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Original Article

Patterns of beetle (Coleoptera) diversity in arid environments of Margarita Island, Venezuela

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ABSTRACT. Measuring biodiversity remains a fundamental yet challenging issue in conservation biology. Drylands, major components of terrestrial biomes, are particularly susceptible to desertification due to climate change and human activities. In Venezuela, the highly threatened arid ecosystems of Margarita Island harbor unique biodiversity, yet beetle diversity remains poorly known, despite the value of beetles as models to guide conservation actions. Most beetle diversity and ecological studies in arid and semiarid ecosystems worldwide focus on ground-dwelling beetles. Therefore, beetle diversity in the arid environments of Margarita Island was assessed using three methods: pitfall trapping, yellow pan traps, and beating. The diversity patterns recorded for each sampling technique were compared in a one-year survey from May 2012 to April 2013, including dry and rainy seasons. Asymptotic species richness estimation was used to assess beetle richness at the study site. Coverage-based rarefaction curves and generalized linear mixed models were employed to compare variations in richness, abundance, and Shannon-Wiener diversity between methods and seasons. Compositional differences in assemblages were also assessed using multivariate methods. Some 152 species were found, and asymptotic richness was 185 species. Previous work listed 21 species of Tenebrionidae. We recorded 16 tenebrionids, of which 6 are new for the island. *Eufallia seminivea* (Motschulsky, 1866) (Latridiidae), *Hyperaspis octomaculata* (González, 2024), and the genera *Zilus* (Mulsant, 1850), *Tiphysa* (Mulsant, 1850) (Coccinellidae), *Trichodesma* (LeConte, 1861) (Anobiidae), and *Neolitochrus* (Gimmel, 2013) (Phalacridae) are recorded for the first time in Venezuela. Yellow-pan traps and beating showed the highest estimations of species diversity, highlighting the important contribution of vegetation-dwelling beetles to arid ecosystem diversity despite inherent methodological constraints.

KEYWORDS: Biodiversity, Caribbean, Drylands, Ground-dwelling beetles, Vegetation-dwelling beetles

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INTRODUCTION

The threat of extinction posed by climate change and habitat transformation raises the urgency of assessing global biodiversity. For plants and vertebrates, this goal may be achieved by integrating accumulated knowledge from faunistic and floristic surveys, biogeography, and systematics (Colwell & Coddington 1994; Brummitt et al. 2021; Murali et al. 2021; Shao et al. 2021). For hyperdiverse groups, the current state of taxonomic and biogeographic knowledge represents a challenge and may not allow reliance on traditional approaches (Colwell & Coddington 1994; Haack et al. 2021; Meier et al. 2024). Therefore, the design of biodiversity inventories for such diverse groups requires not only the use of effective sampling but also estimation and extrapolation procedures (Colwell & Coddington 1994; Gerlach et al. 2014; Haack et al. 2021; Meier et al. 2024). In this context, the evaluation of the levels of

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richness and the distribution of diversity in different environments can help identify areas of richness and endemism and guide conservation actions (Ramírez-Hernández et al. 2018; Pizarro-Araya et al. 2023). Drylands cover more than 45% of Earth's terrestrial surface, making them a major component of global biomes (Marasco et al. 2023), and support nearly half of global food production (Shukla et al., 2019). Despite the common misperception that arid ecosystems are biodiversity-poor, they harbor remarkable diversity, including endemic species uniquely adapted to natural environmental fluctuations (Maestre et al. 2021). However, these ecosystems face escalating threats from climate change and anthropogenic activities, with increasing risk of changes in ecosystem functionality, including declining soil fertility, plant productivity, and biodiversity (Fajardo et al. 2013; Berdugo et al. 2020). In Venezuela, dryland ecosystems are highly threatened, with Margarita Island experiencing the most extensive habitat losses. Open-cast sand mining represents the primary driver of habitat degradation in these ecosystems (Fajardo et al. 2013).

The island of Margarita (10°59'13"N and 63°56'08"W), with an area of 952 km^2, is separated from South America by a channel approximately 25 km wide (Sanz et al. 2011). The island consists of two sectors: the larger eastern sector and the western Macanao peninsula, which are connected by an isthmus mainly composed of mangrove swamps (Sugden, 1986; Sanz et al. 2011). Thirty land cover types, nine different types of vegetation covers, and eleven land uses were described for the island by Sanz et al. (2011). The predominant and less fragmented vegetation covers are shrubland and xerophytic shrubland (Sanz et al. 2011; Proyecto MapBiomas Venezuela, 2024). Tropical dry forests are well-developed in seasonal riverbeds but cover small areas and show higher fragmentation levels compared with other types of vegetation (Sanz et al. 2011; Fajardo et al. 2013). Within the Caribbean, Margarita Island's biodiversity stands out as unique, which has been related to its closeness to the mainland, diverse topography, and island size (Sanz 2007; Briceño-Linares et al. 2011). The island is larger than the Lesser Antilles, which, along with the West Indian islands, are considered a biodiversity hotspot (Peck 2016). According to Peck (2016), these islands present 7,000 species of endemic plants and 779 species of endemic vertebrates. While a high level of endemism has been established for plants and terrestrial vertebrates, levels of endemism for most insect groups are poorly documented (Peck 2016). Information on beetles of the Lesser Antilles was reported by Peck (2016), indicating that 1572 species are limited to one or more of the Lesser Antilles islands. Margarita Island is part of South America and its continental shelf islands, which are supposed to have had land connections with the continent during the Pleistocene low sea levels and are considered a different biogeographic unit from the Lesser Antilles (Peck 2016). The most likely origin of Coleoptera in these regions may be South America (Peck 2016). The uniqueness of Margarita Island's biodiversity has been shown mainly by its vertebrates, but arthropods are poorly known. The available information on beetles was compiled during the second half of the last century, including Tenebrionidae of the Caribbean region and listing 21 species of this family (Marcuzzi 1954, 1959, 1977).

Coleoptera is the most successful and species-rich insect group, with around 380,000 species described (Zhang et al. 2018). Beetles exhibit extraordinary morphological and ecological diversity, occupying nearly every niche in terrestrial and freshwater ecosystems (Peck 2016; Zhang et al. 2018). They have ecological value as scavengers and recyclers of organic materials, wood borers, pollinators, plant feeders, and parasites. Therefore, they have been recognized as models to guide conservation actions (Gerlach et al. 2014; Peck 2016). However, most beetle diversity studies in arid and semiarid ecosystems worldwide have focused primarily on ground-dwelling species, potentially underestimating the contribution of vegetation-associated beetles to overall diversity (Doblas-Miranda et al. 2009; Liu et al. 2012; Liu et al. 2016; Pizarro-Araya et al. 2023).

To update the information on beetle diversity from Margarita Island, a survey was carried out in the Macanao Peninsula using three complementary sampling techniques to capture beetle diversity across different microhabitats, from ground-dwelling to vegetation-associated species. The peninsula is representative of the predominant shrublands of the island. Beetle diversity (richness and abundance) was examined using different statistical procedures. The diversity patterns recorded through each method were compared, including the effects of seasonality. We present an updated list of Coleoptera for the island.

MATERIAL AND METHODS

Study site. The study was carried out in the Macanao Peninsula (10°55'–11°11'N, 63°46'–64°24'W), Margarita Island, on the northeastern coast of Venezuela. This research forms part of a broader multidisciplinary project aimed at assessing the vulnerability of Macanao's dryland ecosystems to environmental degradation driven by extractive activities, particularly open-cast sand mining. The Peninsula has an area of 331 km^2. The average annual temperature is 27°C (range: 24°C to 31°C); mean annual rainfall is 522 mm (± 224 mm), with a major peak in August and a distinct dry season from January to June (Sanz & Ferraro-Rodríguez, 2006; Fajardo et al. 2013). The vegetation type corresponds to the predominant shrublands of the island. It is composed of a mixture of open cactus assemblages and thorn forests, with columnar cacti such as *Stenocereus griseus* and Fabaceae (*Prosopis juliflora*, *Caesalpinia coriaria*, and *Parkinsonia praecox*) as the dominant vegetation. A landcover map and images of the study site are presented in Figure 1.

Sampling. Monthly samplings from May 2012 to April 2013 were done in two sites located on opposite sides of the island (Comején sector 11°02'20" N, 64°13'34" W, Chacaracual sector 11°02'18" N, 64°13'36" W, Fig. 1). In each site, twelve plots of 10×10 m were placed randomly. Six plots were placed at the north side of the seasonal riverbeds, and the other six plots were placed at the south side. Beetles were collected using three sampling methods: beating (BT), pitfall traps (PTF), and yellow-pan traps (YPT). BT was performed by beating vegetation in five random points within the plots twice a day. Fallen insects on a piece of white fabric (1×1 m) below the vegetation were collected with tweezers and stored in the same vial with 70% alcohol. PFTs were 9 cm in diameter and 14 cm deep. They were one-third filled with ethylene glycol as a preservative and buried. Four traps were placed per plot under two types of microhabitats: two traps under cacti and two traps under other types of vegetation (non-cacti). Due to logistical issues, PFTs were placed only in the Comején sector. On the other hand, two YPTs were placed per plot; these consisted of yellow containers with a soap solution that were placed in vegetation branches. Both PFT and YPT were active for 24 hours, and the material collected from each trap was stored in separate vials with 70% alcohol. The sampling design afforded 288 beating samples (1 sample × 24 plots × 12 months), 576 PTF samples (4 samples × 12 plots × 12 months), and 576 YPT samples (2 samples × 24 plots × 12 months).

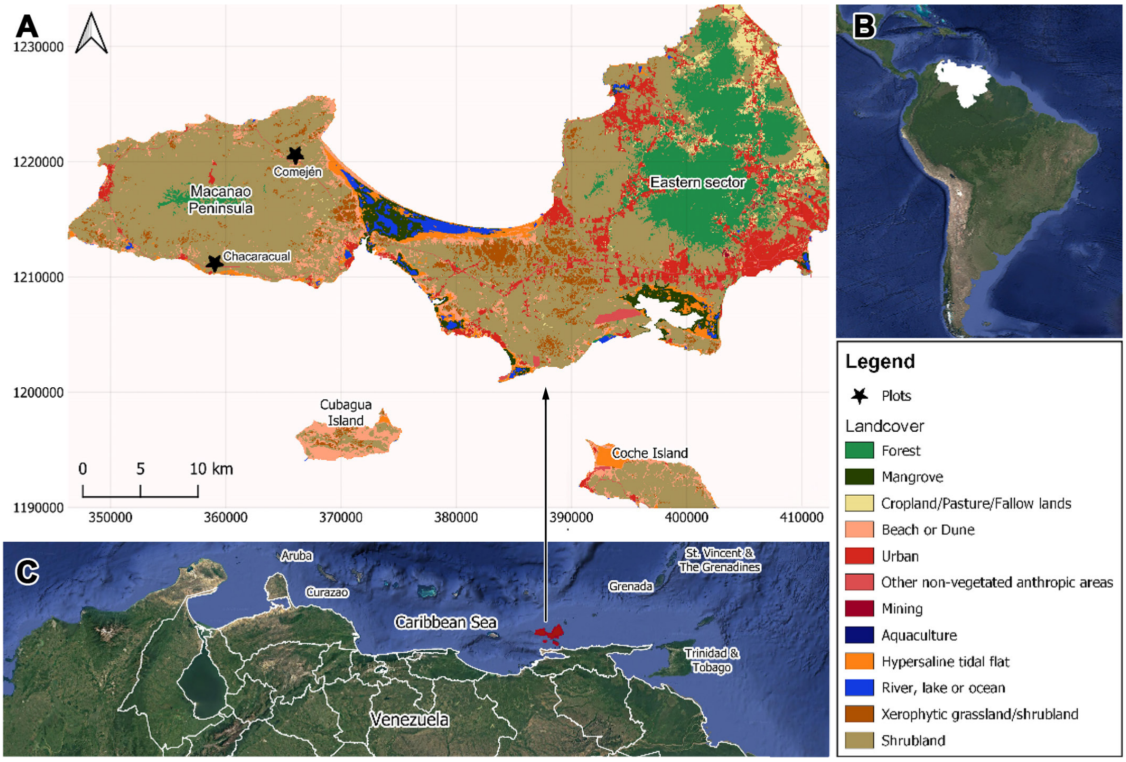

Figure 1. Map of the study site. **A.** Margarita Island landcover map (2013) with sampling plots locations (UTM coordinates) (Source: Proyecto MapBiomas Venezuela, 2024); **B.** Relative situation of Venezuela in South America. **C.** Relative situation of Margarita Island in the Caribbean Sea and Venezuela.

Taxonomic identification. All individuals were assigned to morphologically recognizable units (morphospecies, referred to as species for simplicity), which were used in diversity estimations. Some morphospecies were excluded from the dataset when morphological similarities prevented confident delimitation as single or multiple morphospecies. Additionally, all Scolytinae were excluded from analyses because it has been suggested that morphological convergence and polyphyly within this subfamily may complicate accurate species delimitation without molecular data (Pistone et al. 2018). Taxonomic determination of specimens was done to the lowest possible taxon name, based on available literature (e.g., Fisher 1925; Marcuzzi 1954, 1959, Werner 1970; Campbell 1971; Marcuzzi 1977; White 1971; Moldenke 1981; Háva 2004; Kingsolver 2004; Martínez 2005; González 2015; Vaz-de-Mello et al. 2011; Constantin 2013, 2017; Ivie & Hart 2016; Cortés-Hernández & Morrone 2019; Legalov 2018, 2020). Cerambycidae, Coccinellidae, Cleridae, and some Chrysomelidae were determined by specialists. Although the Museo del Instituto de Zoología Agrícola "Francisco Fernández Yepez", Universidad Central de Venezuela (MIZA - UCV) has the largest entomological collection in Venezuela, with more than three million specimens, there are no accessible records of Margarita Island. A reference collection of the island's recorded species is housed at the Laboratorio de Biología de Organismos (Instituto Venezolano de Investigaciones Científicas).

Data Analysis. Data analyses were carried out in R (R Team Core 2024). To estimate the number of species expected in the sampling area, asymptotic richness (Chao1) was computed in iNEXT package (Chao 1984; Chao et al. 2014; Hsieh et al. 2025) using a pooled data set with the three sampling methods. Sample coverage was also computed with the same R package. For comparisons of species richness and diversity (Shannon-Wiener) between sampling methods, coverage-based rarefaction curves with 95% confidence intervals based on 100 randomizations were generated. Extrapolations were done up to twice the reference sample sizes (Chao & Jost 2012). Following Chao & Jost (2012), sample coverages were computed, and comparisons were done at the lowest final sample coverage among the three assemblages. These analyses were also performed using iNEXT (Hsieh et al. 2025). The observed diversity was obtained by calculating the Shannon-Wiener diversity index per sample using the *vegan* package (Oksanen et al. 2019). Generalized linear mixed models (GLMMs) were used to compare abundance, observed richness, and diversity between sampling methods, including the season (dry and rainy) as a second factor to assess variations in diversity patterns due to season. Since PFT also accounted for the microhabitat variability, a separate analysis of this effect was done before comparing the patterns obtained by the three sampling methods. Data per plot were pooled. To account for the non-independence of data points due to the repeated sampling per site and date, random intercepts were added to the models. GLMMs were fitted using the *lme4* package (Bates et al. 2015). For models for which no overdispersion was detected, Poisson distributions of errors were used for abundance and species richness. In some cases, overdispersion was detected, and the negative binomial distribution was used instead. Normal distribution was used for Shannon-Wiener diversity. Significant differences were assessed by multiple *post hoc* comparisons through the *multcomp* package (Hothorn et al. 2008). For significant interaction method *x* season, user-defined *post hoc* comparisons were used, since we were interested in differences of the same methods between seasons and different methods within seasons.

To evaluate variations in assemblages recorded with each sampling technique and seasons, several procedures were carried out using the *vegan* package. First, a non-metric multidimensional scaling (NMDS) was performed based on species abundance added up per month (each observation represents a month). Multivariate differences in species assemblages were tested employing a two-way (method *x* season) Permutational Multivariate Analysis of Variance (PERMANOVA). Sampling methods complementarity (distinctness) was calculated using Marczewski-Steinhaus (M-S) distance (Colwell & Coddington 1994). M-S distance for pairwise calculations was given by the formula:

$$C_{MS} = \frac{a + b - 2j}{a + b - j}$$

Where for a pair A and B, $\boldsymbol{a}$ is the number of species in A, $\boldsymbol{b}$ is the number of species in B, and $\boldsymbol{j}$ is the number of species in common. Finally, range-abundance curves with log-transformed relative abundances were constructed for each sampling technique.

RESULTS

From a one-year survey, 3706 beetle individuals were collected. We recorded 152 (morpho) species in 31 families, of which 92 genera were determined, and 26 were named at the species level. The remaining species could not be determined beyond the family, subfamily, or tribe level. The most species-rich families were Curculionidae (26), Coccinellidae (18), Tenebrionidae (16), Chrysomelidae (15), and Cerambycidae (8). Twelve families have a richness between 3 and 6 species, while the remaining 14 families were represented by one or two species (Fig. 2). Chrysomelidae, Tenebrionidae, and Curculionidae represent about 82% of all individuals collected (Fig. 2). Five genera are added to the tenebrionid fauna of Margarita Island: *Paratenetus* (Spinola, 1844), *Strongylium* (Kirby, 1819), *Lobopoda* (Solier, 1835), *Lystronychus* (Latreille, 1829), and *Hymenorus* (Mulsant, 1852). *Paratenetus* was represented by two undetermined species, whereas each *Strongylium, Lobopoda, Lystronychus,* and *Hymenorus* was represented by one undetermined species. These increase the number of tenebrionid species on the island to 27. Regarding other families, *Eufallia seminivea* (Motschulsky, 1866) (Latridiidae), *Hyperaspis octomaculata* (González, 2024), and the genera *Zilus* (Mulsant, 1850), *Tiphysa* (Mulsant, 1850) (Coccinellidae), *Trichodesma* (LeConte, 1861) (Anobiidae), and *Neolitochrus* (Gimmel, 2013) (Phalacriidae) are recorded for the first time in Venezuela. A list of recorded beetles can be found in Appendix 1. Asymptotic richness estimation for the study site (the three methods pooled) converged in an estimated richness of 185 species (95% *CI*: 153, 218). The proportion of singletons was 26% (Table 1).

BT recorded the highest observed richness with 114 species, followed by YPT with 71 species, whereas PFT only recorded 36 species. The proportions of singletons were higher for PFT (58%), followed by YPT (44%), whereas BT showed the lowest value (37%) (Table 1). Of PFT singletons, 43% were ground-dwelling beetle species (scarabs, carabids, and curculionids), and the remaining 57% were vegetation-dwelling species (some coccinellids, curculionids, and tenebrionids), likely incidental in PFT. Most of the singletons found in BT samples (60%) were species exclusively recorded for this method and included some Coccinellidae, Curculionidae, Buprestidae, Chrysomelidae, Bostrichidae, and Anobiidae species. The remaining BT singletons were also found in YPT samples. Regarding YPT, most of the singletons in these samples were also recorded in BT samples (61%), while the remaining ones were also found in PFT (curculionids and chrysomelids associated with vegetation).

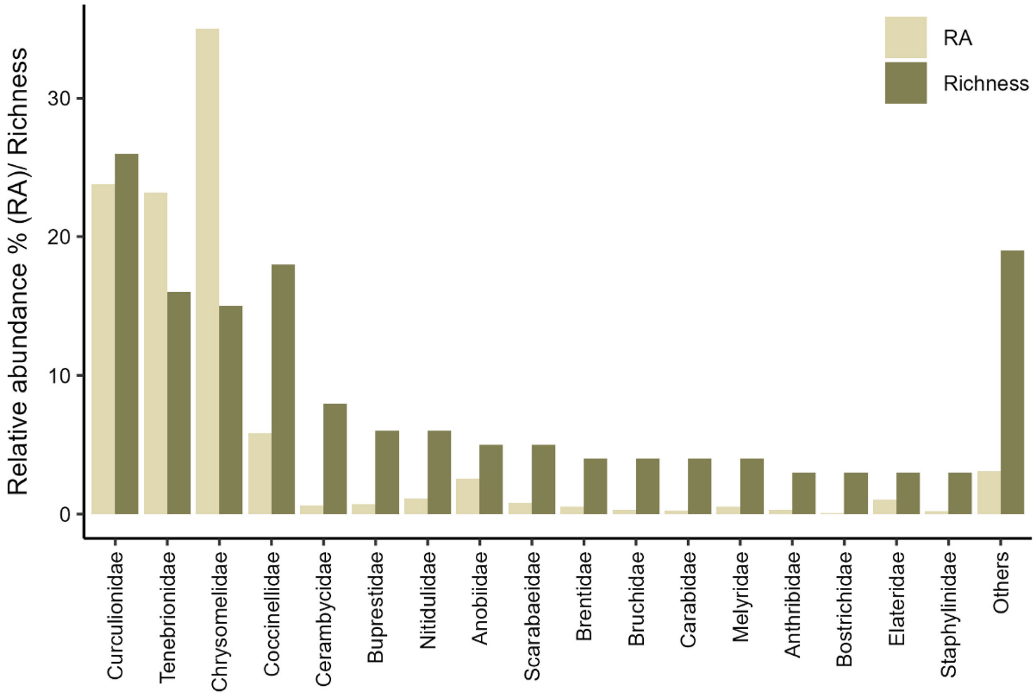

Figure 2. Species richness and relative abundance (RA) of the beetle families collected in the Macanao Peninsula, Margarita Island, Venezuela. The category "Others" includes 14 families represented by one or two species.

Regarding coverage-based comparisons, vegetation-dwelling beetles (BT and YPT) showed higher species richness than ground-dwelling beetles (PFT). Following Chao & Jost (2012), we standardized comparisons at the lowest sample coverage level that does not exceed twice the reference sample size of any assemblage. This yielded a base sample coverage of SC = 0.9558, at which YPT and PFT required extrapolation while BT remained within the interpolation range (Table 2). At this standardized coverage, YPT showed the highest richness, followed by BT and PFT. However, PFT exhibited substantial uncertainty in the extrapolated range, with confidence intervals overlapping zero at the lower bound. To provide a more conservative comparison based entirely on observed (interpolated) data, we also compared assemblages at SC = 0.9074, the lowest coverage among methods within their original sample sizes (Table 1, Fig. 3A). At this coverage level, YPT recorded 71 species, BT recorded 37 species, and PFT recorded 17 species. The 95% confidence intervals for PFT did not overlap with those of either vegetation-dwelling method at this coverage level or at any lower coverage values (Fig. 3A, Table 2), indicating statistically significant differences in species richness. Rarefied species diversity (Shannon-Wiener) was higher for vegetation-dwelling than for ground-dwelling beetles at both values of standardized coverage (Table 2, Fig. 3B). 95% CI did not overlap at any point below these coverage values (Fig. 3B).

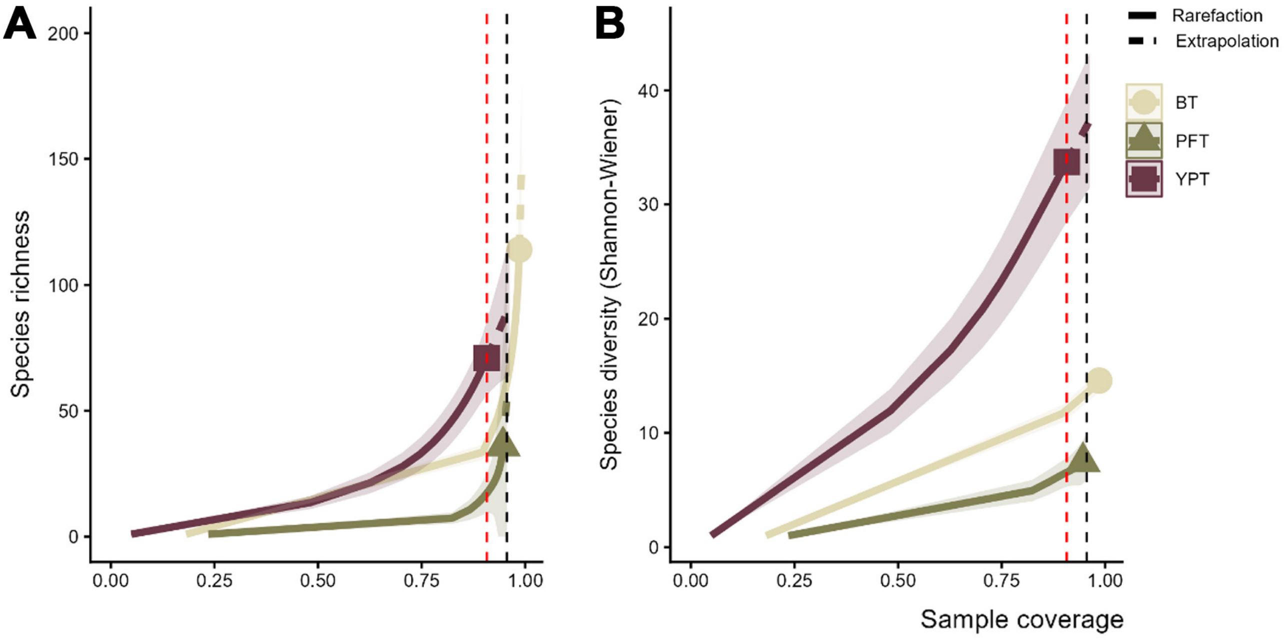

Figure 3. Coverage-based rarefaction curves for the three sampling methods with 95% CI (shaded areas represent 95% CI). **A.** Beetle species richness. **B.** Beetle diversity (Shannon-Wiener). Vertical dashed lines indicate the base coverages used for comparisons (red dashed line SC = 0.9074, black dashed line SC = 0.9558). BT: beating, YPT: yellow-pan traps, PFT: pitfall traps.

Table 1. Summary statistics of species assemblages, including number of individuals, observed richness, sample coverage (SC), and number of singleton species across three assemblages (BT, PFT, YPT) and the combined dataset (ALL).

Assemblage	Individuals	Obs. Rich	SC	Singletons
BT	2979	114	0.9859	42
PFT	393	36	0.9466	21
YPT	334	71	0.9074	31
ALL	3706	152	0.9892	40

Table 2. Comparison of species richness and diversity across assemblages at equal sample coverage. Comparisons are shown at two coverage levels: SC = 0.9074 (lowest coverage achieved within original sample sizes for all methods) and SC = 0.9558 (base coverage following Chao & Jost 2012, requiring extrapolation for YPT and PFT). R: rarefaction. E: extrapolation.

Assemblage	SC	Individuals	Method	Richness (95% CI)	Diversity (95% CI)
BT	0.9074	196	R	37 (33, 40)	5.39 (5.06, 5.72)
PFT	0.9074	103	R	17 (7, 27)	4.12 (3.57, 4.67)
YPT	0.9074	334	R	71 (57, 85)	33.70 (29.35, 38.05)
BT	0.9558	595	R	61 (56, 67)	13.50 (12.43, 14.58)
PFT	0.9558	783	E	55 (0, 127)	7.88 (6.23, 9.52)
YPT	0.9558	607	E	89 (70, 107)	36.87 (31.70, 42.04)

Microhabitats where pitfall traps were placed did not affect ground-dwelling beetles' diversity patterns (Fig. 4A–C). Models results indicated non-significant effects at the 5% level after controlling for random effects on observed richness (*microhabitat:* $\text{chisq}_{(1)}$ = 0.76, p = 0.38; *season*: $\text{chisq}_{(1)}$ = 3.39, p = 0.07; *microhabitat x season:* $\text{chisq}_{(1)}$ = 1.03, p = 0.31), abundance (*microhabitat:* $\text{chisq}_{(1)}$ = 1.59, p = 0.21; *season*: $\text{chisq}_{(1)}$ = 3.01, p = 0.08; *microhabitat x season:* $\text{chisq}_{(1)}$ = 2.20, p = 0.13) and Shannon-Wiener diversity (*microhabitat:* $\text{chisq}_{(1)}$ = 0.92, p = 0.33; *season*: $\text{chisq}_{(1)}$ = 3.04, p = 0.08; *microhabitat x season:* $\text{chisq}_{(1)}$ = 2.45, p = 0.12, Fig. 4C).

GLMMs results partially accord with rarefaction curves in Fig. 3. Statistically significant effects on beetle observed richness were found for the method ($\text{chisq}_{(2)}$ = 236.47, $p < 0.001$) and its interaction with the season ($\text{chisq}_{(2)}$ = 16.61, $p < 0.001$), but not for the season itself ($\text{chisq}_{(1)}$ = 0.22 p = 0.64). In contrast with the rarefied species richness, where YPT showed the highest values among methods, the BT method showed the highest observed richness in both seasons (*Dry*: $z_{\text{BT-PFT}}$ = 9.44, $p < 0.001$, $z_{\text{BT-YPT}}$ = 6.94, $p < 0.001$; *Rainy*: $z_{\text{BT-PFT}}$ = 11.35, $p < 0.001$, $z_{\text{BT-YPT}}$ = 7.33, $p < 0.001$; Fig. 4D), followed by YPT which caught a higher number of species than PFT during both seasons (*Dry*: $z_{\text{PFT-YPT}}$ = -3.32, p = 0.007, *Rainy*: $z_{\text{PFT-YPT}}$ = -6.83, $p < 0.001$, Fig. 4D). No differences were observed between seasons for BT and YPT ($BT_{dry\text{-}rainy}$: z = -0.61, p = 0.99, $YPT_{dry\text{-}rainy}$: z = -0.31, p = 0.99), but PFT caught more species during the dry season (z = 3.86, $p < 0.001$, Fig. 4D).

Beetle abundance showed a similar pattern to the one observed for richness (Fig. 4E). There were a statistically significant effect of method and the interaction with season (*method:* $\text{chisq}_{(2)}$ = 205.07, $p < 0.001$; *season*: $\text{chisq}_{(1)}$ = 2.83, $p < 0.09$; *method x season:* $\text{chisq}_{(2)}$ = 14.21, $p < 0.001$). Abundance recorded with the BT method was the highest in both seasons (*Dry*: $z_{\text{BT-PFT}}$ = 6.56, $p < 0.001$, $z_{\text{BT-YPT}}$ = 6.53, $p < 0.001$; *Rainy*: $z_{\text{BT-PFT}}$ = 11.89, $p < 0.001$, $z_{\text{BT-YPT}}$ = 7.70, $p < 0.001$), whereas PTF and YPT showed differences in abundance during the rainy season, but not during the dry season (*Dry*: $z_{\text{PFT-YPT}}$ = -1.11, p = 0.84, *Rainy*: $z_{\text{PFT-YPT}}$ = -5.56, $p < 0.001$). BT and YPT did not differ in beetle abundance between dry and rainy seasons ($BT_{dry\text{-}rainy}$: z = 0.35, $p > 0.99$, $YPT_{dry\text{-}rainy}$: z = 0.78, p = 0.96), while PFT caught more individuals during the dry season (z = 3.77, p = 0.001).

For the observed Shannon-Wiener diversity index, significant effects of method and its interaction with season were found *(method*: $\text{chisq}_{(2)}$ = 189.20, $p < 0.001$; *season*: $\text{chisq}_{(1)}$ = 0.13, p = 0.72; method × season: $\text{chisq}_{(2)}$ = 8.16, p = 0.02). Although rarefaction curves suggested that YPT may record the highest diversity, pairwise comparisons revealed a significantly higher observed diversity for BT in comparison to PFT and YPT during both seasons, (*Dry*: $z_{\text{BT-PFT}}$ = 8.09, $p < 0.001$, $z_{\text{BT-YPT}}$ = 3.87, $p < 0.001$; *Rainy*: $z_{\text{BT-PFT}}$ = 11.46, $p < 0.001$, $z_{\text{BT-YPT}}$ = 3.71, p = 0.002, Fig. 4F). YPT showed higher diversity than PFT during both seasons (*Dry*: $z_{\text{PFT-YPT}}$ = -4.26, $p < 0.001$, *Rainy*: $z_{\text{PFT-YPT}}$ = -7.79, $p < 0.001$, Fig. 4F). All the sampling methods showed non-significant differences in the recorded diversity between seasons ($BT_{dry\text{-}rainy}$: z = -0.70, p = 0.98, $YPT_{dry\text{-}rainy}$: z = -0.82, p = 0.95, $PFT_{dry\text{-}rainy}$: z = 2.29, p = 0.15).

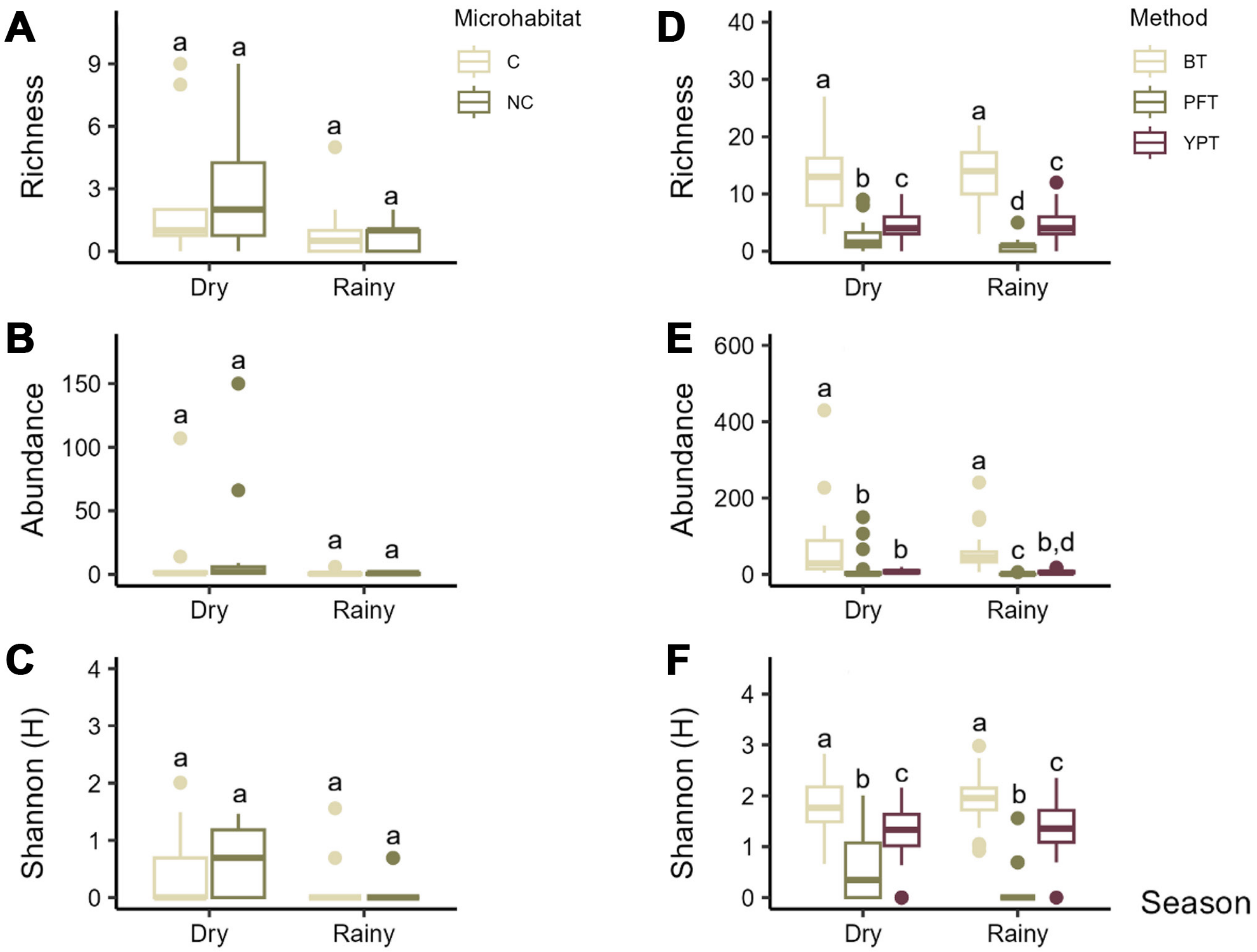

Figure 4. Boxplots. Plots on the left display comparisons for pitfall traps microhabitats, and seasons: **A.** Richness; **B.** Abundance; **C**. Shannon-Wiener diversity. Plots on the right display comparisons for sampling methods and seasons: **D.** Richness; **E.** Abundance; **F.** Shannon-Wiener diversity. Comparisons were done between different methods within seasons and the same methods between seasons. Legends for all left and right panels are presented at the top. Letters above boxplots indicate statistical significance for pairwise comparisons (different letters indicate statistically significant results), C: Cacti, NC: Non-cacti vegetation, BT: beating, YPT: yellow-pan traps, PFT: pitfall traps.

The BT method recorded the highest number of exclusive species (58), whereas PFT and YPT showed a lower number of exclusive species (18 and 12, respectively). Complementarity was 67% between BT and YPT, 97% between BT and PFT, and 92% between PFT and YPT. The ordination obtained by NMDS indicated compositional differences between methods but not between seasons (Fig. 5). Monthly samples belonging to each method showed clustering, with ground-dwelling assemblages (PFT samples) showing higher temporal variability than vegetation-dwelling assemblages (BT and YPT samples). The range-abundance curves (Fig. 6) show the assemblages of dominant species. Vegetation-dwelling assemblages recorded with BT were dominated by *Yingaresca ornata* (Jacoby, 1889) (Chrysomelidae), one species of *Pandeleteius* (Schoenherr, 1834) (Curculionidae), and *Epitragus aurulentus* (Kirsch, 1866) (Tenebrionidae). *Trichoton lapidicola* (Champion, 1885) (Tenebrionidae) was the dominant species in ground-dwelling assemblages; other Tenebrionidae and Curculionidae were also abundant, but the species were different from those in BT (Fig. 6). Abundances in YPT samples were low in general, and dominant species were also found in BT samples. Nonetheless, species such as *Achryson surinamun* (Linné, 1767) (Cerambycidae), one species of *Pachyschelus* (Solier, 1833), *Chrysobothris* (Eschscholtz, 1829) (Buprestidae), *Neolitochrus* (Phalacriidae), and *Cymatodera* (Gray, 1832) (Cleridae) were exclusively recorded with this method. In agreement with NMDS results, PERMANOVA found significant differences in assemblages between methods (*pseudo-F* = 7.09, $p < 0.001$), but not between seasons (*pseudo-F* = 1.24, $p = 0.20$) or the interaction (*pseudo-F* = 1.35, $p = 0.08$).

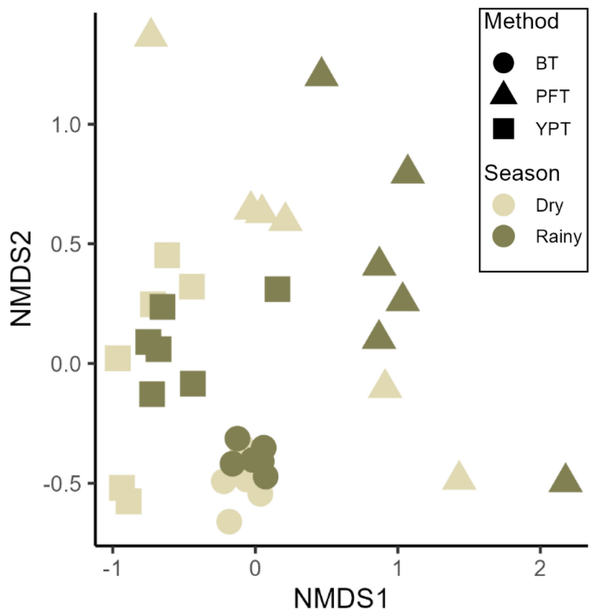

Figure 5. Scatter plot showing the ordination obtained from the NMDS (Stress = 0.15). BT: beating, YPT: yellow-pan traps, PFT: pitfall traps.

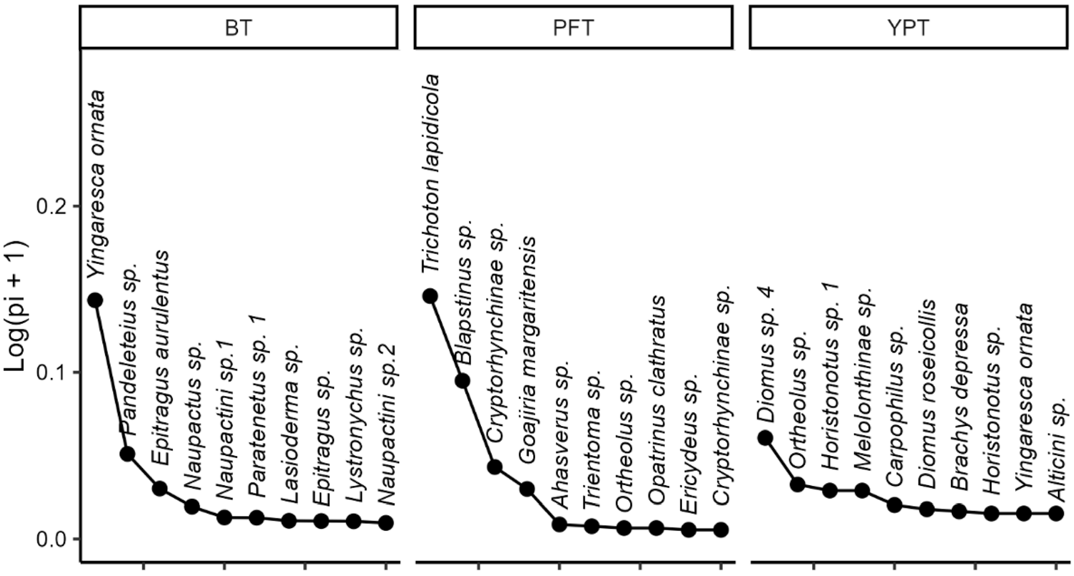

Figure 6. Range-abundance curves. The first 10 ranks are represented. The species presented for BT and PFT represent more than 80% of the total abundance recorded with these methods. The species presented for YPT represent 52% of the total abundance since this method showed many species with low abundances. BT: beating, YPT: yellow-pan traps, PFT: pitfall traps, pi: relative abundance.

DISCUSSION

A total of 152 beetle species were recorded in the study area, with the asymptotic richness estimation converging at 185 species. These estimations suggest that the arid environments of the Macanao Peninsula were under-represented in the number of species observed. The proportion of singletons found (26%) may indicate incomplete sampling (Kirmse 2024), though this pattern is common in highly diverse ecosystems and may reflect the presence of rare and transient species with low detection probabilities

(Haack et al. 2021; Kirmse 2024). The overall proportion of singletons in our study (26%) was lower than commonly reported for beetle assemblages in arid ecosystems, where ground-dwelling taxa have shown singleton proportions between 30% and 49% (Guthrie et al. 2010; Ahrens et al. 2016; Pizarro-Araya et al. 2023). This difference is attributable to our inclusion of vegetation-associated beetles, which showed lower singleton proportions than ground-dwelling assemblages. Ground-dwelling beetles showed the highest proportion of singletons (58%), though this may be inflated by incidental captures of vegetation-dwelling species in PFT (e.g., *Epitragus* sp., *Diomus* sp., *Longitarsus* sp.). Additionally, ground assemblages were highly dominated by two species, *Trichoton lapidicola* and *Blapstinus* sp., which together accounted for 64% of all collected individuals. Vegetation-dwelling assemblages exhibited different diversity patterns. When considered separately, BT (37% singletons) and YPT (44% singletons) appeared to have substantial singleton proportions. However, most singletons from YPT were shared with BT. Notably, YPT captured unique species such as *Pachyschelus* sp., *Mimocestes* sp., Cybocephalinae, and *Chrysobothris* sp. Considering the complete vegetation-dwelling assemblage (combining BT and YPT), the singleton proportion decreases to 28%, highlighting the need to employ multiple suitable sampling techniques to obtain comprehensive inventories in species-rich tropical ecosystems (Kirmse 2024). The incidence of singletons may also reflect ecological processes beyond sampling incompleteness. Aggregated distribution patterns are common in insect communities and can generate apparent rarity at local scales (Basset & Novotny, 1999). Rare species at one site may reflect source-sink dynamics or mass effects (Novotny & Basset, 2000). For instance, species rare on a particular host plant may be more abundant on alternative hosts or distributed across multiple host species at low densities, maintaining local populations through immigration from source populations on other plants (Novotny & Basset, 2000). Plant species richness in our sampling plots ranged from 7 to 14 species. Sampled plants included shrubs and small trees such as *Prosopis juliflora*, *Bastardia viscosa*, *Caesalpinia coriaria*, *Cordia curassavica*, *Guaiacum officinale*, *Lycium nodosum*, *Melochia tomentosa*, *Croton conduplicatus*, and *Gossypium hirsutum*. Variation of plant composition and individual plant size across plots could have created heterogeneous microhabitat conditions that likely contribute to patterns of beetle rarity and aggregation.

The three sampling methods captured distinct beetle assemblages, reflecting both their inherent biases and the ecological stratification of beetle communities. PFT, as expected, primarily captured ground-dwelling beetles, with tenebrionids dominating collections; *T. lapidicola*, *Blapstinus* sp., and *Goajiria margaritensis* (Marcuzzi, 1986) accounted for 70% of pitfall abundance. This dominance of Tenebrionidae aligns with patterns observed in arid ecosystems worldwide, where this family constitutes a major component of epigeal beetle assemblages (Pfeiffer & Bayannasan, 2012; Pizarro-Araya & Cepeda-Pizarro 2013; Niu et al. 2020). It has been noted that the importance of considering microhabitat-scale responses in sampling design for pitfall traps (Mehrabi et al. 2014). However, we did not find differences in beetle abundance, richness, and diversity recorded under cacti and non-cacti vegetation. The trapping liquid has also been pointed out as an important source of bias in dry conditions (Ruiz-Lupión et al. 2019), which may explain the higher richness and abundance we observed for ground-dwelling beetles during the dry season. Beating collected the highest number of species (75% of total observed richness), capturing primarily vegetation-associated taxa, including phyllophagous, xylophagous, anthophilous, and predatory species. Despite potential biases toward larger or less mobile insects (Ozanne 2005), this method successfully recorded minute coccinellids (*Scymnus*, *Diomus*) and weevils (*Sibinia*), as well as active, difficult to sample species such as Anthribidae (Valentine 2002). YPT showed lower performance in observed richness and abundance, but capturing some unique species absent from BT samples (e.g., *Pachyschelus* sp., *Chrysobothris* sp.). Despite the lower complementarity observed between BT and YPT (M-S distance), their unique captures and differences in assemblage patterns (NMDS results) demonstrate their value as complementary vegetation-sampling approaches.

Coverage-based rarefaction at standardized sample coverage (SC = 0.9074) suggested that vegetation-dwelling assemblages harbored a higher species richness than ground-dwelling assemblages (Table 2, Fig. 3A). The large confidence intervals for PFT at higher coverages reflect greater uncertainty in richness estimation, which is expected when assemblages contain many rare species with extremely small relative abundances that are difficult to detect (Chao et al. 2014; Colwell et al. 2012). This uncertainty is consistent with the highly uneven abundance distribution observed in the ground-dwelling assemblage, where two tenebrionid species accounted for 64% of all individuals. It has been pointed out that overlapped intervals do not guarantee non-significance (Colwell et al. 2012). For mega-diverse communities, a significant difference in richness across assemblages may not be detected statistically with rarefaction/extrapolation methods. Extrapolated richness estimates are subject to large uncertainties due to small sample sizes, leading to wide and overlapped confidence intervals, indicating that data may be inconclusive (Colwell et al. 2012; Chao et al. 2016).

In arid ecosystems, shrubs are recognized as primary drivers of spatial heterogeneity, creating patches with favorable microclimatic conditions and higher nutrient and water availability compared to bare soil (Doblas-Miranda et al. 2009; Niu et al. 2020; Pizarro-Araya et al. 2023). However, research has focused on how this vegetation structure affects ground-dwelling arthropod assemblages (Doblas-Miranda et al. 2009), while the diversity associated with vegetation itself has been ignored. Most beetle diversity studies in arid regions employ sampling methods designed to capture epigeal fauna or active fliers (Pizarro-Araya & Cepeda-Pizarro, 2013; Guedes et al. 2019; Pizarro-Araya et al. 2023). Our results suggest that an important component of dryland beetle diversity remains poorly documented in the existing literature. This is exemplified in the case of Tenebrionidae. We found that some species (*T. lapidicola*, *Blapstinus* sp., *G. margaritensis*) were captured exclusively in PFT, while others (*Epitragus aurulentus*, *Lystronychus* sp., *Paratenetus* sp.) were associated with vegetation samples. This indicates that both major ecological groups of Tenebrionidae, ground-dwelling and vegetation-dwelling, are well represented in the Macanao arid region. Other examples are *Sibinia* species, which can be monophagous or oligophagous and are strictly bound to vegetation with specific habitat demands, which also provides them with significant bioindicative value (Koštálová & Szénási 2015). It is worth noting that 22 genera recorded in this study, as well as *Achryson surinamun and Amphicerus cornutus* (Pallas, 1772), have been previously collected on *Prosopis* species (Ward, 1977; see Appendix 1), highlighting the importance of particular plant species for beetle assemblages in this arid environment. The observed richness in Macanao is considerably lower than that of other South American continental shelf islands with similar areas. For instance, Peck et al. (2002) recorded 672 beetle species in 69 families for Tobago Island (~300 km²), with only 22 genera and one species shared with our study. This difference is likely due to our small sampling area and the more extensive forest cover in Tobago (nearly 60% of total area), including evergreen forests and one of the best-preserved tropical dry forest ecosystems in the eastern Caribbean and northern South America (Baban et al. 2009; Boodram & Oatham, 2013). Similarly, richness in the Lesser Antilles exceeds our findings; for Saint Vincent Island (342 km²), 536 beetle species in 62 families were recorded (Peck, 2010). Macanao shares 61 genera and 8 species with the Lesser Antillean islands, where approximately 50% of beetle species show wide distributions across the Antilles and Neotropics (Peck, 2009, 2010, 2016).

Despite lower overall richness, some beetle diversity patterns found in Macanao align with patterns observed in continental South American drylands. Curculionidae, Chrysomelidae, Tenebrionidae, and Coccinellidae were the most species-rich and abundant families, consistent with findings from other South American arid and semiarid ecosystems (Guedes et al. 2019; Pizarro-Araya et al. 2023). These families are also among the most diverse in the Lesser Antilles (Peck 2016). The lower richness in Macanao likely reflects the limited sampling area, ongoing habitat degradation from mining activities, and methodological limitations of our study, highlighting the conservation importance and the need for continued inventory efforts in this dryland ecosystem. Among the methodological limitations, the use of morphospecies may have led to underestimation of true species richness, as morphospecies approaches often miss cryptic diversity as revealed by molecular methods (Hendrich et al. 2010; Pistone et al. 2018; Zhou et al. 2019, Ren & Zhang, 2024). However, morphospecies sorting by non-specialists can yield diversity estimates comparable to those produced by taxonomic experts, and some research suggests that the monitoring and assessment of insect diversity may be achieved by the careful use of morphospecies (Oliver & Beattie 1996; Derraik et al. 2002; Obrist & Duelli, 2010; Hackman et al. 2017; Kirmse 2024). In our study, morphospecies classification was performed by researchers with formal training in beetle morphology and taxonomy. Furthermore, some problematic groups were excluded. Another main limitation was the absence of light traps in our sampling design, causing an inadequate sampling of nocturnal beetle species, potentially missing an important component of the beetle diversity. The limited spatial extent of our sampling area further constrains the extrapolation of our findings to the entire peninsula. Despite these limitations, our study provides the most comprehensive assessment of beetle diversity in Margarita Island drylands to date and establishes a valuable baseline for future monitoring and conservation efforts.

The lower beetle richness compared to other Caribbean islands with better preserved habitats, combined with the ongoing threat from open-cast mining, highlights the vulnerability of the Macanao dryland ecosystem. The contribution of vegetation-dwelling beetles to overall diversity highlights that conservation strategies must target not only the requirements of ground-dwelling beetles but also the vegetation structure that supports diverse vegetation-dwelling beetle assemblages. It is worth noting that, for Venezuela, there are not many sources available for identifying beetle species for many groups. In some cases, literature from the Antilles, the United States, Mexico, and Colombia was used with caution, supplemented with descriptions to corroborate the determination. Although in most cases species identification was not possible, listing higher taxa still represents valuable baseline data for this poorly explored region. Such inventories are essential for monitoring biodiversity change. Future studies incorporating nocturnal sampling and replication across a larger area would further refine our understanding of beetle diversity patterns and their responses to environmental change in this insular arid ecosystem.

AUTHOR'S CONTRIBUTION

The authors confirm their contribution to the paper as follows: Virginia Sanz; conceptualization, investigation, methodology, funding acquisition, supervision, drafting & editing; Génesis Yánes; investigation, Writing, reviewing & editing; Wilber Bernay: investigation, Writing, reviewing & editing; Abimel Moreno: formal analysis and visualization, drafting, revising and correspondence. The authors read and approved the final version of the manuscript.

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AVAILABILITY OF DATA AND MATERIAL

The specimens listed in this study are deposited in Laboratorio de Biología de Organismos, Instituto Venezolano de Investigaciones Científicas, Venezuela, and are available from the curator upon request. Raw data are also available from the authors.

ETHICS APPROVAL AND CONSENT TO PARTICIPATE

This study only included arthropod material, and all required ethical guidelines for the treatment and use of animals were strictly adhered to in accordance with international, national, and institutional regulations. No human participants were involved in any studies conducted by the authors for this article.

CONSENT FOR PUBLICATION

Not applicable.

CONFLICT OF INTERESTS

The authors declare that there is no conflict of interest regarding the publication of this paper.

GENERATIVE AI STATEMENT

No generative AI tools were used in the preparation of this paper.

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الگوهای تنوع زیستی سخت‌بالپوشان (Coleoptera) در محیط‌های خشک جزیره مارگاریتا، ونزوئلا

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چکیـده: سنجش تنوع زیستی همچنان یک موضوع اساسی و چالش‌برانگیز در زیست‌شناسی حفاظتی است. مناطق خشک، اجزای اصلی بیوم‌های سرزمینی، به ویژه به دلیل تغییرات اقلیمی و فعالیت‌های انسانی به بیابان‌زایی حساس هستند. در ونزوئلا، اکوسیستم‌های خشک بسیار تهدیدشده جزیره مارگاریتا، تنوع زیستی منحصر به فردی را در خود جای داده‌اند. با این حال، تنوع سخت‌بالپوشان، با وجود جایگاه مهم شان به عنوان مدل‌های اقدامات حفاظتی، هنوز به خوبی شناخته نشده است. بیشتر مطالعات تنوع و بوم‌شناسی سخت‌بالپوشان در اکوسیستم‌های خشک و نیمه‌خشک در سطح جهانی بر سوسک‌های زمین‌زی تمرکز دارند. بنابراین، تنوع سخت‌بالپوشان در محیط‌های خشک جزیره مارگاریتا با استفاده از سه روش تله‌های گودالی، تله‌های زرد و ضربه زدن ارزیابی شد. الگوهای تنوع ثبت شده برای هر تکنیک نمونه‌برداری در یک بررسی یک ساله از اردیبهشت ۱۳۹۱ تا فروردین ۱۳۹۲ شامل فصل‌های خشک و بارانی مقایسه شد. تخمین غنای گونه‌ای ناهمگن برای ارزیابی غنای سخت‌بالپوشان در منطقهٔ مطالعاتی استفاده شد. منحنی‌های نادرسازی مبتنی بر پوشش و مدل‌های مختلط خطی عمومی برای مقایسه تغییرات در غنا، فراوانی و تنوع شانون–وینر بین روش‌ها و فصل‌ها به کار گرفته شدند. تفاوت‌های ترکیبی در مجموعه‌ها نیز با استفاده از روش‌های چندمتغیره ارزیابی شد. حدود ۱۵۲ گونه یافت شد و غنای ناهمگن ۱۸۵ گونه بود. در مطالعات قبلی تعداد ۲۱ گونه از سوسک‌های زمین‌زی Tenebrionidae فهرست شده بودند. ما ۱۶ گونه از این سوسک‌ها را ثبت کردیم که در بین آنها ۶ گونه برای جزیره جدید هستند. دو گونهٔ *Eufallia seminivea* (Motschulsky, 1866) (Latridiidae) و *Hyperaspis octomaculata* (González, 2024) و جنس‌های *Zilus* (Mulsant, 1850)، *Tiphysa* (Mulsant, 1850) (Coccinellidae)، *Trichodesma* (LeConte, 1861) (Anobiidae) و *Neolitochrus* (Gimmel, 2013) (Phalacridae) برای اولین بار در ونزوئلا ثبت شدند. تله‌های زرد و روش ضربه زدن، علی‌رغم محدودیت‌های ذاتی روش‌شناختی نشان‌دهندهٔ بالاترین تخمین‌های تنوع گونه‌ای و سهم بالای سوسک‌های گیاه‌زی را در تنوع اکوسیستم‌های خشک هستند.

واژگـان کلیدی: تنوع زیستی، کارائیب، مناطق خشک، سوسک‌های زمین‌زی، سوسک‌های گیاه‌زی