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Species richness and ecogeographic patterns of Scarabaeinae (Coleoptera: Scarabaeidae) in Jalisco, Mexico

BENJAMÍN HERNÁNDEZ^{1,4*}, DIANA MARÍA RIVERA-RODRÍGUEZ^{1,5}, CUAUHTEMOC DELOYA^{2,6}, MIGUEL VÁSQUEZ-BOLAÑOS^{3,7} & JOSÉ LUIS NAVERRETE-HEREDIA^{3,8}

¹*Departamento de Ciencias Básicas, Instituto Tecnológico de Tlajomulco, Tecnológico Nacional de México. Carretera Tlajomulco–San Miguel Cuyutlán Km. 10, C.P. 45640, Tlajomulco de Zúñiga, Jalisco, México*

²*Red de Interacciones Multitróficas, Instituto de Ecología, A. C., Carretera antigua a Coatepec 351, El Haya, Xalapa, 91073 Veracruz, México*

³*Centro de Estudios en Zoología, Centro Universitario de Ciencias Biológicas y Agropecuarias, Universidad de Guadalajara. Apdo. Postal 134, 45100 Zapopan, Jalisco, México*

⁴✉ bhm.hdez@gmail.com; <https://orcid.org/0000-0003-0283-1206>

⁵✉ dinaris@hotmail.com; <https://orcid.org/0000-0002-3638-8401>

⁶✉ aristeodel@gmail.com; <https://orcid.org/0000-0002-4774-140X>

⁷✉ miguel.vasquez@academicos.udg.mx; <https://orcid.org/0000-0002-6494-5199>

⁸✉ glenusmx@gmail.com; <https://orcid.org/0000-0002-3336-8528>

*Corresponding author

Abstract

We analyzed species richness and ecogeographic patterns of Scarabaeinae (Coleoptera: Scarabaeidae) in Jalisco, Mexico. Occurrence data were compiled from digital databases, literature, and entomological collections, yielding 6,042 records for 86 species. A current richness model was generated using 100 km² grid cells, and species distribution models were constructed using MaxEnt to estimate potential richness. We also performed a principal component analysis based on 23 climatic variables to identify climatic affinity groups. Our results show that the areas with the highest current and potential richness are located in the Sierra Madre del Sur and the Pacific Coast provinces. We identified four main climatic groups that correspond to biogeographic provinces. These findings provide a comprehensive overview of Scarabaeinae diversity in Jalisco and highlight both sampling gaps and priority areas for future studies. The classification of species based on climatic affinities reveals a richness gradient and suggests distinct assemblage structures driven by environmental conditions.

Key words: Species distribution, climatic affinity, biogeographic provinces

Introduction

Mexico is located between tropical and subtropical latitudes in North America and presents an outstanding orographic complexity due to its mountain ranges, diverse climates, and vegetation types. These have resulted in a high richness and number of endemic species (Halffter 1987; Mastretta-Yanes *et al.* 2015; Morrone 2020). Recent studies emphasize the need to rethink how such environmental heterogeneity shapes species distribution and richness gradients and informs conservation strategies (Pessôa *et al.* 2021; Villalobos *et al.* 2022; Ojeda *et al.* 2021; Moctezuma *et al.* 2024a).

The Mexican territory comprises distinct physiographic regions, terrestrial ecoregions, and biogeographic provinces (Rodríguez 2017). One of the most influential frameworks is Halffter's (1984) Mexican Transition Zone (MTZ), which has been conceptualized as an area for dynamic contact and overlap between the Neotropical and Nearctic biotas. This zone is now recognized as a natural biogeographic laboratory that facilitates the study of biotic assembly and diversification processes (Morrone 2020). Recent multi-taxon analyses have confirmed that the MTZ hosts complex biogeographic transitions and species turnover zones, underscoring its importance for biodiversity conservation in Mesoamerica (Moctezuma *et al.* 2018; Escalante *et al.* 2021; Díaz-García *et al.* 2025). Recent phylogenetic frameworks support the role that the MTZ has performed as a diversification center (Lizardo *et al.* 2024; Moctezuma *et al.* 2024b).

Mountain formation during the Late Cretaceous and the rise of the Trans-Mexican Volcanic Belt have divided the country into major physiographic and climatic zones, creating a complex mosaic of habitats that shaped the evolutionary and ecological history of many taxa (Halffter 1987; Mastretta-Yanes *et al.* 2015; Moctezuma *et al.* 2024b). Transitional areas within the MTZ are defined by environmental gradients and overlapping biotas, making them essential for understanding patterns of species richness and turnover (Moctezuma *et al.* 2018; Morrone 2020; Lizardo *et al.* 2022). Recent studies highlight the role of environmental filters in structuring dung beetle communities across elevational and precipitation gradients (Soberón & Peterson 2020; Cultid-Medina & Escobar 2020; Moctezuma *et al.* 2021; Lizardo *et al.* 2024a; Lizardo *et al.* 2024b).

In this context, ecogeographic analyses are powerful tools to identify richness patterns and interpret the influence of environmental variables on species distributions. Such analyses, grounded in ecological niche theory and species distribution modeling, help clarify richness-environment relationships (Peterson *et al.* 2018, Soberón & Peterson 2020; Lizardo *et al.* 2022; Lizardo *et al.* 2024a; Lizardo *et al.* 2024b). In regions with limited sampling or taxonomic resolution, like much of Mexico, these tools also contribute to reducing the Wallacean shortfall for insect taxa such as Scarabaeinae (Lizardo *et al.* 2022; Moctezuma 2021; Moctezuma *et al.* 2024c).

Scarabaeinae dung beetles have been used as indicators of habitat quality due to their sensitivity to disturbance and their role in nutrient cycling and secondary seed dispersal (Halffter & Matthews 1966, Favila & Halffter 1997, Spector 2006; Griffiths *et al.* 2015; Noriega *et al.* 2018; Rivera & Favila 2022; Noriega *et al.* 2023). Meta-analyses show that dung beetle richness and composition respond strongly to forest fragmentation, land-use change, and cattle grazing pressures in the Neotropics (Nichols *et al.* 2019, Cultid-Medina & Escobar 2020). However, beyond local disturbance, understanding how these species are distributed along broad climatic gradients (particularly in a region where several biogeographical provinces converge) is crucial to identifying the specific environmental drivers of their spatial patterns. Their geographic patterns in mountainous landscapes such as Mexico's sky islands provide critical insights into conservation planning (Moctezuma *et al.* 2018; Moctezuma *et al.* 2024c).

Despite being one of the regions with the highest recorded species richness in Mexico, the specific ecogeographic patterns of the Scarabaeinae fauna remain largely unexplored. Although national checklists exist, regional-scale analyses remain essential to fill information gaps and identify biodiversity hotspots. For example, in the state of Jalisco, a previously published checklist (Navarrete-Heredia *et al.* 2001) has recently been expanded through database compilation, literature review, and taxonomic verification. Jalisco lies at the confluence of three mountain systems such as: Sierra Madre Occidental, Sierra Madre del Sur, and the Trans-Mexican Volcanic Belt and includes parts of the Pacific Coast, the Balsas Basin, and the Mexican High Plateau (Morrone 2017). This makes it a representative case within the MTZ to study richness patterns and climatic affiliations of Scarabaeinae beetles.

Moreover, in the past decade, taxonomic knowledge has increased significantly with the description of several new species. These new species have been identified within the genera *Onthophagus* (Moctezuma & Halffter 2020a; Moctezuma & Halffter 2020b; Moctezuma & Halffter 2021; Moctezuma *et al.* 2021; Moctezuma *et al.* 2023a; Moctezuma *et al.* 2023b), *Phanaeus* (Moctezuma *et al.* 2017; Halffter *et al.* 2022), and *Canthon* (Halffter *et al.* 2015; Rivera-Gasperín *et al.* 2025), leading to a substantial increase in our understanding of Scarabaeinae biodiversity in western Mexico. This progress contrasts sharply with the knowledge available prior to 2015 and has opened the door to further discoveries in other genera. Consequently, the objective of this study was to analyze the species richness of Scarabaeinae in Jalisco through an ecogeographic perspective. Specifically, we aimed to 1) identify areas of high species richness, 2) evaluate the climatic factors driving distribution, and 3) classify species based on their climatic affinity to assess their relationship with the biogeographic provinces of the MTZ.

Material and methods

Study Area. The state of Jalisco is located in western Mexico, between 18°48'N and 22°48'N latitude and 105°42'W and 101°24'W longitude, covering an area of 78,588 km² (INEGI 2023). The dominant vegetation types include tropical deciduous forest, pine-oak forest, and xerophytic shrubland (Rzedowski 2006). Approximately 70% of the state experiences a warm subhumid climate, with rainfall concentrated in the summer and an average annual precipitation of 850 mm. Elevation ranges from sea level to 4,260 m above sea level (García 2004).

A key feature of the state is that it lies at the convergence of six biogeographic provinces. Three belong to the Mexican Transition Zone (*sensu* Morrone *et al.* 2017): the Sierra Madre del Sur, Sierra Madre Occidental, and the Trans-Mexican Volcanic Belt. Two belong to the Neotropical region (the Pacific Coast and Balsas Basin), and one belongs to the Nearctic region (the Mexican High Plateau) (Arriaga *et al.* 1997; Morrone *et al.* 2017) (Fig. 1).

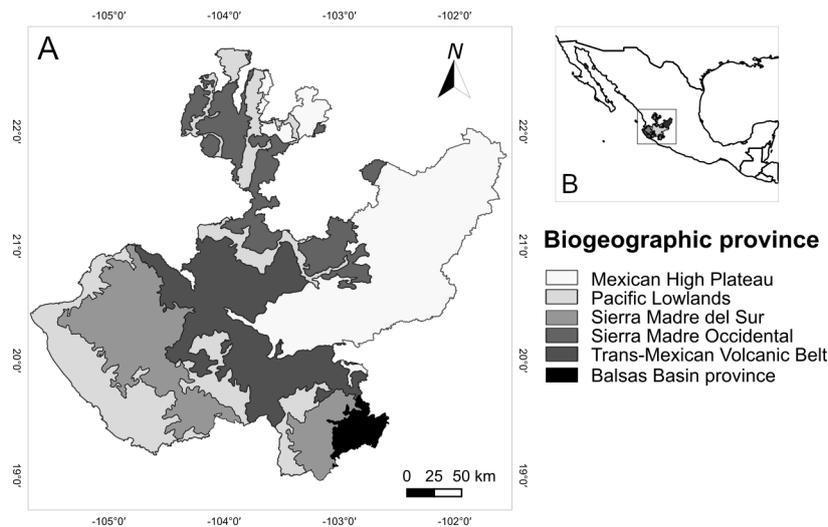


Figure 1. Study area: The divisions indicate the biogeographic provinces of Jalisco sensu Morrone, 2017.

Occurrence data. Occurrence data for Scarabaeinae species were obtained from the digital databases of the Sistema Nacional de Información sobre Biodiversidad of the Comisión Nacional para el Conocimiento y Uso de la Biodiversidad (SNIB-CONABIO 2015) and the Global Biodiversity Information Facility (GBIF.org 2015). Additionally, we consulted specimens housed in the Colección de Entomología del Centro de Estudios en Zoología, Universidad de Guadalajara (CZUG), which contains the largest number of records for the state. A thorough literature review (Matthews & Halffter 1968; Zunino & Halffter 1988; Génier 1996; Howden & Génier 2004; Navarrete-Heredia & Cortés-Aguilar 2004; Kohlmann & Solís 2006; Delgado & Kohlmann 2007; González-Hernández *et al.* 2015; Halffter *et al.* 2015; Moctezuma & Halffter 2020a; Moctezuma & Halffter 2021; Halffter *et al.* 2022; Rivera-Gasperín *et al.* 2025) was also conducted up to September 2025. For records derived from literature sources with detailed locality information but lacking coordinates, we georeferenced the localities using Google Earth. We also standardized locality names and verified and corrected coordinates using Geographic Information Systems (QGIS 2023).

Taxonomic identity was verified based on current literature. Records involving synonymies or doubtful occurrences (based on natural history or distribution inconsistencies) were excluded from analysis but preserved in a secondary database for future verification.

Climatic variables. Because the political boundaries of Jalisco are irregular, we defined a rectangular area based on minimum and maximum coordinates (18°48'N to 22°48'N, 105°42'W to 101°24'W) to improve modeling accuracy. This area was used to clip all climatic and altitudinal raster layers. We used 19 bioclimatic and elevation variables from WorldClim (Hijmans *et al.* 2005), and data from the Environmental Information System from Instituto Nacional de Investigaciones Forestales, Agrícolas y Pecuarias, which contains climatological information for Mexico and Central America from 1961 to 2010 (Ruíz *et al.* 2018). Monthly raster layers of potential evapotranspiration and relative humidity were processed to calculate annual averages.

We also calculated the annual aridity index, defined as the ratio between annual precipitation (bio1) and evapotranspiration, to represent water stress at the surface and atmospheric levels (Ruíz *et al.* 2018). All rasters were processed at a 30 arc-second resolution using map algebra in the raster package (Hijmans 2020) within R (R Core Team 2023).

Current and potential richness models. To build the current richness model, the Jalisco state shapefile was divided into 100 km² grid cells. Each occurrence point was assigned to the centroid of its nearest grid cell using the nearest-neighbor method. The number of species per cell was then calculated and mapped using QGIS (QGIS 2023). For the potential richness model, we modeled the potential distribution of each species using the MaxEnt algorithm (version 3.4.1; Phillips *et al.* 2006). MaxEnt is widely recognized for its robustness in handling small datasets and complex variable interactions (Wisz *et al.* 2008). It estimates habitat suitability based on relationships between occurrence points and environmental variables. Species records were randomly split into 50% training and 50% testing datasets with 10 replications to validate model accuracy using Area Under the Curve (AUC) values. Binary presence-absence maps were generated using a 10th percentile training threshold to minimize omission rates. Final richness was estimated by summing binary maps for each species using map algebra in the raster packages (Hijmans 2020) within R (R Core Team 2023).

Species with too few records to allow model calibration were included only as presence points in the final potential richness map.

Ecogeographic Analysis. From each occurrence point, we extracted values from all climatic and elevation raster layers. Then, we calculated species-specific averages for each variable. To identify patterns of climatic affinity among species, we performed a Principal Component Analysis (PCA). We also applied an unsupervised k-means clustering algorithm, specifying four groups ($k = 4$), based on proximity in climatic space.

To spatially represent these groups, we summed the binary potential distribution maps of all species within each group, generating composite distribution layers by climatic affinity. This analysis was made with raster packages (Hijmans 2020) within R (R Core Team 2023).

Climatic Descriptors for Group Classification. To characterize the climatic groups, we selected four variables: mean annual temperature (bio1), mean annual precipitation (bio12), potential evapotranspiration (PET), and aridity index ($AI = bio12 / PET$). We calculated the range of values for each group by subtracting the minimum from the maximum and dividing by two, and we also calculated group-level averages. Based on these descriptors, we applied the climate zone classification proposed by García (2004) and the aridity zone classification by UNEP (1992) to name the groups. All calculations were conducted using the raster package in R (R Core Team 2023).

Results and Discussion

A total of 6,042 records were obtained, corresponding to 18 genera and 86 species verified through literature and specimens deposited in collections (Appendix 1). Seven species with few records were excluded from the final database; taxonomic review classified them as doubtful due to their location far outside their known distribution ranges. These include: *Copris incertus* Say, 1835, which ranges from eastern Mexico to Costa Rica and Colombia; *Copris mexicanus* Halffter and Matthews, 1959, known exclusively from the state of Michoacán (Matthews 1961); *Canthon viridis* Palisot de Beauvois, 1805, does not occur in Mexico, as its distribution is restricted to the United States (Rivera-Cervantes & Halffter 1999); *Onthophagus carpophilus* Pereira & Halffter, 1961, is widely known from southwestern Mexico (Capello & Halffter 2019); *Onthophagus incensus* Say, 1835, known from central to southern Mexico (Zunino 2003); *Eurysternus mexicanus* Harold, 1869, reported from the Gulf of Mexico coast to South America; *Eurysternus magnus* Castelnau, 1840, recorded from the lowlands of northwest Mexico to Central America (Génier 2009); and *Phanaeus tridens* Castelnau, 1840 was reported for Jalisco (Navarrete-Heredia et al. 2001); however, this record does not correspond to the species' distribution, which ranges from northern to southern Veracruz (Moctezuma et al. 2021).

Classifying these species as doubtful rather than erroneous in this study serves to highlight possible new records or the existence of undescribed taxa; however, confirmation and precise locality data are necessary. In some cases, apparent geographical gaps, as seen in the well-defined species *Onthophagus anewtoni* Howden & Génier, 2004 (Moctezuma & Halffter 2021). Conversely, recent studies suggest that true disjunct distributions can indicate distinct species rather than species complexes, as shown by *Phanaeus huichol* Moctezuma, Sánchez-Huerta & Halffter, 2017, previously known as *Phanaeus endymion* Harold, 1863 (Moctezuma et al. 2017).

Knowledge Status and Sampling Coverage. Most records were obtained from the SNIB–CONABIO database (53%), followed by material deposited at CZUG (37%), while the remaining 10% originated from literature and GBIF. Duplicate records were identified between the GBIF and SNIB–CONABIO databases, leading to prioritization of the SNIB–CONABIO dataset.

Jalisco comprises 125 municipalities, with data available for 86. Notable municipalities include Ameca, Atenguillo, Autlán de Navarro, Casimiro Castillo, Chapala, Hostotipaquillo, La Huerta, Lagos de Moreno, Mascota, Tequila, Tuxcueca, and Zapopan, collectively representing 60% of the records (Fig. 2). Several of these municipalities contain important protected natural areas, such as the Chamela Biological Station in La Huerta, Sierra de Manantlán in Autlán de Navarro, Bosque de la Primavera in Zapopan, and Volcán de Tequila in Tequila (Appendix 1). Additionally, the database includes significant records from faunistic studies (Quiroz-Rocha et al. 2008; Navarrete-Heredia et al. 2012; González-Hernández et al. 2015; Hernández & Navarrete 2018; Hernández et al. 2021; Hernández et al. 2022). Beyond these, 188 additional sites are summarized based on grid cells dividing the state's surface. Out of 816 total cells, only 178 contained records, indicating a known sampling coverage of Scarabaeinae in Jalisco of 21%. Most cells with records are concentrated in the Trans-Mexican Volcanic Belt, where medium species richness is observed in the central part. Although less sampled, the Sierra Madre del Sur is the biogeographic province with cells exhibiting high species

richness, similar to the Pacific Coast. The Mexican High Plateau and Sierra Madre Occidental remain comparatively underexplored (Fig. 3A). Similar patterns of under sampling and potential richness concentration have been reported in central Mexican mountains. For example, Moctezuma *et al.* (2024c) documented significant Wallacean shortfalls in dung beetle distributions in high-altitude sky-island national parks, using predictive models to identify biodiversity gaps above 3,000 m. Their findings reinforce the importance of targeted sampling in montane regions such as the Sierra Madre Occidental, which remains poorly represented in current datasets for Jalisco.

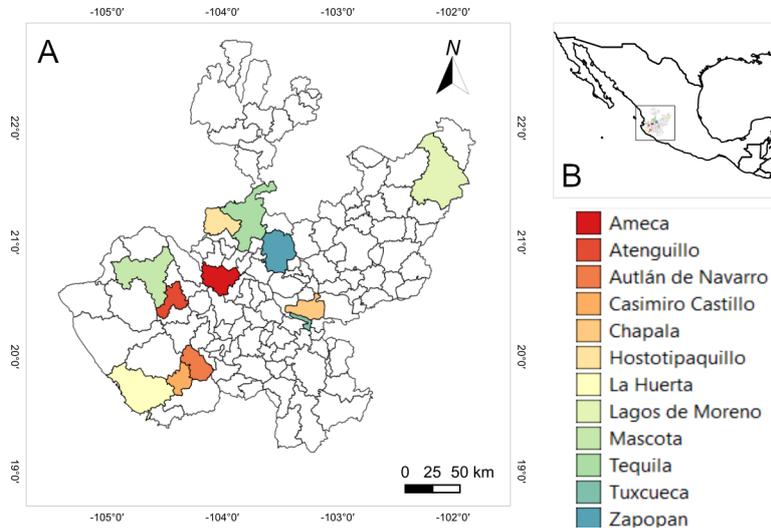


Figure 2. Map of the municipalities in the state of Jalisco with the highest number of records.

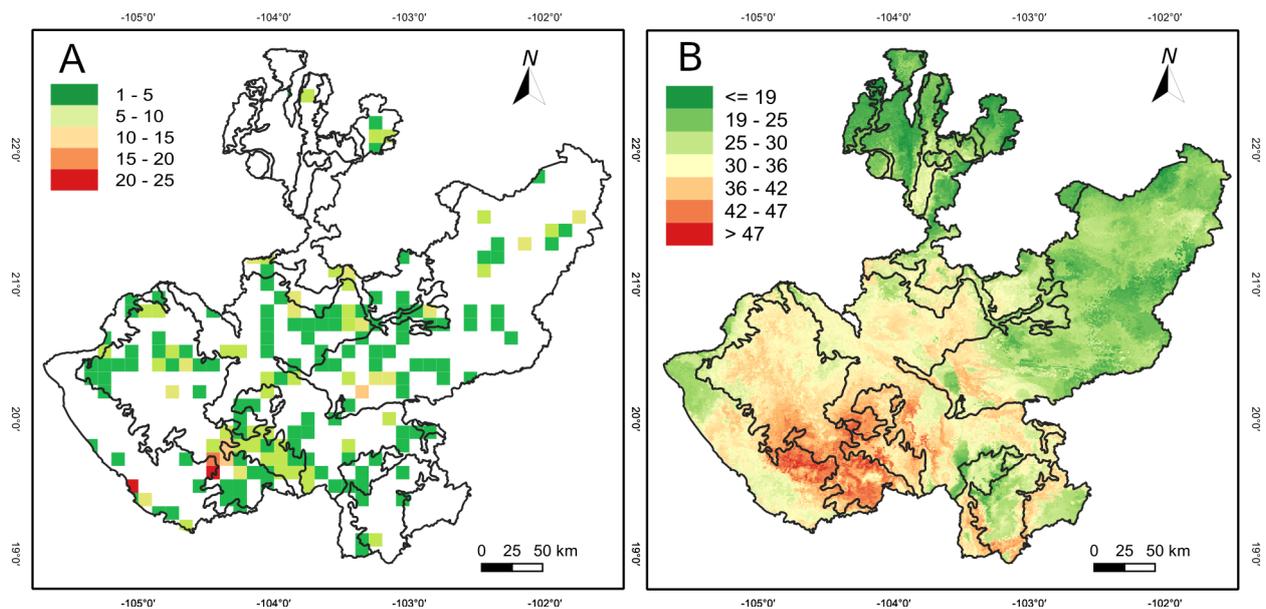


Figure 3. Scarabaeinae richness of the Jalisco state. **A**, current richness at 10km²; **B**, potential richness through the sum of the potential distribution of each reported species.

The number of records per species shows a marked contrast: 57 species represent less than 1% of the records, whereas 65% of records belong to the most frequently collected species within the state (*Oniticellus rhinocerus* Bates, 1887, *Coprophanaeus pluto* (Harold, 1863), *Phanaeus huichol* Moctezuma, Sánchez-Huerta & Halffter 2017, *P. amithaon*, *P. furiosus*, *Canthon humectus assimilis* Robinson, 1946, *Euoniticellus intermedius* Reiche, 1849, *Digitonthophagus gazella* (Fabricius, 1787), *Canthon indigaceus* LeConte, 1866). However, this high frequency in datasets may reflect sampling bias due to the widespread use of baits, which can lead to the under-representation of non-coprophage and specialist species (Moctezuma 2021b). Additionally, a significant portion of the data is derived from previous surveys in which the principal sampling method consisted of carrion traps baited with squid. (Quiroz-Rocha *et al.* 2008; Navarrete-Heredia *et al.* 2012; González-Hernández *et al.* 2015; Hernández & Navarrete-Heredia

2018; Hernández *et al.* 2022) that predominantly used squid meat as bait. Knowledge of Scarabaeinae species in Jalisco has advanced significantly since the publication of the initial checklist (Navarrete–Heredia *et al.* 2001), with an increase of 27 species.

Potential Richness Patterns. Due to insufficient records, the distributions of 30 species could not be modeled; thus, only pixels where these species were present were considered. Their occurrences were rasterized and directly added to the final species richness map, contributing only to the specific grid cells where they were recorded. Of the 56 species modeled, the average AUC values were 0.84 (omission) and 0.80 (test), supporting model validity (see Appendix 1). Summing the binary maps of potential distributions yielded a potential species richness map for the state.

Within the portion of the state occupied by Scarabaeinae, 35% of the area exhibits potential presence of up to 30 species, primarily concentrated in the Trans–Mexican Volcanic Belt and the northern Sierra Madre del Sur. At least 40% of the territory hosts 19 to 25 species in the Sierra Madre Occidental and Mexican High Plateau. The remaining 25% represents areas of high potential richness, with over 40 species in the southern Sierra Madre del Sur and adjacent Pacific Coast, coinciding with current areas of high richness such as the Sierra de Manantlán near the Chamela region (Fig. 3B).

Potential richness represents a hypothetical model of community structure based on species’ environmental tolerances. This model assumes that the distribution of coexisting species depends on their abiotic requirements, excluding the influence of other processes that could alter the final richness or composition (Peterson *et al.* 2011).

This modeling approach has also been applied to other taxonomic groups. Such as, Lizardo *et al.* (2017, 2022) employed Species Distribution Models (SDM) to mitigate sampling biases and propose biogeographical regionalization for beetles of genus *Phanaeus*, effectively reducing the Wallacean shortfall. Lizardo *et al.* (2024) utilized niche modeling to explore evolutionary drivers, such as niche conservatism and convergence, in bird assemblages within the Mexican Transition Zone. Similarly, Moctezuma *et al.* (2024c) used SDM methods to highlight areas of unrecorded richness in high-elevation parks of central Mexico, suggesting that potential diversity in montane regions may be systematically underestimated. Their work underscores the relevance of predictive modeling in guiding sampling efforts and conservation focus, especially in areas with steep elevational gradients like southern Jalisco.

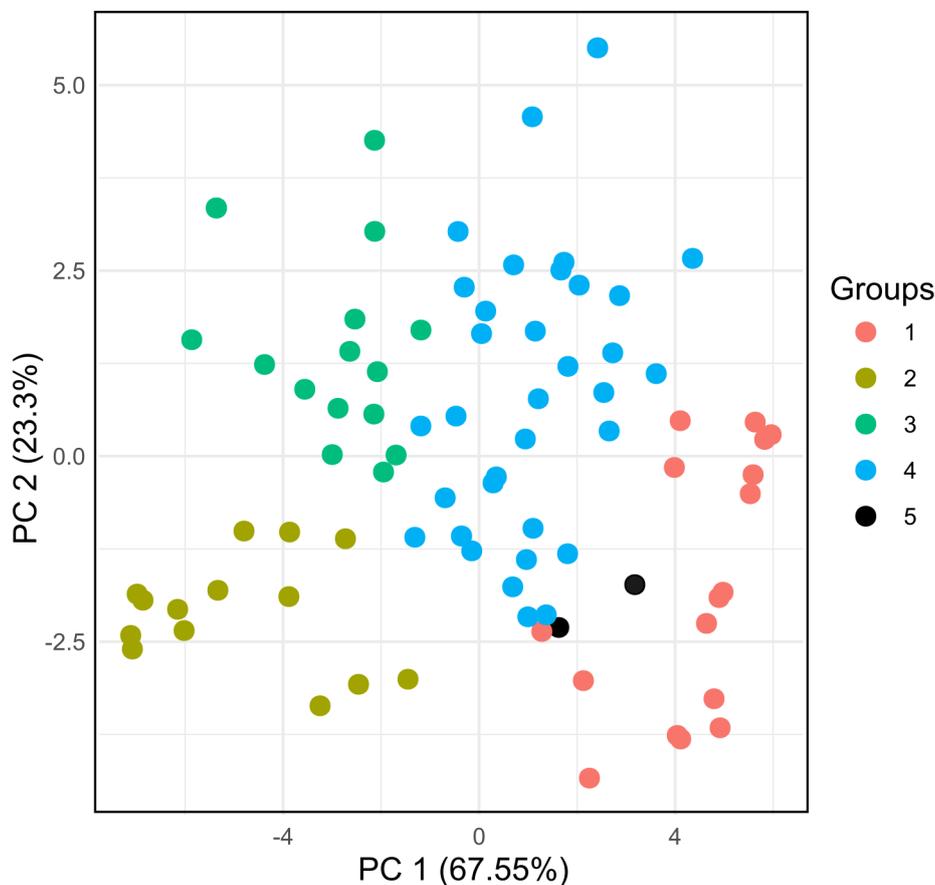


Figure 4. Analysis of principal components based on the 21 bioclimatic and altitude variables. The colors indicate the climatic groups: Red: group1, Green: group 2, Yellow: group 3, Blue: group 4, Black: group 5 exotic species.

Ecogeographic Patterns. In the Principal Component Analysis (PCA), the first component explained 67.55% of variation, and the second component 23.3%. Hierarchical clustering revealed four distinct species groups associated with climatic variables. In the biplot (Fig. 4), the first component separates groups by altitude: groups 1 and 4 correspond to species distributed at higher altitudes (1000–2200 m), while groups 2 and 3 correspond to species below 1000 m. This altitudinal difference aligns with temperature ranges: groups 1 and 4 associate with lower temperature variables, whereas groups 2 and 3 align with higher temperature variables (Table 1, Fig. 5). The second component separates groups by precipitation variables; groups in the lower biplot (group 1 and part of group 2) inhabit sites with lower precipitation and potential evapotranspiration.

Table 1. Summary of the range of climate descriptors by groups based on their distribution pattern.

Group	Altitude	AAT (bio1)	AP (bio12)	PET	AI
	Min–Max	Min–Max	Min–Max	Min–Max	Min–Max
Group 1	1565–1986	16.5–18.7	603–752	1618.1–1787.7	0.37–0.42
Group 2	11–1212	23.4–25.8	727–1334	1719.7–2009	0.42–0.66
Group 3	626–1792	17.6–23.8	907–1374	1502.4–1869.8	0.6–0.73
Group 4	813–2214	17.5–22.6	700–1070	1467.4–1969	0.48–.54
Group 5	1423–1726	18.8–20.4	774–776	1696.5–1772.6	0.45–0.43

Altitude (m.a.s.l); AAT: Average Annual Temperature (°C); AP: Annual precipitation (mm); PET: Annual Potential Evapotranspiration (mm/min); AI: Aridity index (AP/PET).

Notably, exotic species (*D. gazella* and *E. intermedius*) were analyzed as a separate group in the hierarchical analysis due to their introduced status and wide ecological adaptability from the United States to South America (Montes de Oca *et al.* 1994; Noriega *et al.* 2017; Pablo-Cea *et al.* 2017). They clustered near groups 1 and 4 (black dots in Fig. 4), but without a clear climatic or geographic association. Their broad colonization ability suggests approximately 90% of the state is suitable for these species when projecting potential distributions.

Mexican Scarabaeinae species are closely associated with the rainy season. The PCA based on 23 bioclimatic variables identified four affinity groups with distinct climatic requirements. Ambient temperature is the most important variable, highly correlated with beetle body temperature, enabling physiological processes throughout their life cycle (Hanski & Cambefort 1991; Verdú *et al.* 2007).

This association and annual environmental variability manifest in reproductive cycles, with adult activity peaking during favorable seasons. Together with seasonal precipitation and relative humidity ranges, these factors strongly influence reproduction at both population and community levels (Vernes *et al.* 2005). Species vary in environmental sensitivity; some are highly sensitive with narrow distributions, while others show broad adaptation and wide distribution.

The four groups correspond somewhat to biogeographic regions with some overlap in adjacent areas and dominant vegetation types (Fig. 6). Based on climatic descriptors (Table 1), the groups are: Temperate semi-arid (group 1), warm dry-subhumid (group 2), semi-warm moist-subhumid (group 3), semi-warm dry-subhumid (group 4), following García (2004) and UNEP (1992), plus exotic species (group 5).

Temperate semi-arid (Fig. 6A): Seventeen species distributed in the Mexican High Plateau and Sierra Madre Occidental, extending into the Trans–Mexican Volcanic Belt at 1500–2000 m elevation, with cold, dry climates, highly seasonal precipitation, and vegetation including xerophytic shrubland, tropical deciduous forest, and pine–oak forests (Appendix 1). These mostly follow The Mexican Plateau Paleoamerican sub-pattern and Mexican Plateau distributional pattern. *Canthon leechi* was the sole species that diverged from the previously described patterns, as it is characterized by a Typical Neotropical pattern (Halffter & Morrone 2017).

Warm dry-subhumid (Fig. 6B): Twenty-two species in tropical lowlands (0–1000 m) with moderate precipitation and higher temperatures. Associated with tropical deciduous forests in the Pacific Coast province, extending into southern Sierra Madre del Sur (Appendix 1). Patterns align with Typical Neotropical a Paleoamerican distributions (Halffter & Morrone 2017).

Semi-warm moist-subhumid (Fig. 6C): Fifteen species at intermediate altitudes (700–1800 m) with seasonal precipitation and moderate mean annual temperatures. Associated with pine–oak forests in Sierra Madre del Sur and Trans–Mexican Volcanic Belt. These follow Typical Neotropical and the Paleoamerican pattern (Halffter & Morrone 2017).

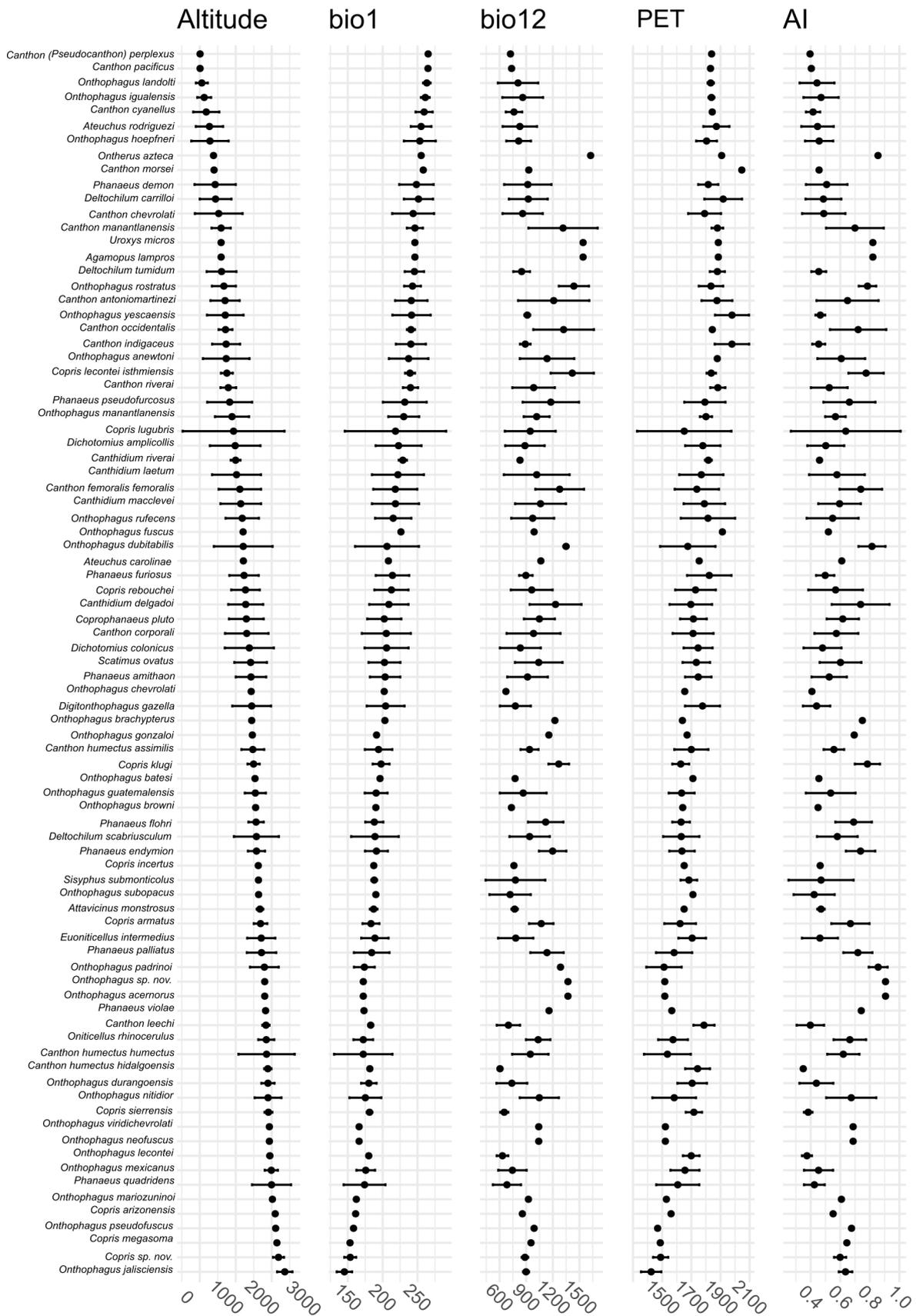


Figure 5. Average value of climatic descriptors by Scarabaeinae species recorded in the state of Jalisco. Bars indicate standard deviation.

Semi-warm dry-subhumid (Fig. 6D): The largest group with 30 species, broad environmental tolerance (800–2200 m), seasonal precipitation, and moderate temperatures. This includes 1) species broadly distributed following Typical Neotropical patterns in Sierra Madre del Sur and Trans–Mexican Volcanic Belt, inhabiting tropical deciduous and secondary vegetation near pine–oak forests, tolerant of extreme environments though rarely recorded; and 2) Paleoamerican Mountain species frequent at high altitudes in Sierra Madre del Sur and Trans–Mexican Volcanic Belt, such as the *Onthophagus chevrolati* group, associated with pine–oak forests.

The climatic affinity groups identified in this study exhibit a strong spatial concordance with the biogeographic provinces and patterns defined for the Mexican Transition Zone (Halffter & Morrone 2017; Morrone 2020). Group 1 aligns closely with the Mexican High Plateau and the eastern slopes of the Sierra Madre Occidental; ecologically, this corresponds to the *Plateau Pattern* described by Halffter (1987), characterized by species adapted to more arid conditions. In contrast, Group 2 is geographically restricted to the Pacific Coast province and the lower Balsas Basin. This group represents the Typical Neotropical Pattern (Halffter *et al.* 2019), composed of lowland species with high thermal requirements that cannot cross the altitudinal barriers of the MTZ. Meanwhile, Groups 3 and 4 reflect the complexity of the Trans-Mexican Volcanic Belt. These areas act as diversification centers where *Paleoamerican* patterns overlap (Halffter & Morrone 2017). The statistical separation of these groups confirms that, although the Trans-Mexican Volcanic Belt acts as a biogeographic filter, climatic variables are the primary drivers structuring these assemblages at a local level, reflecting the historical limits of the cenocrons proposed by Morrone (2020).

Classifying species by climatic affinity is a novel approach that warrants further development and could be highly useful for future regional studies. The patterns represent a regionalization based on current environmental data, highlighting the role of the Trans-Mexican Volcanic Belt in species distribution. This ecogeographic resolution also unveiled a marked longitudinal richness gradient driven by the Trans-Mexican Volcanic Belt role as both a corridor and a barrier (Moctezuma *et al.* 2018). While richness peaks in the humid West, our analysis detected a functional turnover towards the East, where species richness decreases but is replaced by assemblages adapted to aridity and disturbance (Hernández & Navarrete-Heredia 2018; Hernández *et al.* 2021). Consequently, the proposed climatic grouping represents a functional regionalization based on current environmental data, demonstrating that the intersection of topography and climate is the primary driver of community structure and species distribution in the state.

The classification of Scarabaeinae into climatic affinity groups enables the development of differentiated conservation strategies based on species' environmental tolerance, altitudinal distribution, and ecological sensitivity. Each group represents a set of species with distinct climatic requirements, reflecting different vulnerabilities to climate change and anthropogenic disturbance.

The temperate–semiarid group (Group 1) includes species distributed in high-elevation and low-precipitation areas such as the Mexican High Plateau and the Sierra Madre Occidental, where temperatures are moderate to cool. These species are particularly susceptible to habitat fragmentation and climate warming due to their narrow elevational ranges. Therefore, conservation strategies should prioritize connectivity among montane forest remnants and the protection of microclimatic refugia, which can sustain isolated populations. Similar recommendations have been made for Phanaeini dung beetles in Bolivia, where species with restricted elevational distributions are at high risk of extinction due to range-shift gaps and mountaintop extinctions (Herzog *et al.* 2013).

The warm–subhumid dry group (Group 2) comprises species mainly found in tropical lowlands along the Pacific Coast, characterized by high temperatures and a distinct rainy season. This region is under severe pressure from land-use change and deforestation. Conservation actions should focus on protecting remnants of tropical dry forests and restoring ecological corridors between forest patches, particularly for functionally specialized species that exhibit high sensitivity to habitat fragmentation (Villamarín-Cortez *et al.* 2022).

The humid warm–subhumid group (Group 3) includes species at intermediate altitudes associated with moist temperate forests, such as pine–oak forests in the Sierra Madre del Sur. These species are closely linked to ambient humidity and dense vegetation cover. Conservation efforts should aim to maintain canopy structure and preserve local moisture regimes, as these conditions are critical for population persistence. Similar findings have been reported for Scarabaeinae communities in Afromontane forests, where habitat heterogeneity was essential to maintaining diversity across elevation bands (Stanbrook *et al.* 2021).

Finally, the dry warm–subhumid group (Group 4) is the largest and most environmentally tolerant. It includes species ranging from lowlands to montane areas, some widely distributed generalists and others restricted to transitional zones between tropical and temperate vegetation. Here, conservation strategies should be dual-pronged: supporting generalist species that enhance ecosystem resilience, while also implementing focused protection for montane endemics, which despite being less disturbance-sensitive may be threatened by rapid land-use changes.

These climatic and biogeographic patterns underscore the need for a regionalized conservation approach that accounts not only for species richness but also for ecological requirements and adaptive capacities. By integrating climatic and altitudinal criteria, conservation planning can be better aligned with the ecological vulnerability and evolutionary constraints of Scarabaeinae assemblages across Mexico.

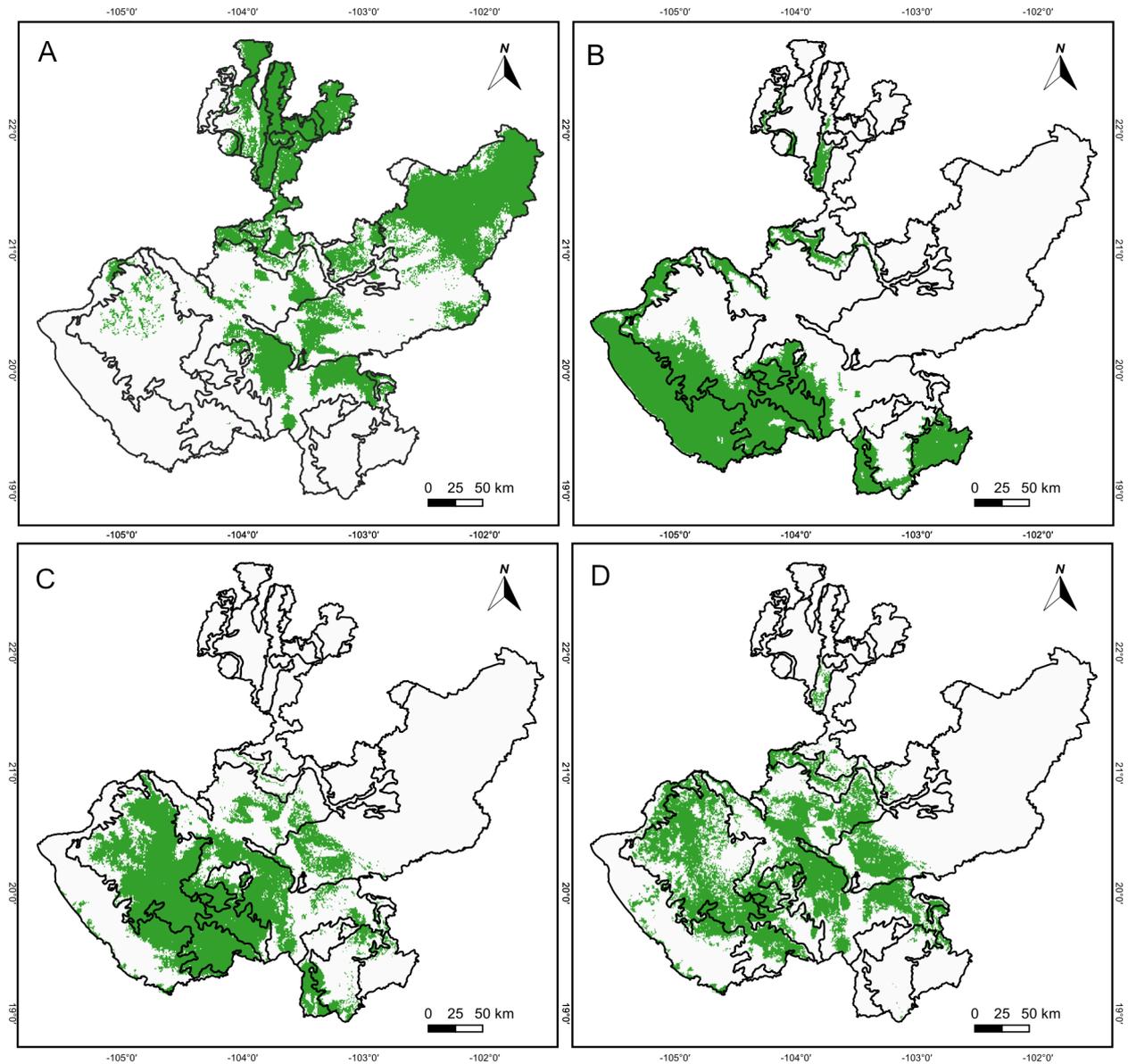


Figure 6. Maps of distribution patterns by climatic groups excluding exotic species. **A**, group1; **B**, group2; **C**, group 3, **D**, group 4.

Conclusion

The results represent a comprehensive synthesis of knowledge on Scarabaeinae species in Jalisco. Compilation of data allowed assessment of current knowledge, identification of data gaps, and formulation of research perspectives. Despite being relatively well-studied, Scarabaeinae distributional data are biased towards collections from major protected areas. Species record distribution is uneven, likely reflecting this bias. Targeted sampling in underexplored regions such as northern Jalisco (Sierra Madre Occidental) and southern Jalisco (Balsas Basin) is necessary. The proposed climatic classification revealed a longitudinal richness gradient and possible shifts in community structure due to the intersection of major biogeographic provinces and climatic conditions in the state.

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Appendix 1. Update of Annotated checklist of Scarabaeinae species from Jalisco state. AUC: Area Under Curve. Vegetation Type: TDF: Tropical Deciduous Forest; POF: Pine-Oak Forest; XSI: Xeric Shrublands. Biogeographic province: PL: Pacific Lowlands; SMS: Sierra Madre del Sur; SMOc: Sierra Madre Occidental; TMVB: Trans-Mexican Volcanic Belt; MHP: Mexican High Plateau; BB: Balsas Basin.

Specie	Climatic group	AUC	Record number	Vegetation type	Biogeographic province	Municipally
<i>Attavicinus monstrosus</i> (Bates, 1887)	1	0.93	41	TDF, POF	TMVB, MHP	Chapala, San Cristóbal de La Barranca, Teocuitatlan de Corona
<i>Canthon humectus hidalgoensis</i> (Bates, 1889)	1	0.94	16	XSI	MHP	Lagos de Moreno, Teocaltiche,
<i>Canthon humectus humectus</i> (Say, 1831)	1	0.76	40	TDF, POF	PL, TMVB, MHP, BB	Autlán de Navarro, Casimiro Castillo, Jilotlan de Los Dolores, La Huerta, Tapalpa, Tomatlan, Tuxcueca,
<i>Canthon leechi</i> Martínez, Halfpter & Halfpter, 1964	1	0.89	14	XSI, TDF, POF	MHP	Arandas, Lagos de Moreno, Teocaltiche, Tepatitlan de Morelos
<i>Copris arizonensis</i> Schaeffer, 1906	1	NM	1	POF	TMVB	Guadalajara
<i>Copris lecontei isthmiensis</i> Matthews, 1961	1	0.94	2	TDF	SMS	Cuautitlán de García Barragan
<i>Copris megasoma</i> Matthews & Halfpter, 1959	1	NM	1	POF	TMVB	Mazamitla
<i>Copris sierrensis</i> Matthews, 1961	1	0.9	49	TDF	SMOc, MHP	Jalostotitlán, Lagos de Moreno, Mezquitic, Santa Maria de Los Angeles, Teocaltiche
<i>Copris</i> sp. nov.	1	0.97	15	POF	MHP	Tuxcueca, Mazamitla
<i>Onthophagus batesi</i> Howden & Cartwright, 1963	1	NM	1	TDF	TMVB	La Barca
<i>Onthophagus durangoensis</i> Balthasar, 1939	1	0.83	139	XSI, TDF, POF	MHP, SMS, TMVB	Autlán de Navarro, Casimiro Castillo, Jalostotitlán, Lagos de Moreno, Mascota, Teocaltiche, Tepatitlan de Morelos, Tuxcueca, Zapopan
<i>Onthophagus jaliscensis</i> Zunino & Halfpter, 1988	1	0.94	38	POF	MHP, TMVB	Atequique, Tuxcueca
<i>Onthophagus lecontei</i> Harold, 1871	1	0.88	56	XSI, TDF, POF	MHP	Jalostotitlán, Lagos de Moreno, San Juan de Los Lagos, Teocaltiche, Tepatitlan de Morelos
<i>Onthophagus mexicanus</i> Bates, 1887	1	0.88	79	XSI, TDF, POF	SMOc, MHP, TMVB	Cocula, Colotlan, Lagos de Moreno, San Cristobal de La Barranca, Tepatitlan de Morelos, Tuxcueca
<i>Onthophagus subopacus</i> Robinson, 1940	1	0.83	4	TDF, POF	TMVB, SMOc	Guadalajara, Mezquitic, Zapopan
<i>Phanaeus quadridens</i> (Say, 1835)	1	0.62	5	XSI, POF	MHP, TMVB, SMOc	Chapala, Colotlan, Lagos de Moreno, Magdalena
<i>Sisyphus submonticolus</i> Howden, 1965	1	0.76	3	TDF, POF	SMS, SMOc	Mascota, Mezquitic
<i>Ateuchus rodriguezii</i> (Preudhomme de Borre, 1886)	2	0.87	27	TDF	PL	Casimiro Castillo, Hostotipaquillo, La Huerta, Puerto Vallarta

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Appendix 1. (Continued)

Specie	Climatic group	AUC	Record number	Vegetation type	Biogeographic province	Municipally
<i>Canthon cuixmala</i> Escobar-Hernández 2025	2	NM	99	TDF	PL	El Grullo, La Huerta
<i>Canthon cyanellus</i> LeConte, 1859	2	0.91	22	TDF, POF	PL	El Grullo, La Huerta, Tomatlan
<i>Canthon chevrolati</i> Harold, 1868	2	0.93	65	TDF, POF	PL	Autlán de Navarro, Casimiro Castillo, Cihuatlán, El Grullo, Juchitlán, La Huerta, Pihuamo, Puerto Vallarta, San Gabriel, Tolimán, Tomatlan, Tuxcacuesco, Unión de Tula, Zapotitlan de Vadillo
<i>Canthon indigaceus</i> LeConte, 1866	2	0.9	234	TDF, POF	SMS, TMVB, PL	Ameca, Chapala, Guadalajara, Hostotipaquillo, La Manzanilla de La Paz, Mascota, Mezquic, San Cristobal de La Barranca, San Sebastián del Oeste, Tequila, Tomatlan, Tuxcueca, Zapopan
<i>Canthon morsei</i> Howden, 1966	2	NM	1	TDF	PL	Hostotipaquillo
<i>Canthon pacificus</i> Rivera-Cervantes & Halfpfer, 1999	2	0.99	9	TDF	PL	Cihuatlán, La Huerta
<i>Deltochilum carrilloi</i> González-Alvarado & Vaz-de-Mello, 2014	2	0.86	132	TDF, POF	MHP, PL, TMVB	Autlán de Navarro, Casimiro Castillo, El Grullo, Hostotipaquillo, La Huerta, La Manzanilla de La Paz, Mezquic, Pihuamo, Puerto Vallarta, San Cristobal de La Barranca, San Gabriel, Tolimán, Tuxcacuesco, Tuxcueca
<i>Deltochilum tumidum</i> (Howden, 1966)	2	0.8	7	TDF, POF	PL	El Grullo, Hostotipaquillo, La Huerta, Tuxcacuesco
<i>Onthophagus hoepfneri</i> Harold, 1869	2	0.86	42	TDF, POF	PL	Autlán de Navarro, La Huerta, Puerto Vallarta, Tolimán, Tonaya
<i>Onthophagus igualensis</i> Bates, 1887	2	0.89	56	TDF, POF	PL	Casimiro Castillo, La Huerta, Tuxcacuesco
<i>Onthophagus landolti</i> Harold, 1880	2	0.92	24	TDF	PL	Casimiro Castillo, La Huerta
<i>Onthophagus yescaensis</i> Moctezuma, Hernández & Sánchez-Huerta, 2022	2	0.96	5	TDF	PL	Hostotipaquillo, Zapotlanejo
<i>Phanaeus demon</i> Castelnau, 1840	2	0.86	97	TDF, POF	PL, SMS	Autlán de Navarro, Casimiro Castillo, Cihuatlán, Hostotipaquillo, Juanacatlán, Juchitlán, La Huerta, La Manzanilla de La Paz, Ocotlan, San Gabriel, Zapotitlan de Vadillo
<i>Canthon (Pseudocanthon) perplexus</i> (LeConte, 1847)	2	0.61	3	TDF	PL	La Huerta
<i>Agamopus lampros</i> Bates, 1887	3	NM	1	TDF	PL	Casimiro Castillo

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Appendix 1. (Continued)

Specie	Climatic group	AUC	Record number	Vegetation type	Biogeographic province	Municipally
<i>Canthidium delgadoi</i> Kohlmann & Solis, 2006	3	0.86	9	TDF, POF	SMS	Autlán de Navarro, Atenguillo, Casimiro Castillo, Tuxpan
<i>Canthon antoniomartinezi</i> Rivera-Cervantes & Halffter, 1999	3	0.87	23	TDF, POF	PL	Ameca, Autlán de Navarro, Casimiro Castillo, Mixtlán, Tuxcacuesco
<i>Canthon femoralis femoralis</i> (Chevrolat, 1834)	3	0.89	51	TDF, POF	SMS	Atenguillo, Autlán de Navarro, Casimiro Castillo, Cuautitlán de García Barragan, La Huerta, Talpa de Allende, Tecalitlán, Tlajomulco de Zúñiga, Tolimán, Tuxpan
<i>Canthon manantlanensis</i> Rivera-Cervantes & Halffter, 1999	3	0.94	21	TDF, POF	SMS, PL	Autlán de Navarro, Casimiro Castillo
<i>Canthon riverai</i> Halffter & Halffter, 2003	3	0.87	99	TDF	PL	Autlán de Navarro, Casimiro Castillo, El Grullo, El Limón, Tapalpa, Tuxcacuesco, Unión de Tula
<i>Canthon occidentalis</i> Halffter & Rivera 2015	3	0.82	6	TDF, POF	PL	Cuautitlán de García Barragan, Ejutla
<i>Copris lugubris</i> Boheman, 1858	3	0.85	8	TDF	PL	Autlán de Navarro, La Huerta, San Gabriel, San Sebastián del Oeste
<i>Ontherus azteca</i> Harold, 1869	3	NM	2	TDF	PL	Cihuatlán, Casimiro Castillo
<i>Onthophagus anewtoni</i> Howden & Génier, 2004	3	NM	2	POF	PL	Autlán de Navarro, Guadalajara
<i>Onthophagus brachypterus</i> Zunino & Halffter, 1997	3	NM	4	TDF	SMS	Cuautitlán de García Barragan
<i>Onthophagus dubitabilis</i> Howden & Génier, 2004	3	NM	3	POF	SMS	Autlán de Navarro, Talpa de Allende
<i>Onthophagus manantlanensis</i> Sánchez-Huerta, Moctezuma & Hernández, 2021	3	0.93	3	TDF, POF	PL, SMS	Autlan De Navarro, Casimiro Castillo, Tamazula de Gordiano
<i>Onthophagus pseudoguatemalensis</i> Moctezuma & Halffter, 2021	3	0.86	56	TDF, POF	SMS, TMVB	Autlán de Navarro, Casimiro Castillo, Gómez Farías, Mascota, Talpa de Allende
<i>Onthophagus rostratus</i> Harold, 1869	3	0.91	7	TDF	PL, BB	Casimiro Castillo, Tecalitlán, Tomatlan
<i>Phanaeus pseudofurcosus</i> Balthasar, 1939	3	0.95	31	TDF, POF	PL, SMS	Autlan De Navarro, Casimiro Castillo, San Gabriel, Tecalitlán, Unión De Tula, Tuxcueca
<i>Ateuchus carolinae</i> Kohlmann, 1981	4	NM	1	POF	SMS	Talpa de Allende

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Appendix 1. (Continued)

Specie	Climatic group	AUC	Record number	Vegetation type	Biogeographic province	Municipally
<i>Canthidium laetum</i> Harold, 1867	4	0.69	10	TDF, POF	TMVB, PL	Ajjic, Autlán de Navarro, Cihuatlán, Casimiro Castillo, La Huerta, Chapala, La Manzanilla de La Paz, Tolimán
<i>Canthidium macclevei</i> Kohlmann & Solis, 2006	4	0.6	17	TDF, POF	TMVB, MHP, PL	Ameca, Casimiro Castillo, El Grullo, Tecalitlán, Tepatitlan de Morelos, Tuxcacuesco, Tuxcueca
<i>Canthidium riverai</i> Kohlmann & Solis, 2006	4	NM	3	TDF, POF	PL	Autlán de Navarro, Ejutla
<i>Canthon corporaali</i> Balthasar, 1939	4	0.74	37	TDF, POF	PL, MHP, TMVB	Ameca, Autlán de Navarro, Casimiro Castillo, El Limón, La Huerta, Mixtlán, San Gabriel, Tuxcueca
<i>Canthon humectus assimilis</i> Robinson, 1946	4	0.85	307	TDF, POF	MHP, SMS, TMVB	Acatic, Ameca, Chapala, Cocula, Colotlan, Guachinango, Guadalajara, Hostotipaquillo, Mascota, Mezquitic, Mixtlán, Poncitlán, San Cristobal de La Barranca, San Sebastián del Oeste, Tala, Tequila, Tuxcueca, Zapopan
<i>Copris armatus</i> Harold, 1869	4	0.73	8	TDF	SMS, TMVB	Autlán de Navarro, Cocula, El Salto, Guadalajara, Mascota, Zapopan
<i>Copris klugi</i> Harold, 1869	4	0.82	24	TDF	SMS, TMVB	Autlán de Navarro, Casimiro Castillo, Cocula, El Salto, Mascota, Talpa de Allende
<i>Copris rebouchei</i> Harold, 1869	4	NM	3	TDF, POF	TMVB, SMS	Autlán de Navarro, Tonaya
<i>Coprophanæus pluto</i> (Harold, 1863)	4	0.79	476	XSI, TDF, POF	MHP, SMS, PL, TMVB	Ameca, Atenguillo, Autlán de Navarro, Cabo Corrientes, Casimiro Castillo, Chapala, El Grullo, Gómez Farías, Hostotipaquillo, Jalostotitlán, La Huerta, La Manzanilla de La Paz, Lagos de Moreno, Mascota, Mixtlán, Pihuamo, Puerto Vallarta, San Cristobal de La Barranca, San Gabriel, Talpa de Allende, Tecalitlán, Teocaltiche, Tepatitlan de Morelos, Tequila, Tolimán, Tuxcacuesco, Tuxcueca, Zapopan
<i>Deltochilum scabriusculum</i> Bates, 1887	4	0.84	50	TDF, POF	MHP, PL, SMS, SMOc, TMVB	Autlán de Navarro, Casimiro Castillo, La Huerta, Puerto Vallarta, San Cristobal de La Barranca, Talpa de Allende, Tuxcueca, Tuxpan
<i>Dichotomius amplicollis</i> (Harold, 1869)	4	0.76	156	XSI, TDF, POF	SMS, SMOc, TMVB, PL	Cabo Corrientes, Casimiro Castillo, Chapala, Cocula, El Limón, Gómez Farías, Guadalajara, Hostotipaquillo, Jocotepec, La Huerta, Lagos de Moreno, Mascota, Mezquitic, San Cristobal de La Barranca, San Gabriel, San Sebastián del Oeste, Talpa de Allende, Tepatitlan de Morelos, Tequila, Tizapan El Alto, Tonaya, Tuxcueca, Unión de Tula, Zapopan

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Appendix 1. (Continued)

Specie	Climatic group	AUC	Record number	Vegetation type	Biogeographic province	Municipally
<i>Dichotomius colonicus</i> (Say, 1835)	4	0.78	175	XSI, TDF, POF	SMS, SMOc, TMVB, PL	Autlán de Navarro, Cabo Corrientes, Casimiro Castillo, Chapala, Colotlan, Guachinango, Guadalajara, Hostotipaquillo, Jocotepec, La Barca, La Huerta, Lagos de Moreno, Ocotlan, Puerto Vallarta, Quitupan, San Cristobal de La Barranca, San Ignacio Cerro Gordo, San Sebastián del Oeste, Tepatitlan de Morelos, Tequila, Tizapan El Alto, Tlajomulco de Zúñiga, Tolinán, Tonaya, Tuxcacuesco, Tuxcueca, Zapopan, Zapotitlan de Vadillo, Zapotlanejo
<i>Oniticellus rhinocerus</i> Bates, 1887	4	0.88	907	TDF, POF	SMS, TMVB	Ameca, Atenguillo, Cocula, Gómez Farías, Mascota, Mezquitic, Mixtlán, San Sebastián del Oeste, Talpa de Allende, Tecolotlán, Tequila, Zapopan
<i>Onthophagus acernorus</i> Moctezuma, Hernández, & Sánchez-Huerta, 2021	4	NM	20	POF, AC	SMS	Talpa de Allende
<i>Onthophagus browni</i> (Howden & Cartwright, 1963)	4	NM	2	TDF	TMVB	
<i>Onthophagus chevrolati</i> Harold, 1869	4	NM	1	POF	TMVB	Zapotitlan de Vadillo
<i>Onthophagus fuscus</i> Boucomont, 1932	4	NM	1	POF	TMVB	Tequila
<i>Onthophagus gonzaloi</i> Moctezuma, Hernández & Sánchez-Huerta, 2022	4	NM	6	POF	SMS	Mascota
<i>Onthophagus mariozuninoi</i> Delgado, Navarrete & Blackaller-Bages, 1993	4	NM	1	POF	TMVB	Tequila
<i>Onthophagus neofuscus</i> Moctezuma & Halfiter, 2020	4	NM	1	POF	TMVB	Tecolotlán, Tuxpan
<i>Onthophagus nitidior</i> Bates, 1887	4	0.83	115	TDF, POF	MHP, SMS, TMVB	Autlán de Navarro, Casimiro Castillo, Cocula, Colotlan, Jalostotitlán, Jilotlan de Los Dolores, La Barca, Mascota, Poncitlán, San Cristobal de La Barranca, Talpa de Allende, Tepatitlan de Morelos, Tuxcueca, Valle de Juarez, Zapopan
<i>Onthophagus padrinoi</i> Delgado, 1999	4	NM	2	POF	SMS	Autlán de Navarro, San Sebastián del Oeste
<i>Onthophagus pseudofuscus</i> Zunino & Halfiter, 1988	4	NM	1	POF	TMVB	Atequique

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Appendix 1. (Continued)

Specie	Climatic group	AUC	Record number	Vegetation type	Biogeographic province	Municipally
<i>Onthophagus rufescens</i> Bates, 1887	4	0.67	7	TDF, POF	MHP, SMS	Lagos de Moreno, San Cristobal de La Barranca, San Sebastián del Oeste, Talpa de Allende
<i>Onthophagus sp. nov.</i>	4	NM	2	POF, BM	SMS	Talpa de Allende
<i>Onthophagus viridichevrolati</i> Moctezuma & Halffter, 2020	4	NM	1	POF	TMVB	Tecolotlán
<i>Phanaeus amithaon</i> Harold, 1875	4	0.83	496	XSI, TDF, POF	MHP, TMVB, SMS, SMOc	Ajijic, Ameca, Arandas, Atoyac, Autlán de Navarro, Casimiro Castillo, Chapala, Cocula, Colotlan, Cuautitlán de García Barragan, Cuquio, Ejutla, El Arenal, El Salto, Etzatlán, Guadalajara, Ixtlahuacan de Los Membrillos, Jocotepec, Juanacatlán, La Barca, Lagos de Moreno, Magdalena, Mascota, Mazamitla, Mixtlán, Poncitlán, Quitupan, San Cristobal de La Barranca, San Sebastián del Oeste, Tala, Tamazula de Gordiano, Tapalpa, Tecalitlán, Tecolotlán, Tepatitlan de Morelos, Tequila, Tlajomulco de Zúñiga, Tonaya, Tuxcacuesco, Tuxcueca, Unión de Tula, Villa Purificación, Zapopan, Zapotlán El Grande, Zapotlanejo
<i>Phanaeus flohri</i> Nevinson, 1892	4	0.9	120	TDF, POF	MHP, TMVB, SMS, MHP	Ameca, Atenguillo, Autlán de Navarro, Chapala, Gómez Farías, Guadalajara, Mascota, Mazamitla, Talpa de Allende, Tequila, Tuxcueca
<i>Phanaeus furiosus</i> Bates, 1887	4	0.92	327	XSI, TDF, POF	MHP, TMVB, SMS, SMOc	Ahualulco Del Mercado, Ameca, Chapala, Cocula, Colotlan, Ejutla, Etzatlán, Guadalajara, Hostotipaquillo, La Huerta, Lagos De Moreno, Magdalena, Mascota, Poncitlán, San Cristobal De La Barranca, San Sebastián Del Oeste, Tala, Talpa De Allende, Tecolotlán, Tequila, Tlajomulco De Zúñiga, Tuxcacuesco, Tuxcueca, Zapopan, Zapotlanejo
<i>Phanaeus huichol</i> Moctezuma, Sánchez-Huerta & Halffter, 2017	4	0.9	468	TDF, POF	TMVB, SMS	Ameca, Atenguillo, Autlán de Navarro, Casimiro Castillo, Cocula, Cuautitlán de García Barragan, Gómez Farías, Mascota, Mixtlán, San Cristobal de La Barranca, Talpa de Allende, Tecalitlán, Tecolotlán, Tecoman, Tequila, Zapopan
<i>Phanaeus obliquans</i> Bates, 1887	4	NM	2	TDF	PL	Cihuatlán, La Huerta
<i>Phanaeus palliatus</i> Sturm, 1843	4	0.92	218	TDF, POF	MHP, TMVB, SMS	Autlán de Navarro, Casimiro Castillo, Chapala, Cocula, Mascota, Mazamitla, Talpa de Allende, Tapalpa, Tolimán, Tuxcacuesco, Tuxcueca
<i>Phanaeus violae</i> Halffter, Moctezuma & Nogueira, 2022	4	Nm	1	TDF	BB	Tamazula de Gordiano

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Appendix 1. (Continued)

Specie	Climatic group	AUC	Record number	Vegetation type	Biogeographic province	Municipally
<i>Scatimus ovatus</i> Harold, 1862	4	0.68	29	TDF, POF	MHP, TMVB, SMS	Cabo Corrientes, Casimiro Castillo, Chapala, Cocula, San Cristobal de La Barranca, San Sebastián del Oeste, Talpa de Allende, Tepatitlan de Morelos
<i>Uroxys deavilai</i> Delgado & Kohlmann, 2007	4	NM	1	TDF	PL	Casimiro Castillo
<i>Digitonthophagus gazella</i> (Fabricius, 1787)	5	0.83	251	XSI, TDF, POF	SMS, SMOc, TMVB, PL	Acatlan de Juarez, Ameca, Atoyac de Álvarez, Autlán de Navarro, Casimiro Castillo, Chapala, Cihuatlán, Ciudad Guzmán, Colotlan, Cuautitlán de García Barragan, Ejutla, El Grullo, El Limón, El Salto, Guadalajara, Hostotipaquillo, Ixtlahuacan del Rio, Jalostotitlán, Jocotepec, La Huerta, Lagos de Moreno, Pihuamo, San Cristobal de La Barranca, San Gabriel, Tenamaxtlán, Teocaltiche, Tequila, Teuchitlan, Tlajomulco de Zúñiga, Tolimán, Tonaya, Unión de Tula, Zapopan, Zapotitlan de Vadillo
<i>Euoniticellus intermedius</i> (Reiche, 1848)	5	0.8	269	XSI, TDF, POF	SMS, SMOc, TMVB, PL	Atoyac de Álvarez, Autlán de Navarro, Casimiro Castillo, Chapala, Colotlan, Cuautitlán de García Barragan, El Grullo, El Limón, Hostotipaquillo, Ixtlahuacan del Rio, Jalostotitlán, Jocotepec, La Huerta, Lagos de Moreno, Mascota, San Cristobal de La Barranca, San Gabriel, San Ignacio Cerro Gordo, San Sebastián del Oeste, Tala, Talpa de Allende, Tecalitlán, Tecolotlán, Teocaltiche, Tepatitlan de Morelos, Tequila, Tolimán, Tonaya, Tuxcueca, Unión de Tula, Zapopan