008), there is little doubt that the species should now be widespread on Saint Martin, occurring in both the Dutch and the French areas.

[7] Schoolmeesters (2022) listed no species for Saint Kitts and Nevis, overlooking the records for the island of St. Kitts of *Ateuchus illaesus* (Harold, 1868) by Matthews (1966) and Peck (2011a, 2016) and of *Digitonthophagus gazella* by Peck (2011a, 2016).

[8] Schoolmeesters (2022) assigned no species to Antigua and Barbuda, overlooking Peck's (2011a, 2016) record of *Digitonthophagus gazella* from the island of Antigua.

[9] Schoolmeesters (2022), following Matthews (1966), listed only one species, Ateuchus illaesus, from Montserrat, overlooking Ivie et al.'s (2008a, 2008b) record of *Digitonthophagus gazella* from there, a record also repeated by Peck (2016).

[10] Schoolmeesters (2022) overlooked the presence of *Digitonthophagus gazella* and *Canthon perseverans* Matthews, 1966 in Saint Vincent and the Grenadines (Peck, 2016).

[11] Schoolmeesters (2022) overlooked the presence of *Onthophagus antillarum* and *Digitonthophagus gazella* in Grenada (Matthews, 1966; Woodruff et al., 1998; Peck, 2016). Schoolmeesters (2022) also recorded *Canthon perseverans* uniquely from Grenada, implying that it was endemic to the island. Although it was indeed originally described solely from there (Matthews, 1966) and this situation remained unchanged for many decades, Peck (2016) has recently added a new record from the island of Union, in Saint Vincent and the Grenadines.

[12] Colijn et al. (2019) mentioned the existence of a photo of a dung beele from Curaçao that they identified as *Pseudocanthon* sp., possibly belonging to *P. chlorizans*.

[13] Schoolmeesters's (2022) list of species present in Chile contains a number of errors related both to species incorrectly assigned to the country and species erroneously omitted from it. Among the former are *Sulcophanaeus imperator* (Chevrolat, 1844) (actually endemic to Bolivia, Paraguay and Argentina; Edmonds, 2000), *Deltochilum variolosum* Burmeister, 1873 (apparently restricted to the same countries as *S. imperator*), and *Onthophagus ptox* Erichson, 1847 (range still dubious, but certainly not encompassing Chile; Rossini et al., 2018a). The ones incorrectly omitted, in turn, are two introduced species, *Onitis vanderkelleni* Van Lansberge, 1886 and *Digitonthophagus gazella*, both of which are present in Chile only on the island of Rapa Nui (i.e., Easter Island) (Mondaca, 2023). In addition to these inaccuracies, we have two changes recently established by Mondaca (2023) that Schoolmeesters could obviously not have incorporated into the 2022 version of his catalog: the new junior subjective synonymy of *Pinotus dahli* Landin, 1955 under *Homocopris torulosus* (Eschscholtz, 1822) (the name is listed as valid in Schoolmeesters for a Chilean species as *Dichotomius dahli*) and the revalidation of *Copris punctatissimus* Curtis, 1844 for a endemic species of *Homocopris* (the name is listed by Schoolmeesters as an invalid junior synonym of *Homocopris torulosus torulosus*). Altogether, this leaves us with 10, as indicated by Mondaca (2023), rather than 11 species as listed in Schoolmeesters (2022). Due to these errors and modifications, we use Mondaca's more recent and accurate figure for our calculations, including for the number of endemic species.

to characters now known to hold poor diagnostic value such as details in colouration and punctation, whereas more informative characters such as, as mentioned above, the shape of the endophallites (the term itself has a recent history; Génier, 2019b) and secondary sex characteristics were most often ignored. To overcome this difficulty, all the taxonomic revisions listed in Table 1 have sought to study the original type specimens, designating, when necessary, neotypes. Further nomenclatural problems, including, but not always limited to, the identity of the types, have also been dealt with in papers outside revisions (e.g., Génier, 2001; Génier and Vaz-de-Mello, 2002; Vaz-de-Mello and Génier, 2005; Cupello, 2013; Cupello and Vaz-de-Mello, 2014a; Cupello et al., 2016; Cupello and Génier, 2017; Génier and Krell, 2017; Hielkema, 2017; Maldaner et al., 2017; Cupello, 2018; Cupello and Vaz-de-Mello, 2019; Cupello, 2020; Kohlmann et al., 2020; Cupello et al., 2021b, 2022, 2023b). Two of us have also started a

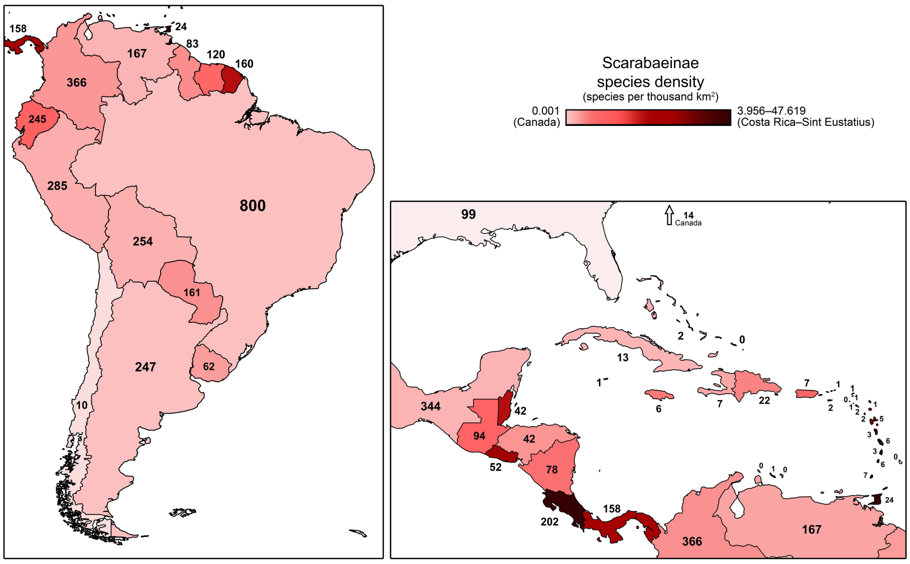

FIGURE 9
Species richness of each New World country and other territories. Numbers indicate the number of species so far recorded for each political entity, color grade marks species/area ratios. Brazil has the largest number of species, but it is one of the poorest countries in terms of species per area. The richest from the latter point of view include Costa Rica, Trinidad and Tobago, and most of the small Antillean islands. But note that no native scarabaeines are known for some of the latter, the recent invader *Digitonthophagus gazella* being their sole representative of the subfamily. See Table 5 for more details.

series dedicated to the study of historical type specimens (Vaz-de-Mello and Cupello, 2018a, b).

Lastly, while most of the taxonomic novelties in this Revolution have appeared in revisions and monographs and later papers published to complement them as listed in Table 1, smaller, independent works have also appeared addressing a single or a few species, usually new ones, in supraspecific taxa yet to be revised (e.g., Zunino and Halffter, 1988c; Delgado-Castillo and Deloya, 1990; Ivie and Philips, 1990; Martínez and Clavijo, 1990; Martínez and Martínez, 1990; Warner, 1990; Martínez, 1991, 1992; Delgado

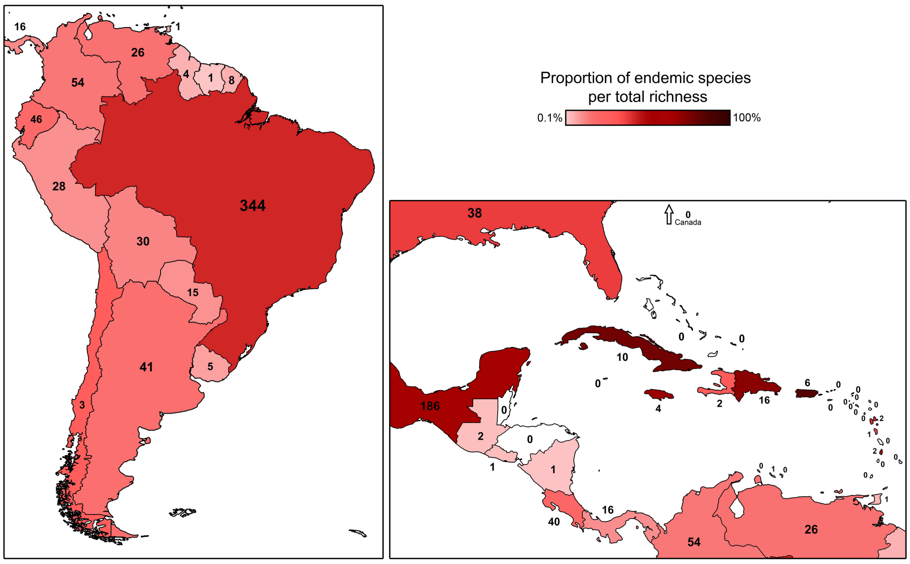

FIGURE 10
Species endemicity in each New World country and other territories. Numbers indicate the number of endemic species so far recorded from each political entity; color grade marks the percentage of endemic species in the fauna. Brazil is the country with the highest number of endemic species, as well as that in South America with the highest proportion of endemics. In the entire New World, the insular countries of Jamaica, Cuba, the Dominican Republic, and Saint Lucia, as well as the Commonwealth of Puerto Rico, are the political entities with the highest proportion of endemic species. See Table 5 for more details.

et al., 1993; Delgado, 1995; Verdú and Galante, 1997; Zunino and Halffter, 1997; Delgado and Pensado, 1998; Ratcliffe, 1998; Ratcliffe and Smith, 1999; Génier, 2000a, b; Aguilar-Julio, 2001; Delgado and Kohlmann 2001; Vaz-de-Mello et al., 2001; Halffter and Halffter, 2003; Kohlmann et al., 2003; Solís and Kohlmann, 2003; Howden and Génier, 2004; Vaz-de-Mello and Génier, 2005; Delgado et al., 2006; Peraza and Deloya, 2006; Ivie and Philips, 2008; Philips and Ivie, 2008; Halffter and Halffter, 2009; Gandini and Aguilar-Julio, 2009; González-Alvarado et al., 2009; Arias-Buriticá and Vaz-de-Mello, 2012; Figueroa et al., 2012; Génier, 2012; Nunes and Vaz-de-Mello, 2013; Chamorro et al., 2014; Delgado and Curoe, 2014; Génier and Howden, 2014; Silva and Vaz-de-Mello, 2014; Génier, 2015; Mora-Aguilar and Delgado, 2015; Moctezuma et al., 2016; Nunes and Vaz-de-Mello, 2016a; Vaz-de-Mello and Nunes, 2016; Kohlmann and Vaz-de-Mello, 2018; Moctezuma et al., 2018; Arriaga-Jiménez et al., 2019; Génier, 2019a; Moctezuma et al., 2019a, b; Montoya-Molina and Vaz-de-Mello, 2019b; Mora-Aguilar and Delgado, 2019; Lopera-Toro et al., 2020; Moctezuma and Halffter, 2020a; Moctezuma et al., 2020; Vaz-de-Mello et al., 2020; Boilly and Vaz-de-Mello, 2021; Chamorro et al., 2021; González-Alvarado and Vaz-de-Mello, 2021a; Moctezuma, 2021; Moctezuma et al., 2021a, d), including some fossil species (Tarasov et al., 2016; Tello et al., 2021a; Tello et al., 2021b; see also Zunino, 2013; Cantil et al., 2018). And while faunistic rather than phylogenetic, Bert Kohlmann and Ángel Solís' successive revisions of the Costa Rican species have also played a key role in pushing forward the systematics of the group (Kohlmann, 1997; Kohlmann and Solís, 1997, 2001; Solís and Kohlmann, 2002; Kohlmann and Solís, 2006b, 2009, 2012; Solís and Kohlmann, 2013; Kohlmann et al., 2019; Solís and Kohlmann, 2023). Thanks to their effort, today, the Costa Rican fauna is likely the best known in the New World, with the highest number of known species per area in all of the continent (Figure 9). Also valuable are the faunistic revisions of the North American *Canthidium* (Kohlmann and Solís, 2006a; Kohlmann et al., 2018), the Mexican *Canthon* (*Glaphyrocanthon*) (Rivera-Cervantes and Halffter, 1999), the Mexican and Guatemalan *Uroxys* (Delgado and Kohlmann, 2007), the South American *Pseudocanthon* Bates, 1887 (Nazaré-Silva and Silva, 2021b), and the Colombian *Dichotomius* (Sarmiento-Garcés and Amat-García, 2014). Adding the numbers from these independent works and the faunistic revisions to those from the revisions and their supplements, 614 new species-group taxa have so far been discovered during the Revolution, increasing by more than 47% the number of species and subspecies known to exist in the New World in 1987.

Expanding the frontiers

Despite the past 30 years of splendid progress, much still has to be done to modernize the systematics of the New World dung beetles. This is most obvious when we check what has been done with the most speciose groups. Of the twelve genera with 50 species or more in the Americas, only five have modern complete revisions published, one of them in need of being redone, while another four are being revised in parts (Table 8; Figures 11, 12). The remaining three, as argued by Cupello (2018), are the major gaps in the taxonomic knowledge of the American Scarabaeinae: *Uroxys* Westwood, 1842, *Canthidium* Erichson, 1847, and *Ateuchus* Weber, 1801. All three, while abundant in collections, have been sidelined by a number of difficulties they present to taxonomists. They are mostly composed of small (2–15 mm), black, and externally homogeneous beetles whose main taxonomic characters are found in the male genitalia, thus requiring careful dissection and anatomical study. The last global revision for each of them dates back to the works of Harold, in the mid-19th century, and neither has so far benefited from all the progress in theory, techniques, and material stored in collections made over the last 150 years. But precisely because of this, it is expected that, once properly studied, it

TABLE 8 The most speciose dung beetle genera in the New World fauna.

Genera	Number of recognized species in the Americas	Taxonomic status (percentage of species revised)
Onthophagus Latreille, 1802	226 (2,257 worldwide)	Partly revised (49.5%)
Dichotomius Hope, 1837	200	Partly revised (52.5%)
Canthidium Erichson, 1847	178	Under revision (F. Génier)
Canthon Hoffmannsegg, 1817	163	Partly revised (15.9%)
Deltochilum Eschscholtz, 1822	114	Partly revised (49%)
Ateuchus Weber, 1801	102	Under revision (M. Cupello)
Phanaeus MacLeay, 1819	83	Revised
Anomiopus Westwood, 1842	63	In need of a new revision
Ontherus Erichson, 1847	60	Revised
Uroxys Westwood, 1842	59	In need of revision
Eurysternus Dalman, 1824	53	Revised
Coprophanaeus d'Olsoufieff, 1924	50	Revised

Limited to genera with at least 50 species in the area. Numbers from Schoolmeesters (2022).

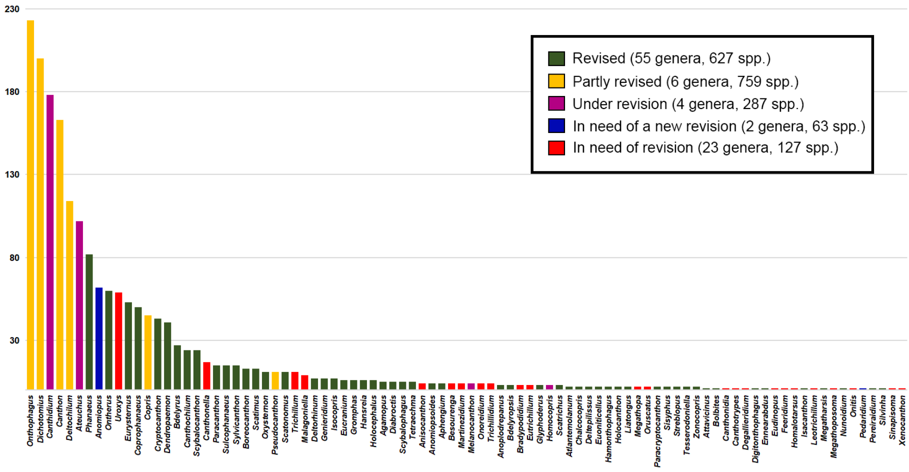

FIGURE 11
Number of currently recognized species and status of taxonomic resolution of each genus in the New World fauna. Notice that these numbers shall likely increase for most genera still unrevised or incompletely revised. At the same time, one of us (MC) feels that the numbers for a few of the groups, particularly *Phanaeus* and *Onthophagus*, are likely inflated under his preferred species definition (see Cupello and Vaz-de-Mello, 2018; Cupello et al., 2021a). Note also that whereas a relatively great number of medium- and small-sized genera have already been revised during the Revolution, the six most speciose groups either have only partial revisions published (ranging from ~16% to ~52% of their species composition; see Table 8) or, though currently under study, still have to see the first results of their revisions published. *Uroxys* is the largest genus still needing to attract any taxonomic attention other than that of faunistic revisions (Delgado and Kohlmann, 2007; Solís and Kohlmann, 2013). It is important to keep in mind, however, that having been revised does not mean being fully resolved: the revision is expected, for more difficult cases, to be just the first step in the investigation; more research will be needed to solve many of the problems still existing with the revised groups (see, e.g., Cupello et al.'s [2023a] comments about the revised *Sylvicanthon*). Finally, notice that six of the genera also encompass species in other parts of the globe: *Onthophagus*, *Copris*, *Euonitcellus*, *Onitis*, *Digitonthophagus*, and *Hamonthophagus*. The latter three are human-introduced in the Americas. The other three, though arriving on the continent spontaneously, are, in geological terms, newcomers, and only one, *Onthophagus*, has experienced significant radiation beyond North and Central America. As a likely result of this recent arrival in the Western Hemisphere, all of them are more diverse in the Old World.

will be these groups that will likely reveal the most interesting discoveries. The first author has been working for the past five years on a revision of one of these genera, *Ateuchus*, and can confirm that the predictions are indeed precise.

Progress must also be made in terms of fieldwork. Although, as we have seen, the places explored by dung beetle specialists have been broadening over the past decades, there are still areas mostly untouched. These include especially the northern Amazon,

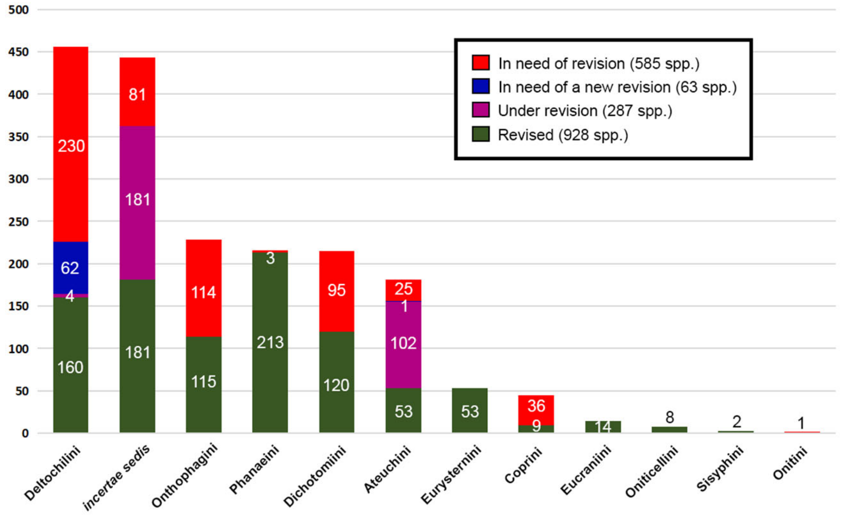

FIGURE 12
Status of taxonomic resolution of each tribe in the New World fauna. Bars show, for each tribe or the group of *incertae sedis* genera, the number of species classified by us in each of the four resolution categories. Phanaeini is, by far, the best resolved among the six most diverse groups; in contrast, Ateuchini, as far as published works are concerned, is, with only ~29% of its species revised during the Revolution, in the most precarious situation.

particularly in the Upper Rio Negro area of northwestern Brazil and Colombia, as well as the entire Venezuelan Amazon. Also almost entirely unexplored are the xerophytic forests of the Dry Chaco in southern Bolivia, northern Paraguay, and northwestern Argentina. As previously noted by Cupello et al. (2021a), distribution maps of South American taxa usually present a great void over the Dry Chaco (see, e.g., *Bolbites onitoides* Harold, 1868, *Holocanthon fuscorubrus* (Blanchard, 1846), *Ontherus appendiculatus* (Mannerheim, 1829), and *Gromphas inermis* Harold, 1869), and recent examination of the two main collections in Paraguay by the first author has revealed that even they house almost no specimens collected there (Cupello et al., 2023a). Also poorly represented in collections are the faunas of the Bolivian and, especially, Argentinian Yungas, as well as that of the tropical forests of the northern Central American countries, namely Guatemala, Honduras, and Nicaragua.

Efforts are also needed toward the re-discovery of species that, despite increasing collection activity, still fail to be caught. Examples are *Gromphas dichroa* (Blanchard, 1846) and *Deltepilissus diabolicus* (Harold, 1880), both of which have not been encountered in the field since the mid-20th century (Cupello and Vaz-de-Mello, 2013b, 2015; Silva et al., 2022), *Homalotarsus impressus* Janssens, 1932 and *Atlantemolanum costalimai* (Pereira and d'Andretta, 1955), both known exclusively from a few old, likely 19th-century specimens (Edmonds, 1972; González-Alvarado et al., 2019), and *Dendropaemon piceus* (Perty, 1830) and *Ateuchus procerus* (Harold, 1883), two even more drastic cases as they have vanished since the first half of the 19th century (Génier and Arnaud, 2016; Cupello, 2022). What is most curious about the majority of these examples is that these species inhabit one of the most intensively collected areas during the last 20 years in South America, the Brazilian Atlantic Forest. Why have they not been found again? Is it possible that they have become extinct due to the extensive deforestation of their habitat (cf. Ribeiro et al., 2009)? At least some of these vanished taxa have been hypothesized to be social insect inquilines, and it may be that if special attention is paid to investigating ant and termite nests, they will finally be re-discovered. The history of the Mexican endemic *Attavicinus monstrosus* (Bates, 1887) shows that we should be cautious before treating these myrmecophilous dung beetles as extinct simply because they are presumably microendemic and have disappeared for a time (Navarrete-Heredia, 1996).

A further issue that must be tackled by the scarabaeine systematists is their macrotaxonomic criteria and methodology. That is, how they infer supraspecific relationships and convert them into a classification. Of the 150 complete revisions and supplementary works listed in Table 1, just 14 have based their macrotaxonomy on explicit phylogenetic analyses, i.e., by presenting formal lists of characters and the analytical methods employed to infer phylogenetic relationships from them (Génier, 1996; Cook, 1998, 2000, 2002; Génier and Kohlmann, 2003; Vaz-de-Mello, 2007a, 2008; Cupello and Vaz-de-Mello, 2015; Génier and Arnaud, 2016; Roggero et al., 2016; Génier and Moretto, 2017; Maldaner et al., 2018b; Martínez-Revelo et al., 2020a; Halffter et al., 2022a). Eight others have based their macrotaxonomy on the phylogenetic results of previous publications (Ocampo, 2004, 2005, 2007, 2010a, 2010b, who relied upon Philips et al., 2002 and Ocampo and Hawks, 2006, and Cupello et al., 2020, 2021a, who relied on Philips et al., 2004a, Cupello and Vaz-de-Mello, 2015 and Tarasov and Génier, 2015, among others) or on then-unpublished data (Philips and Bell, 2008; finally published by Philips, 2016). The remaining ones have, in contrast, built their classifications following more vague, undisclosed procedures, relying on less disciplined, more superficial morphological comparisons to infer the phylogenetic relationships of the species (if the goal of presenting a phylogenetic classification was stated at all; sometimes, even the kind of classification that is aimed – e.g., if it is a phylogenetic or purely phenetic classification – is left vague). For one of these groups originally revised without such an adequate phylogenetic treatment, the phanaeine genera, subsequent workers have started to investigate its phylogeny using these more sophisticated computational methods (Philips et al., 2004a; Price, 2007, 2009; Maldaner et al., 2018b; Gillett and Toussaint, 2020), though this still has to be reflected in a revised macrotaxonomy (Maldaner et al., 2018b is an exception). Incipient treatment has also been given to *Dichotomius* (Pardo-Diaz et al., 2019).

The challenge, then, is to improve this scenario. First, authors, including ourselves, should strive to be more formal and disciplined in our phylogenetic analyses. This is not simply a formal need, the necessity to comply with a more explicit methodology and principles simply for the sake of it or to publish in journals with higher impact factors, but because these methods – i.e., those involved with computational parsimony and parametric (i.e., model-based) phylogenetic analyses – have demonstrated over the decades to be much better at inferring phylogenetic hypotheses that seem to be correct than the unaided, undisciplined human impression. Also, new character systems will be open to exploration once these more sophisticated techniques are dominated by us, scarabaeine systematists, including genetic and morphometric characters. Finally, we should seek to establish formal ranking criteria. What is a genus, a tribe, or a subtribe? Why is it that a taxon is ranked, let us say, as a subgenus and not as a genus or species group? Zunino and Halffter (1981), Génier (2017), and Cupello (2022) have given the first steps in this direction, but much is still to be done. By applying these methods and criteria explicitly and exploring a broad array of data, we will better understand the phylogenetic relationships of the New World dung beetles, and this will, in turn, lead us to a truly phylogenetic macrotaxonomy.

The level of classification that is currently most in need of such an advanced treatment is, no doubt, that of the tribe. This is a truly monumental task, for, since the New World fauna has a polyphyletic origin, the problem actually goes beyond the realm of the local fauna, encompassing the global diversity of the subfamily. Tarasov and Dimitrov (2016), in their groundbreaking phylogenetic study of the Scarabaeinae, have started the revisionary process, and now, with subsequent contributions, the number of recognized tribes in the whole subfamily has increased to 19, 11 of which, as listed in the Appendix, are present in the Americas (one, Onitini, introduced, six, Ateuchini, Dichotomiini, Deltochilini, Eucraniini, Eurysternini, and Phanaeini, endemic) (Scholtz et al., 2009; Tarasov and Dimitrov, 2016; Tarasov, 2017; Davis et al., 2019;

Daniel et al., 2020; Rossini et al., 2022). But the work is still far from being complete, and a great number of New World genera remain *incertae sedis* in the subfamily (Tarasov and Dimitrov, 2016; see the Appendix). And though we are calling special attention to the problems of the tribes, we should not lose sight that the genus-level classification is also in dire need of a more methodologically rigorous systematic treatment: the problems involving *Canthon* and related genera have been exposed 20 years ago by Medina et al. (2003) and are still to be resolved (cf. Cupello and Vaz-de-Mello, 2018), and it is well possible that, when investigated more seriously, genera like *Uroxys* and *Ateuchus*, as currently defined, may also prove to be polyphyletic (Vaz-de-Mello, 2007b).

Finally, the principles and methods of the microtaxonomic investigation – i.e., the delimitation and naming of species and subspecies – must also seek advancement. As we said above for macrotaxonomy, systematists must have clear definitions for the microtaxonomic ranks. That is to say, they need to have clear in their minds as to what kind of entities they want to apply the species and subspecies levels in the Linnean hierarchy (cf. Dubois, 2011). This is pivotal for two main reasons. First, for different taxonomies to be comparable, they have to share the same definitions for the taxonomic ranks. If different authors employ the term "species" to refer to different biological entities (e.g., reproductive communities versus diagnosable populations versus population lineages), taxonomic disagreements will usually have more to do with semantics than with the reality of the biological world. Saying "I don't agree that taxon A as delimited by author X is a good species" means nothing if the word "species" is not expressly defined and, even if it is, if the debaters do not agree on this definition (or are not at least aware that the word is being employed with different denotations). Second, species delimitation methods and ranking criteria, whatever they may be, derive directly from the definition of what a species (or subspecies) is; one can only have a method for discovering X if one defines what is meant by X. If a taxonomist has not defined what a species is (i.e., what kind of entity should be classified in the species category), delimiting species taxa is logically impossible.

But having a definition per se is not enough. This definition must be based on sound, educated reasoning and criteria, not on vague, intuitive ideas of what a species or subspecies is supposed to be. If our goal as systematists of building a classification system based on the evolution of dung beetles is to succeed, we must be better acquainted with the latest developments in the theory of speciation and other microevolutionary processes (e.g., Avise, 2000; Coyne and Orr, 2004; Price, 2008; Grant and Grant, 2014; Barraclough, 2019). We must also make good use of one of the greatest advantages that we have over our pre-1980s predecessors: the availability of large population and geographical series. They allow us to have a better understanding of the population structure of our species in terms of both connectivity between the populations and how their characters, both phenotypic and genetic, are distributed across the geographical space. In analyzing this material, another obvious advantage of modern systematics is, as mentioned above for macrotaxonomy, our capacity of exploring genetic and morphometric characters. Both of these character systems can provide a much vaster volume of data than the traditional qualitative (or vaguely quantitative) morphology to which our predecessors were mostly limited. And the power of these two character systems, genetics and morphometrics, goes beyond sheer volume of data: they allow us to complement traditional descriptive procedures with sophisticated statistical analyses for species delimitation and the study of population structure (Barraclough, 2019), something so far still rarely applied in taxonomic studies on New World dung beetles (but see, e.g., Nolasco-Soto et al., 2017, 2020; see also Matthews, 1961 for simple morphometrics). Yet, as recently demonstrated by Solís and Kohlmann (2023), difficult cases that defy dung beetle microtaxonomists' abilities to find a proper resolution relying on traditional morphological analyses can be clarified with the help even of the simplest molecular analyses. A study of the taxonomic literature listed in Table 1 will show many other cases that would benefit from these approaches, both simple and more sophisticated ones (see, e.g., discussions in Edmonds and Zídek, 2012, Cupello et al., 2021a, 2023a). Though still not easily accessible, behavioral, ecological, spectrophotometric, and biochemical characters shall also play a central role in microtaxonomy once proper methodology is learned or developed. The future will say which new character systems will be opened up by technological advancements for taxonomic exploration.

By paying attention to the population nature of biological diversity, we will put behind old typological biases leading to conceptualizations of species as homogeneous, "minimally diagnosable" units, and, in its place, adopt a biologically grounded conceptualization of species as composed of individuals interacting through interbreeding and so giving emergence to a new level of biological integration, the evolving population and its gene pool. This will have two effects. First, it will make us look for variation, the raw material of evolution, as opposed to present variation in short, almost exculpatory sentences as if recognizing its existence in our species other than in color or size was to admit that the taxonomy is possibly faulty (e.g., "until more evidence is found, we will prefer to treat as these specimens as a single species"). Second, it will make us more cautious before publishing (or accepting) new species taxa based on subtle variation, particularly microgeographic ones and in groups whose taxonomy is still largely unresolved such as *Onthophagus*, *Deltochilum*, and *Canthidium*. Population and geographical variation exist, and our taxonomic methods and concepts must be formulated in accordance.

Species, taxonomists must have in mind, are historically dynamic entities, and the understanding of their nature will remain incomplete until their phylogeographies are fully explored (see Maldaner et al., 2019 and Nolasco-Soto et al., 2017, 2020 for incipient attempts). But, at the same time, we must take care not to confuse population structure with speciation (Sukumaran and Knowles, 2017). Discontinuity in variation may not be due to discontinuity in reproductive connectivity, but an artifact of low geographical sampling of clinally variable, but still connected populations. And even if reproductive discontinuity between (meta)populations is the case, it still may not be evidence of speciation, for the discontinuity may be due to geographical rather than biological reproductive isolation (see Cupello et al., 2021a). All these factors must be taken into account by the microtaxonomist. We must look not only for patterns of variation, but for causes. Not only to know if the organisms or populations are different or "evolving separately", but why they are different and are evolving separately. Our microtaxonomic activities must, in essence, evolve from being solely descriptive to also embracing, like the phylogenetic macrotaxonomy, an explanatory goal.

Why is there a revolution?

Why has the Scarabaeinae Taxonomic Revolution been happening? And why did it start in the late 1980s and not, let us say, in the 2010s or the 1940s? What are the historical factors involved? We suppose that a general increase in scientific funding at least in some of the countries involved, particularly in Brazil in the 2000s, has played a major role. This at least in part was made possible due to the expressive economic growth and rise in general prosperity that most countries across the Americas have been experiencing since WWII (Roser, 2013; Pinker, 2018). Latin America's GDP per capita as a whole has risen by more than 365% since 1940, and this figure is even greater for some of the major countries in the Revolution taken individually such as Costa Rica (~422%), Mexico (~544%), and Brazil (~771%) (Our World in Data, 2020; Figure 7); the situation has been no different for the other two main players in the Americas, the US (~360%) and Canada (~424%) (Our World in Data, 2020). The vast population expansion experienced across much of the continent in the latter half of the 20th century, especially in the US, Mexico, Colombia, and Brazil (Roser et al., 2013), as well as the concomitant increasing participation of women in science (Figure 7) and the widespread rising in literacy and the betterment of education in general (Roser and Ortiz-Ospina, 2016; Pinker, 2018; Roser and Ortiz-Ospina, 2018) have also impacted the field by simply increasing the pool from which new dung beetle taxonomists are drawn. Also important have likely been the sharply declining costs for long-distance transport, particularly airfare (Thompson, 2013; Our World in Data, 2015; Gondim and Daraya, 2016; Pinker, 2018), which enabled much easier access to remote areas for fieldwork and overseas travels for the study of collections. If, before, taxonomists were mostly limited to the museums of their countries and seldom had access to the material housed overseas, including the precious type material, now they have the world before them. This alone could explain the change from a faunistic to a phylogenetic approach during the Revolution.

The advent and spread since the 1990s of personal computers, the internet, and e-mail communication (Roser et al., 2015) has also certainly played a central role in creating and expanding the Revolution. They made the exchange of information between researchers much more efficient, and enabled those based away from the major centers of scientific activity, particularly in Latin America, to effectively be part of the global community of systematists. Another, perhaps even more significant consequence of our digitally connected world has been the growing online accessibility of the taxonomic literature, particularly of historical, rarer works, freely available on websites such as the Biodiversity Heritage Library and Google Books. If, previously, to read a short description written two centuries ago by, say, Fabricius or Blanchard, a researcher may have needed to travel hundreds of kilometers to a library in another city, state, or even country, or endure long weeks of wait until someone mailed (or faxed) him a photograph or photocopy of the page he wanted to see, now the same information can be accessed within a few seconds from almost anywhere on the globe. The digital revolution has also greatly facilitated and reduced the cost of the publication process. Writing and editing a text on a word processing software such as Microsoft Word is undoubtedly easier and faster than using a typewriter or paper and pen. Digital imaging, both digital photography and digital drawing and related digital editors, is much more efficient than traditional line drawing or analog photography. The movement of manuscripts between authors, editors, and reviewers, which formerly had to rely on slow mail services (especially if international and involving third-world countries), is now as quick as a keystroke. And the costliest and slowest phase in the publication process has been pretty much eliminated: since 2012, provided that a few requirements are met, printing is no longer necessary for a taxonomic work to be formally published for nomenclatural purposes (ICZN, 2012). So, from beginning to end, producing a taxonomic revision is, nowadays, a much more practical task than it was a few decades ago.

But how does the history of the modern New World Scarabaeinae taxonomy compare with that of other scarab, beetle, and insect groups in this part of the globe? Is our revolution unique? Or have other groups experienced the same phenomenon? If the Revolution is something special of the Scarabaeinae at least among other scarabs as it seems to be, then there must be additional factors to the ones pointed out above, for they would facilitate the work on any biological group indiscriminately. Perhaps the answer is simply contingency: it just happened that the idiosyncratic interest from a few founding members met the right environment when the above conditions emerged in the late 1980s to the 2000s, and everything simply followed. Another factor to consider, however, is that, simultaneously with the Taxonomic Revolution, there has also been an Ecological Revolution: dung beetles have been transformed during the past decades into one of the major taxa used as bioindicators by ecologists interested in the conservation of tropical biomes (Halffter and Favila, 1993; Favila and Halffter, 1997; Spector, 2006; Nichols et al., 2007; Gardner et al., 2008; Kryger, 2009; Nichols and Gardner, 2011; Rivera and Favila, 2022; Arellano et al., 2023; Mora-Aguilar et al., 2023). This Ecological Revolution itself was largely the result of the emergence of conservation biology as a scientific discipline in the 1980s (Soule and Wilcox, 1980; Soulé, 1985; Quammen 1996; Meine et al., 2006; Van Dyke, 2008; Franco, 2013). The Ecological Revolution has had a two-fold effect on the systematics of the Scarabaeinae: on the one hand, it has put great pressure on the advancement of the discipline, for reliable identifications and identification tools are needed by a community much broader than the taxonomists themselves and museum curators. On the other hand, as we have already discussed, this widespread interest in dung beetles for environmental studies has brought an unprecedented volume of specimens to the collections, a golden opportunity for taxonomic investigations. The great majority of the new populations and species studied by modern taxonomists, particularly in South

America, originate from such ecological inventories. Without this co-evolution of the Taxonomic and Ecological Revolutions, neither could have happened.

And how have the different taxonomic schools in each country been interacting? The first impression is that the current revolution has its root in two major centers of origin, both founded around the 1950s: one in Canada, by Henry F. Howden (1925–2014), and another in Mexico, by Gonzalo Halffter (1932–2022). The latter has greatly flourished, with ramifications throughout Latin America, having been in the partial genesis of at least the modern Brazilian and Costa Rican schools through Halffter's former students Fernando Z. Vaz-de-Mello and Bert Kohlmann, respectively. The Canadian school, in turn, has been active mainly through the work of François Génier. But to what extent has this "polyphyletic" origin influenced the outcome of the Revolution? Are there perceptible differences in style or approaches by the descendants of each of the two schools? Has this influenced their results? And what about the individual researchers in the United States not genealogically related to either of the schools? Have they contributed unique elements? W.D. Edmonds, for instance, one of the major figures in the Revolution, became interested in dung beetle systematics in the early 1960s completely independent of Howden or Halffter, though he came to be close to the latter afterward (e.g., Edmonds and Halffter, 1978; Halffter and Edmonds, 1982). The same could be said of another close US collaborator of Halffter's, Eric Matthews (1932–2022) (Halffter and Matthews, 1966), as well as of Howden's US associate Oscar L. Cartwright (1900–1983) (e.g., Howden and Cartwright, 1963). The influence of Francisco Pereira (1913–1991) in Brazil, Antonio Martínez (1922–1993) in Argentina, and Mario Zunino in Italy in forging their partner Halffter's Mexican school is also worthy of further investigation. The history of the Scarabaeinae Taxonomic Revolution can be itself a subject of fruitful research for those interested in the social dynamics of scientific progress.

Conclusion

While we should all celebrate the progress made in the past three decades, it is important to have clear in our minds that the Scarabaeinae Taxonomic Revolution has just started. It needs to expand to the most difficult groups still unworked in the New World, as well as to grow outwards and reach the faunas of the other parts of the globe, especially those of the Oriental and Ethiopian Regions. In these two latter regions, the hyperdiverse genus *Onthophagus*, with 2,257 species already described (only a small minority in the Americas), is, no doubt, the greatest challenge, and it must eventually be tackled. Closer to home, in the Americas, with the revision of *Ateuchus* nearing completion (though still unpublished; Cupello, 2022), *Dichotomius*, *Canthon*, *Deltochilum*, *Uroxys*, and *Canthidium* remain the most demanding challenges. As these revisions progress, new character systems should also be explored. Is it possible, for example, that, once the female genitalia has been more thoroughly scrutinized, its anatomy will prove to be as important for the systematics of dung beetles as the male endophallus has been since the pioneering works of Mario Zunino and Bert Kohlmann in the 1970s and 1980s? Preliminary results have given support to this idea (e.g., Zunino, 1971, 1972, 1975, 1976, 1978, 1979; Kohlmann, 1984; Zunino and Halffter, 1988a; Marchisio and Zunino, 2012; Cupello et al., 2020). The same may also be true for the mouthparts and wing venation (see, e.g., Philips et al., 2004a, b; Tarasov and Génier, 2015; Cupello et al., 2020; Palestrini et al., 2020). The study of immature stages, which experienced some progress in the latter half of the 20th century (e.g., Edmonds and Halffter, 1978), has, with a few exceptions (e.g., Hernández-Martínez and Martínez, 2003; Martínez and Lumaret, 2005; Sánchez et al., 2010), pretty much stagnated since then. Why can they not prove to be as taxonomically informative as the adults? And what about the molecular data? Will molecular phylogeographical analyses, for example, reveal more complex population dynamics in the scarabaeine species than our morphological studies have so far been capable of detecting? And the macrotaxonomy, will it be revolutionized or only fine-tuned when explicit phylogenetic methodologies, whether employed for molecular or morphological characters, are more widely adopted? Only time and effort will tell. But we are confident that, should funding continue to be available, the Scarabaeinae Revolution will keep producing fascinating discoveries about this so charismatic and ecologically relevant insect group, the dung beetles.

Author contributions

MC conceptualized the paper, reviewed the literature, compiled the data, prepared the figures and tables, and wrote and reviewed the text. FS conceptualized the paper, wrote an early version of the text, and reviewed its final version. FV-d-M conceptualized the paper, provided much of the literature reviewed by MC, and reviewed the text. All authors contributed to the article and approved the submitted version.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

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Appendix: Current macrotaxonomy of the New World Scarabaeinae

Tribal-level classification based on Cupello and Vaz-de-Mello (2013b), Philips (2016), and Tarasov and Dimitrov (2016). Tribal-level nomenclature based on Bouchard et al. (2011) and the updates by Bousquet (2016) and Bouchard and Bousquet (2020).

- **Ateuchini Perty, 1830 (21 gg., 181 spp.)**
  - **Ateuchina Perty, 1830 (3 gg., 113 spp.)**
    - *Aphengium* Harold, 1868 (4 spp.)
    - *Ateuchus* Weber, 1801 (102 spp.)
      - *Ateuchus* s. str. (100 spp.)
      - *Ateuchus* (*Lobidion*) Génier, 2010 (2 spp.)
    - *Deltorhinum* Harold, 1867 (7 spp.)
  - **Scatimina Vaz-de-Mello, 2008 (17 gg., 63 spp.)**
    - *Besourenga* Vaz-de-Mello, 2008 (4 spp.)
    - *Bradypodidium* Vaz-de-Mello, 2008 (3 spp.)
    - *Degallieridium* Vaz-de-Mello, 2008 (1 sp.)
    - *Eutrichillum* Martínez, 1969 (3 spp.)
    - *Feeridium* Vaz-de-Mello, 2008 (1 sp.)
    - *Genieridium* Vaz-de-Mello, 2008 (7 spp.)
    - *Leotrichillum* Vaz-de-Mello, 2008 (1 sp.)
    - *Martinezidium* Vaz-de-Mello, 2008 (4 spp.)
    - *Nunoidium* Vaz-de-Mello, 2008 (1 sp.)
    - *Onoreidium* Vaz-de-Mello, 2008 (4 spp.)
    - *Pedaridium* Harold, 1868 (1 sp.)
    - *Pereiraidium* Vaz-de-Mello, 2008 (1 sp.)
    - *Scatimus* Erichson, 1847 (13 spp.)
    - *Scatrichus* Génier and Kohlmann, 2003 (3 spp.)
    - *Silvinha* Vaz-de-Mello, 2008 (1 sp.)
    - *Trichillidium* Vaz-de-Mello, 2008 (4 spp.)
    - *Trichillum* Harold, 1868 (11 spp.)
  - ***incertae sedis* in Ateuchini (1 g., 5 spp.)**
    - *Agamopus* Bates, 1887 (5 spp.)
- **Coprini Leach, 1815 (1 g., 45 spp.)**
    - *Copris* Geoffroy, 1762 (45 spp.)
      - *Copris* s. str. (45 spp.)
- **Deltochilini Lacordaire, 1855 (20 gg., 457 spp.)**
    - *Anisocanthon* Martínez and Pereira, 1956 (4 spp.)
    - *Anomiopus* Westwood, 1842 (63 spp.)
    - *Atlantemolanum* González-Alvarado et al., 2019 (2 spp.)
    - *Boreocanthon* Halffter, 1958 (13 spp.)
    - *Canthon* Hoffmannsegg, 1817 (163 spp.)
      - *Canthon* s. str. (65 spp.)
      - *Canthon* (*Bajacanthon*) Halffter, 2022 (1 sp.)
      - *Canthon* (*Francmonrosia*) Pereira and Martínez, 1959 (6 spp.)
      - *Canthon* (*Glaphyrocanthon*) Martínez, 1948 (48 spp.)
      - *Canthon* (*Goniocanthon*) Pereira and Martínez, 1956 (3 spp.)
      - *Canthon* (*Nesocanthon*) Pereira and Martínez, 1956 (3 spp.)
      - *Canthon* (*Peltecanthon*) Pereira, 1953 (4 spp.)
      - *Canthon* (*Pseudepilissus*) Martínez, 1954 (14 spp.)
      - *Canthon* (*Trichocanthon*) Pereira and Martínez, 1959 (1 sp.)
      - *incertae sedis* in *Canthon* (18 spp.)
    - *Deltepilissus* Pereira, 1949 (2 spp.)
    - *Deltochilum* Eschscholtz, 1822 (114 spp.)
      - *Deltochilum* s. str. (7 spp.)
      - *Deltochilum* (*Aganhyboma*) Kolbe, 1893 (27 spp.)
      - *Deltochilum* (*Calhyboma*) Kolbe, 1893 (13 spp.)
      - *Deltochilum* (*Deltohyboma*) Lane, 1946 (50 spp.)
      - *Deltochilum* (*Euhyboma*) Paulian, 1938 (1 sp.)
      - *Deltochilum* (*Hybomidium*) Shipp, 1897 (13 spp.)
      - *Deltochilum* (*Parahyboma*) Paulian, 1938 (2 spp.)
      - *Deltochilum* (*Rubrohyboma*) Paulian, 1938 (1 sp.)
    - *Hansreia* Halffter and Martínez, 1977 (6 spp.)
    - *Holocanthon* Martínez and Pereira, 1956 (2 spp.)
    - *Malagoniella* Martínez, 1961 (9 spp.)
      - *Malagoniella* s. str. (4 spp.)
      - *Malagoniella* (*Megathopomima*) Martínez, 1961 (5 spp.)
    - *Megathopa* Eschscholtz, 1822 (2 spp.)
    - *Megathoposoma* Balthasar, 1939 (1 sp.)
    - *Melanocanthon* Halffter, 1958 (4 spp.)
    - *Pseudocanthon* Bates, 1887 (11 spp.)
    - *Scatonomus* Erichson, 1835 (11 spp.)
    - *Scybalocanthon* Martínez, 1948 (24 spp.)
    - *Scybalophagus* Martínez, 1953 (5 spp.)
    - *Sylvicanthon* Halffter and Martínez, 1977 (15 spp.)
    - *Tetraechma* Blanchard, 1841[1] (5 spp.)
    - *Xenocanthon* Martínez, 1952 (1 sp.)
- **Dichotomiini Pereira, 1954 (4 gg., 215 spp.)**
    - *Chalcocopris* Burmeister, 1846 (2 spp.)
    - *Dichotomius* Hope, 1838 (200 spp.)
      - *Dichotomius* s. str. (74 spp.)
      - *Dichotomius* (*Cephagonus*) Luederwaldt, 1929 (40 spp.)
      - *Dichotomius* (*Homocanthonides*) Luederwaldt, 1929 (1 sp.)
      - *Dichotomius* (*Selenocopris*) Burmeister, 1846 (85 spp.)
    - *Holocephalus* Hope, 1838 (6 spp.)

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[1] Nunes and Vaz-de-Mello (2022) stated that the publication date of *Tetraechma* and its type species *T. sanguineomaculata* was February 1842. This is incorrect. These names were made available in plate 10 of Brullé & Blanchard's insect volume of d'Orbigny's series *Voyage dans l'Amérique méridionale*. The entire series was issued into 90 livraisons between 1835 and 1847, 32 of which corresponding to Brullé & Blanchard's volume (Evenhuis, 1997; Bousquet, 2016). Plate 10, authored by Blanchard alone, is part of livraison 54, whose precise publication date is still unknown. However, the Société Géologique de France recorded in the proceedings of its session from 08 November 1841 the receipt of copies of livraisons 51 to 54 from the French ministry of education ("ministre de l'instruction publique") (Anonymous, 1842). Plate 10, therefore, and the new names contained in it, must have been published before that date, not in February 1842 as Nunes and Vaz-de-Mello asserted. Following Articles 21.3 and 21.5 of the ICZN (1999), 08 November 1841 must be adopted as the publication date of *Tetraechma* and *T. sanguineomaculata* until the actual date – or an earlier record – is retrieved.

- *Isocopris* Pereira and Martínez, 1960 (7 spp.)

Eucraniini Burmeister, 1873 (4 gg., 14 spp.)
- *Anomiopsoides* Blackwelder, 1944 (4 spp.)
- *Ennearabdus* Van Lansberge, 1874 (1 sp.)
- *Eucranium* Brullé, 1838 (6 spp.)
- *Glyphoderus* Westwood, 1838 (3 spp.)

Eurysternini Vulcano et al., 1961 (1 g., 53 spp.)
- *Eurysternus* Dalman, 1824 (53 spp.)

Oniticellini Kolbe, 1905 (4 gg., 8 spp.)
- **Attavicina Philips, 2016 (1 g., 1 sp.)**
  - *Attavicinus* Philips and Bell, 2008 (1 sp.)
- **Liatongina Philips, 2016 (1 g., 2 spp.)**
  - *Liatongus* Reitter, 1893 (2 spp.)
- **Oniticellina Kolbe, 1905 (2 gg., 5 spp.)**
  - *Anoplodrepanus* Simonis, 1981 (3 spp.)
  - *Euoniticellus* Janssens, 1953 (2 spp.)

Onitini Castelnau, 1840 (1 g., 1 sp.)
- *Onitis* Fabricius, 1798 (1 sp.)

Onthophagini Streubel, 1846 (3 gg., 229 spp.)
- *Digitonthophagus* Balthasar, 1959 (1 sp.)
- *Hamonthophagus* Roggero et al., 2016 (2 spp.)
- *Onthophagus* Latreille, 1802 (226 spp.)
  - *Onthophagus* s. str. (226 spp.)

Phanaeini Hope, 1838 (11 gg., 216 spp.)
- **Gromphadina Zunino, 1985 (2 gg., 8 spp.)**
  - *Gromphas* Brullé, 1838 (6 spp.)
  - *Oruscatus* Bates, 1870 (2 spp.)
- **Phanaeina Kolbe, 1838 (9 gg., 208 spp.)**
  - *Bolbites* Harold, 1868 (1 sp.)
  - *Coprophanaeus* d'Olsoufieff, 1924 (50 spp.)
    - *Coprophanaeus* s. str. (38 spp.)
    - *Coprophanaeus* (*Megaphanaeus*) d'Olsoufieff, 1924 (4 spp.)
    - *Coprophanaeus* (*Metallophanaeus*) d'Olsoufieff, 1924 (8 spp.)
  - *Dendropaemon* Perty, 1830 (41 spp.)
  - *Dendropaemon* s. str. (9 spp.)
    - *Dendropaemon* (*Coprophanaeoides*) Edmonds, 1972 (10 spp.)
    - *Dendropaemon* (*Crassipaemon*) Cupello and Génier, 2017 (4 spp.)
    - *Dendropaemon* (*Enicotarsus*) Castelnau, 1831 (1 sp.)
    - *Dendropaemon* (*Eurypodea*) Klages, 1906 (2 spp.)
    - *Dendropaemon* (*Glaphyropaemon*) Génier and Arnaud, 2016 (3 spp.)
    - *Dendropaemon* (*Nigropaemon*) Génier and Arnaud, 2016 (1 sp.)
    - *Dendropaemon* (*Paradendropaemon*) Edmonds, 1972 (2 spp.)
    - *Dendropaemon* (*Rutilopaemon*) Génier and Arnaud, 2016 (1 sp.)
    - *Dendropaemon* (*Streblopaemon*) Génier and Arnaud, 2016 (1 sp.)
    - *Dendropaemon* (*Sulcopaemon*) Génier and Arnaud, 2016 (6 spp.)
    - *Dendropaemon* (*Titthopaemon*) Génier and Arnaud, 2016 (1 sp.)
  - *Diabroctis* Gistel, 1857 (5 spp.)
  - *Homalotarsus* Janseens, 1932 (1 sp.)
  - *Megatharsis* Waterhouse, 1891 (1 sp.)
  - *Oxysternon* Castelnau, 1840 (11 sp.)
    - *Oxysternon* s. str. (8 spp.)
    - *Oxysternon* (*Mioxysternon*) Edmonds, 1972 (3 spp.)
  - *Phanaeus* MacLeay, 1819 (83 spp.)
    - *Phanaeus* s. str. (49 spp.)
    - *Phanaeus* (*Notiophanaeus*) Edmonds, 1994 (34 spp.)
  - *Sulcophanaeus* d'Olsoufieff, 1924 (15 spp.)

Sisyphini Mulsant, 1842 (1 g., 2 spp.)
- *Sisyphus* Latreille, 1807 (2 sp.)

***incertae sedis* in Scarabaeinae (19 gg., 443 spp.)**
- *Bdelyropsis* Vulcano et al., 1960 (3 spp.)
- *Bdelyrus* Harold, 1869 (27 spp.)
- *Canthidium* Erichson, 1847 (178 spp.)
  - *Canthidium* s. str. (80 spp.)
  - *Canthidium* (*Neocanthidium*) Martínez et al., 1964 (70 spp.)
  - *incertae sedis* in *Canthidium* (28 spp.)
- *Canthochilum* Chapin, 1934 (24 spp.)
- *Canthonella* Chapin, 1930 (17 spp.)
- *Canthonidia* Paulian, 1938 (1 sp.)
- *Canthotrypes* Paulian, 1939 (1 sp.)
- *Cryptocanthon* Balthasar, 1942 (43 spp.)
- *Eudinopus* Burmeister, 1840 (1 sp.)
- *Homocopris* Burmeister, 1846 (4 spp.)
- *Isacanthon* Pacheco and Vaz-de-Mello, 2019 (1 sp.)
- *Ontherus* Erichson, 1847 (60 spp.)
  - *Ontherus* s. str. (34 spp.)
  - *Ontherus* (*Caelontherus*) Génier, 1996 (24 spp.)
  - *Ontherus* (*Planontherus*) Génier, 1996 (2 spp.)
- *Paracanthon* Balthasar, 1938 (15 spp.)
- *Paracryptocanthon* Howden and Cook, 2002 (2 spp.)
- *Sinapisoma* Boucomont, 1928 (1 sp.)
- *Streblopus* Van Lansberge, 1874 (2 spp.)
- *Tesserodoniella* Vaz-de-Mello and Halffter, 2006 (2 spp.)
- *Uroxys* Westwood, 1842 (59 spp.)
- *Zonocopris* Arrow, 1932 (2 spp.)

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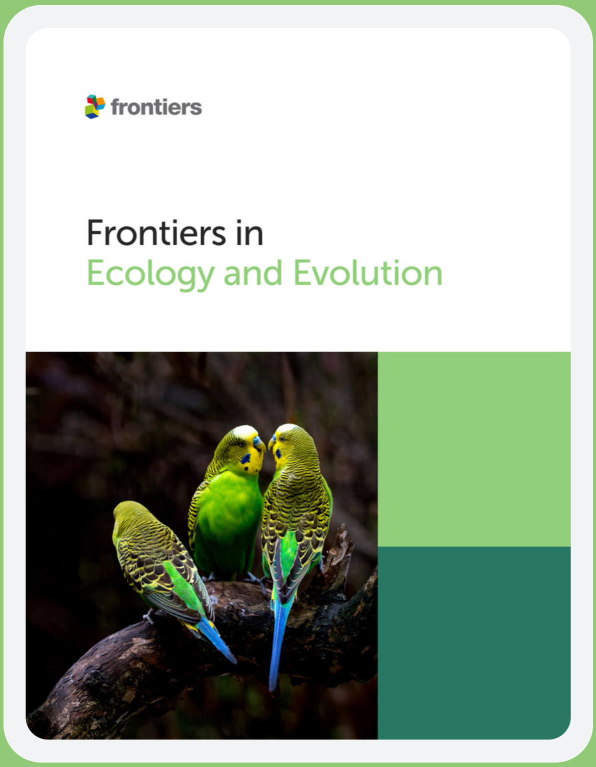

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