



Biodiversity of leaf beetles (Coleoptera: Chrysomelidae) in Ecuador: how many species are there?

Pedro Montes-Gavilán^{1,6} · J. Gómez-Zurita² · M. J. Macía^{3,4} · J. Muñoz⁵ · L. Cayuela^{1,6}

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Abstract Chrysomelidae comprises a highly diverse family of phytophagous beetles that play key roles in ecosystems. Despite their ecological importance, leaf beetles remain understudied in megadiverse tropical regions such as Ecuador. The aim of this study is updating the knowledge on the diversity of Chrysomelidae in Ecuador by: (i) compiling literature and Global Biodiversity Information Facility (GBIF) records; (ii) evaluating temporal, spatial, and taxonomic biases on these data; (iii) exploring spatial patterns of species richness; and (iv) estimating the potential diversity of Chrysomelidae in Ecuador through modelling the distribution of chrysomelid species from Mexico to Paraguay, and using known ratios between plant and leaf beetle species richness from Ecuador, Brazil, El Salvador, Mexico, and Peru. We compiled a dataset of 2,348 records of 871 leaf beetle species from Ecuador, representing different degrees of temporal, spatial, and taxonomic biases. The potential richness of Chrysomelidae in Ecuador shows a clear spatial pattern, with the highest number of species predicted for the extreme NE and NW regions, while this number decreases towards the south and in the inter-Andean valleys. Species distribution models estimated the potential presence of 42 chrysomelid species not previously recorded in Ecuador. Furthermore, the comparison of leaf beetle-vascular plant richness ratios in Ecuador with those of Brazil, El Salvador, Mexico, and Peru, suggests that the actual diversity of Chrysomelidae in Ecuador may be 2–3 times higher than currently known. **Implications for insect conservation** This work improves the knowledge of species diversity of Chrysomelidae in Ecuador, essential information for developing effective conservation strategies for this diverse beetle family, but much more field inventories are still needed.

Keywords Biological record biases · Checklist · Insect conservation · Observed species richness · Potential species richness.

Introduction

Phytophagous insects play a pivotal role in ecosystem services, significantly influencing the structure, functionality, and stability of terrestrial ecosystems. One of their primary functions is contributing to nutrient cycling within ecosystems (Belovsky and Slade 2000; Kitchell et al. 1979; Reynolds et al. 2000; Schowalter et al. 1991). Herbivore insects consume plant biomass, which is transformed and excreted as waste rich in nitrogen, phosphorus, and other essential nutrients facilitating the decomposition of organic matter and the release of nutrients back into the soil, making them available for uptake by plants and other organisms (Fonte and Schowalter 2005; Frost and Hunter 2004; Hollinger 1986; Huntly 1991; Kaukonen et al. 2013; Kitchell et al. 1979; Lovett et al. 2002; Metcalfe et al. 2014; Schowalter 2012). Furthermore, feeding of phytophagous insects can accelerate the breakdown of plant materials, increasing

✉ Pedro Montes-Gavilán
pedro.montes@urjc.es

¹ Departamento de Biología y Geología, Física y Química Inorgánica, Universidad Rey Juan Carlos, Madrid, Spain

² Instituto Botánico de Barcelona (CSIC-CMCNB), Barcelona, Spain

³ Departamento de Biología, Área de Botánica, Universidad Autónoma de Madrid, Madrid, Spain

⁴ Centro de Investigación en Biodiversidad y Cambio Global (CIBC-UAM), Universidad Autónoma de Madrid, Madrid, Spain

⁵ Real Jardín Botánico (CSIC-RJB), Madrid, Spain

⁶ Instituto de Investigación en Cambio Global, Universidad Rey Juan Carlos, Madrid, Spain

decomposition rates and nutrient turnover (Chapman et al. 2003; DeAngelis 1992; Hunter 2001; Reynolds and Hunter 2001; Seastedt and Crossley 1984; Swank et al. 1981). As an important part of nutrient cycling, phytophagous insects contribute to soil fertility, plant growth, and overall ecosystem productivity (Belovsky and Slade 2000; Lerdau 1996; Mattson and Addy 1975; Schowalter 2016; Tschamtker and Greiler 1995). Moreover, phytophagous insects directly influence plant population dynamics through herbivory, which can regulate plant growth, reproduction, and distribution (Brown and Gange 1989, 1992; Brown 1990; Crawley 1989; Lawton 1983; Lewinsohn and Price 1996; Rafes 1973; Schowalter 2000). This interaction shapes vegetation structure and composition, influencing habitat availability for other organisms and overall ecosystem biodiversity (Coley and Barone 1996; Janzen 1970; Siemann et al. 1998; Strong et al. 1984). Additionally, phytophagous insects serve as important prey for a wide range of predators, including birds, mammals, and other arthropods, thereby contributing to energy transfer and trophic dynamics within food webs (Cornell and Hawkins 1995; Van Veen et al. 2006; Hawkins et al. 1997; Janzen 1987).

Within the broad functional group of phytophagous insects, chrysomelids potentially hold particular significance owing to their ecological roles and abundance across various ecosystems (Andrew and Hughes 2004; Basset 2001; Bienkowski 2010). As a family comprising over 40,000 described species (Reid 2017), chrysomelids exhibit an astonishing array of host-plant associations and ecological interactions (Jolivet 1988; Jolivet and Hawkeswood 1995). Their phytophagous habits make them crucial components of plant-insect interactions, putatively influencing plant community dynamics, population demographics, and ecosystem processes (Bacher and Schwab 2000; Futuyma and Mitter 1996; Lewinsohn and Price 1996). Leaf beetles are known to feed on a wide range of host plants, including economically important crops, ornamental plants, and wild flora, thereby impacting agricultural productivity, plant diversity, and ecosystem stability (Anneck and Moran 1982; Hill 1979; Jolivet 1988; Jolivet and Hawkeswood 1995). Furthermore, their interactions with host plants can trigger plant defenses, leading to the induction of secondary metabolites and adaptations that shape plant-herbivore interactions and ecosystem functioning (Farrell and Mitter 1990; Nielsen 1978, 1989). Additionally, certain chrysomelid species can act as pollinators or seed and flower predators, further underlining their ecological significance beyond herbivory (Bienkowski 2010; Gottsberger 2012; Kirmse and Chaboo 2018; Momose 2005; Ribeiro-Costa and Almeida 2012; Samuelson 1994). Given their ubiquity, diversity, and ecological variability, leaf beetles may play

a relevant role in shaping the structure, function, and resilience of terrestrial ecosystems worldwide.

Despite their potential ecological importance, chrysomelids remain relatively understudied, especially in tropical regions, where their diversity is particularly high (Basset 2001; Furth 2006; Sánchez-Reyes et al. 2014; Yang et al. 2024). There are significant gaps in our knowledge of chrysomelid diversity and distributions (Pärtel et al. 2011), with many tropical ecosystems still poorly sampled or entirely unexplored (Larsen et al. 2011; Thormann et al. 2016). This lack of comprehensive information hampers our ability to assess regional patterns of diversity, species composition, and community dynamics (Gómez-Zurita et al. 2016; Pärtel et al. 2011; Pärtel 2014). Moreover, numerous leaf beetle species remain undescribed or poorly documented, highlighting the need for taxonomic revisions and species inventories, especially in tropical regions where species richness is likely underestimated. The relationships between chrysomelids and their host plants further complicate our understanding, as many host associations remain poorly documented or unexplored (Jolivet and Hawkeswood 1995; Yang et al. 2024). Consequently, these knowledge gaps hinder our ability to accurately assess the ecological roles, population dynamics, and conservation status of leaf beetles in tropical ecosystems, impeding effective biodiversity management and conservation initiatives (Gómez-Zurita et al. 2016). This is a common pattern for hidden biodiversity, which includes overlooked organisms that are critical to ecosystem functioning but lack the number of dedicated researchers, or the funding available for larger and more popular species, especially birds and mammals (Delso et al. 2021).

These knowledge gaps are most evident in tropical countries such as Ecuador, despite its status as one of the most biodiverse nations globally (Dangles 2009; Sierra et al. 2002). Remarkably, little is known about the diversity of specific organismal groups, including chrysomelids. These gaps in knowledge contribute to deficiencies within Ecuador's national system of protected areas, leaving certain threatened groups of organisms vulnerable to habitat degradation and loss (Kleemann et al. 2022; Titley et al. 2017). Still today, the most comprehensive list of Chrysomelidae in Ecuador can be extracted from an 80-year-old catalogue of Neotropical Coleoptera (Blackwelder 1946). This list is obviously outdated, with numerous new species having been described, and additional records of Chrysomelidae reported in Ecuador, although research efforts have primarily focused on the subfamily Cassidinae, specifically the tortoise beetles, thoroughly explored by Borowiec (1998).

The main goal of this study is to provide an updated overview of chrysomelid diversity in Ecuador by fulfilling several specific aims: (i) compiling and organizing available

information into an updated checklist of Chrysomelidae species in Ecuador; (ii) evaluating knowledge biases across temporal, spatial, and taxonomic dimensions; (iii) assessing the spatial pattern of Chrysomelidae species richness across Ecuador; and (iv) estimating the potential diversity of Chrysomelidae in this megadiverse country, including predictions of species not yet reported in Ecuador. To accomplish these objectives, we conducted an exhaustive compilation of data available in the literature and combined it with species distribution modeling of Chrysomelidae across the Neotropics. Additionally, we used known ratios between plant and chrysomelid species richness from presumably well-inventoried Neotropical countries to predict the overall number of species in Ecuador. Addressing these knowledge and diversity gaps is imperative to enhance our understanding of leaf beetles ecology and to guide evidence-based conservation strategies in tropical regions. By providing a detailed and systematic account of chrysomelid diversity, this study aims to lay the foundation for future

research and conservation efforts, contributing to the rich biodiversity of leaf beetles in Ecuador.

Materials and methods

Study area

The study area was located in Ecuador, a country in the NW of South America, spanning an area of 256,370 km². Ecuador is geographically diverse, characterized by four major physiographic regions: the Coastal plain, the Andean highlands, the Amazon region, and Galapagos Islands (Cañadas 1983; Tropicos 2025) (Fig. 1). Recognized as a confluence of several of the world's biodiversity hotspots (Myers et al. 2000), its latitudinal position, the presence of the Andean Mountain chain, and the climatic influence of marine currents and Atlantic trade winds contribute to its high environmental heterogeneity. These factors have fostered the development of a wide range of biomes across Ecuadorian

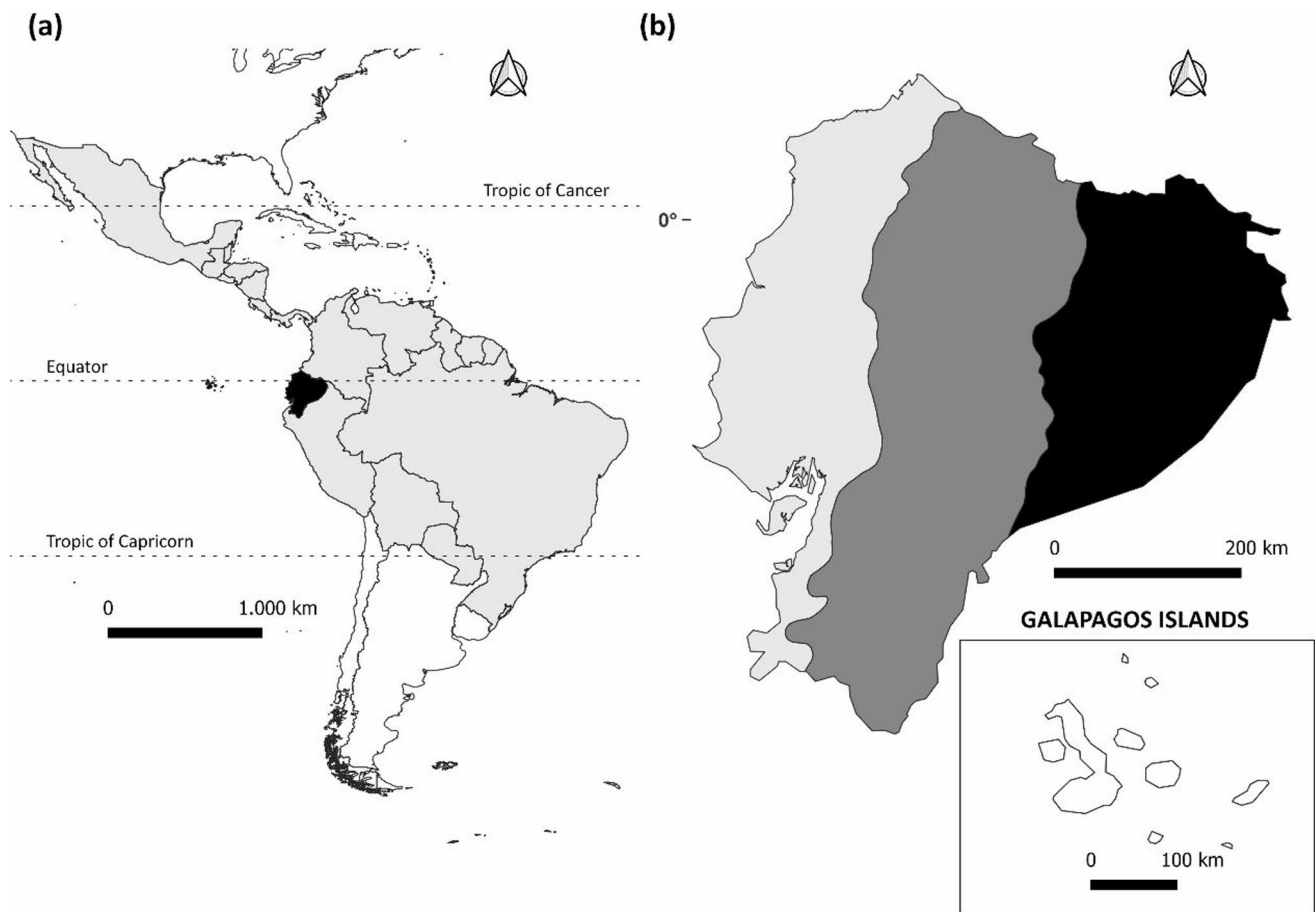


Fig. 1 **a** Map of Central American and tropical South American countries selected in this study (light grey region), and Ecuador (black region) from which leaf beetle records were collected to elaborate the species distribution models (SDM) and **b** four main physiographic

regions within Ecuador: the Coastal plain (light grey region), the Andean highlands (grey region), the Amazon region (black region), and Galapagos Islands (white region)

ecosystems, leading to exceptional biological diversity (Borchsenius 1997; Dangles 2009; Sierra et al. 2002; Skov and Borchsenius 1997).

Biological data compilation and processing

We compiled all published records of Chrysomelidae of Ecuador from three bibliographic databases: Google Scholar, Web of Science, and the Biodiversity Heritage Library. The keywords used in the literature review were pairwise combinations of the keywords “Bruchinae”, “Cassidinae”, “Chrysomelidae”, “Chrysomelinae”, “Criocerinae”, “Cryptocephalinae”, “Eumolpinae”, “Galerucinae”, “Lamprosomatinae”, “leaf beetle”, with the keywords “Ecuador”, and “biological records”. The literature review was conducted between December 2023 and April 2024. In total, we reviewed information from 272 scientific publications, encompassing 2,260 records of Ecuadorian chrysomelid species dating from 1845 to 2023. These records generally included information about the taxonomy, geographic location, collection date, and in some cases, host plants of Chrysomelidae in Ecuador. This bibliographic dataset was reviewed to verify taxonomic accuracy and eliminate obvious misidentifications, such as records of European species.

To assess the spatial pattern of Chrysomelidae species richness across Ecuador and estimate the potential species richness within the country, we collected two datasets from the Global Biodiversity Information Facility (GBIF: www.gbif.org) database. First, we accessed leaf beetle distribution information spanning from Mexico to Paraguay as of March 31, 2024 (doi: <https://doi.org/10.15468/dl.6xah6v>). This dataset included preserved specimens existing in natural history museums, universities, accessible private collections, and research projects, comprising 62,805 records of 1,418 Neotropical chrysomelid species. Second, we downloaded GBIF vascular plant records from Mexico (doi: <https://doi.org/10.15468/dl.sa54ec>), Peru (doi: <https://doi.org/10.15468/dl.hvrz76>), El Salvador, and Ecuador (doi: <https://doi.org/10.15468/dl.6d5a62>), as of May 12, 2024. This dataset contained 1,493,615 records of 61,503 plant species from 550 herbaria. Brazil, El Salvador, Mexico, and Peru were selected as benchmarks due to the availability of relatively recent comprehensive species checklists of all chrysomelid subfamilies also present in Ecuador. The GBIF datasets of leaf beetles and vascular plants were supplemented with data obtained from published species checklists. Specifically, leaf beetle GBIF data were completed with species checklist data from Brazil (Linzmeier and Moura 2025), El Salvador (Van Roie et al. 2019), Mexico (Ordóñez-Reséndiz and López-Pérez 2021), and Peru (Chaboo 2015a, 2015b, Chaboo and Flowers 2015a; 2015b; Chaboo and Schmitt 2015; Chaboo and Schöller 2016; Chaboo and Staines 2015; Furth

et al. 2015), and GBIF data of vascular plants were complemented with species checklist data from Brazil (Flora e Funga do Brasil 2025), Mexico (Villaseñor 2016), Ecuador, El Salvador, and Peru (Ulloa Ulloa et al. 2017).

We used the ‘CoordinateCleaner’ package (Zizka et al. 2019) in R version 4.3.0 (R Core Team 2024) to filter out GBIF records based on the following exclusion criteria: coordinates set to zero, duplicate entries, identical latitude and longitude values, coordinates outside land, discrepancies in coordinate reference systems, low-precision coordinates, and entries located within urban areas or natural history institutions. This process resulted in a Chrysomelidae dataset consisting of 22,161 records of 1,387 Neotropical species. After merging this GBIF dataset with the georeferenced records from the literature review, we obtained a dataset with 23,938 records of 1,842 species. The vascular plant dataset included 1,094,593 records of 61,503 species.

Statistical analyses of data biases

Temporal bias in Chrysomelidae records from Ecuador was assessed by analyzing sampling intensity across seven 25-year time periods spanning from 1845 to 2024. We obtained the number of records for each 25-year time period and performed Pearson’s chi-squared tests using the R packages ‘occAssess’ (Boyd et al. 2021).

The spatial bias of leaf beetle records was assessed through spatial clustering and spatial coverage analyses using 1,848 records of 555 species, each with original or assigned spatial coordinates and an estimate uncertainty in meters. Up to 501 records of 434 species lacked spatial coordinates and were therefore excluded from these analyses. In spatial clustering analysis, the nearest neighbor index was calculated over seven 25-year time periods spanning from 1845 to 2024 using the R package ‘occAssess’ (Boyd et al. 2021). Spatial coverage was analyzed independently for each of the four physiographic regions (Coastal plain, Andes highlands, Amazon, and Galapagos Islands) using the Quantum Geographical Information System (QGIS) v. 3.34.3 program (QGIS Development Team 2024).

Taxonomic bias was assessed by statistically comparing the proportions of species by subfamily in Ecuador with corresponding proportions from the entire Neotropical region, Brazil, El Salvador, Mexico, and Peru using Pearson’s chi-squared tests. The selected countries represent areas where the distribution of species among subfamilies was expected to be similar to that of Ecuador, while the overall Neotropical region was included to assess potential broader-scale differences in subfamily representation. Data was extracted from published species checklists from Brazil (Linzmeier and Moura 2025), El Salvador (Van Roie et al. 2019), Mexico (Ordóñez-Reséndiz and López-Pérez 2021), and

Peru (Chaboo 2015a, 2015b; Chaboo and Flowers 2015a, 2015b; Chaboo and Schmitt 2015; Chaboo and Schöller 2016; Chaboo and Staines 2015; Furth et al. 2015). Species proportions by subfamily in the Neotropics from Mexico to Argentina were derived from Blackwelder (1946).

Analyses of spatial patterns and potential species diversity

To assess the spatial pattern of Chrysomelidae species richness across Ecuador, we generated species distribution models (SDM) for each species, using the GBIF dataset. Initially, we mapped 23,938 literature and GBIF records, totaling 1,842 species, onto a grid of 2,861 cells with a spatial resolution of 10×10 km in QGIS. For species with at least 15 occurrences, SDM were created using maximum entropy (Maxent) and generalized boosted model (GBM) algorithms implemented in the R package ‘biomod2’ (Thuiller et al. 2009). Models for species with 5–14 occurrences were created as a Maxent ensemble of small bivariate models (ESM) using the R package ‘ecospat’ (Di Cola et al. 2017), as Breiner et al. (2018) demonstrated the effectiveness of ESM when dealing with small sample size datasets. Prior to modelling, we identified and removed highly correlated climatic predictor variables ($r > 0.7$) using the R package ‘corrgram’ (Wright 2018). All models were generated using a set of 10,000 random background points and 10 evaluation runs of 80% training splits for model calibration using random partitioning. A final ensemble model was obtained for each species by weighted averaging of models in each replicate, with weights calculated from True Skill Statistic (TSS > 0.7) for species with more than 15 occurrences and Somers’ D (D = 0) for species modeled using the ESM approach. Models with lower TSS or D values were discarded. This resulted in 117 SDM for species with more than 15 occurrences and 274 SDM for species with fewer records across the entire Neotropical region. The continuous habitat suitability values from each ensemble SDM were then transformed into binary raster layers with a pixel resolution of 10×10 km using the threshold that maximized TSS or D. Finally, the binary models were distance-constrained to account for dispersal limitations of leaf beetles. Distance constraint was performed using distance hybrid models with the R package ‘raster’. The Gaussian distance decay function with a sigma of 250 km was used to fit the hybrid models. All distance-constrained binary rasters of potentially distributed species in Ecuador were summed using QGIS ‘Raster calculator’ tool to calculate potential species richness within each 10×10 km grid cell.

Finally, to estimate the potential number of Chrysomelidae species in Ecuador, we used two different approaches. First, we added the number of species identified by SDM as

potentially present but not yet recorded in Ecuador to the current number of species documented from the literature review and GBIF. Second, we compared the ratio of Chrysomelidae to vascular plant species richness in Ecuador to that of relatively well-sampled countries, such as Brazil, El Salvador, Mexico, and Peru. Several studies have demonstrated a relationship between plant richness and herbivorous insect richness (Dinnage et al. 2012; de Freitas et al. 2023; Haddad et al. 2001, 2009; Hertzog et al. 2016; Kemp and Ellis 2017; Knops et al. 1999; Lewinsohn and Roslin 2008; Murdoch et al. 1972; Novotny et al. 2006; Scherber et al. 2010; Siemann et al. 1998; Southwood et al. 1979; Strong et al. 1984), and this assumption allows the estimation of regional and global numbers of insect species (Erwin 1982; Gaston 1992; Hodkinson and Casson 1991; Kirby and Spence 1826; May 1990; Peck 1989; Peck and Kukalova-Peck 1990; Stork 1988; Thomas 1990).

Results

Checklist of Ecuadorian leaf beetles

We compiled a total of 2,260 Chrysomelidae records from the literature, documenting 858 species present in Ecuador, with 75 records corresponding to specimens identified at the genus level (Online Resources 1 and 2). These species belonged to eight subfamilies: Bruchinae, Cassidinae, Chrysomelinae, Criocerinae, Cryptocephalinae, Eumolpinae, Galerucinae, and Lamprosomatinae. Additionally, we obtained 88 records from the GBIF database, increasing the total to 2,348 records and representing 34 chrysomelid species from Ecuador. Of these, 13 species were not documented in the literature, bringing the total number of species recorded in Ecuador to 871.

The number of species by subfamily is shown in Fig. 2. The subfamily Bruchinae accounted for 261 literature records and 11 GBIF records, representing 59 species. Notably, one species, *Amblycerus nigromarginatus* (Motschulsky, 1874), preserved at Texas A&M University Insect Collection was solely recorded in the GBIF dataset and was not found in the literature. Cassidinae exhibited the highest number of records and species, with 1,417 literature and 42 GBIF records, representing 407 species. Borowiec (1998) and Borowiec and Swietojanska (2024) contributed to the literature with 457 records of 200 Cassidinae species. The GBIF records introduced seven new species not documented in the literature. Chrysomelinae comprised 147 literature and four GBIF records, encompassing 99 species in Ecuador. Criocerinae and Cryptocephalinae were only represented by literature records, with 13 records of 12 species of Criocerinae and 20 records of seven species

Fig. 2 a Number of Chrysomelidae records, and **b** species number broken down by subfamily from Ecuador. This figure includes data compiled from both the literature and the Global Biodiversity Information Facility (GBIF) database, representing eight subfamilies: Bruchinae, Cassidinae, Chrysomelinae, Criocerinae, Cryptocephalinae, Eumolpinae, Galerucinae, and Lamprosomatinae. The total number of records for each subfamily is displayed, highlighting the contributions from different sources

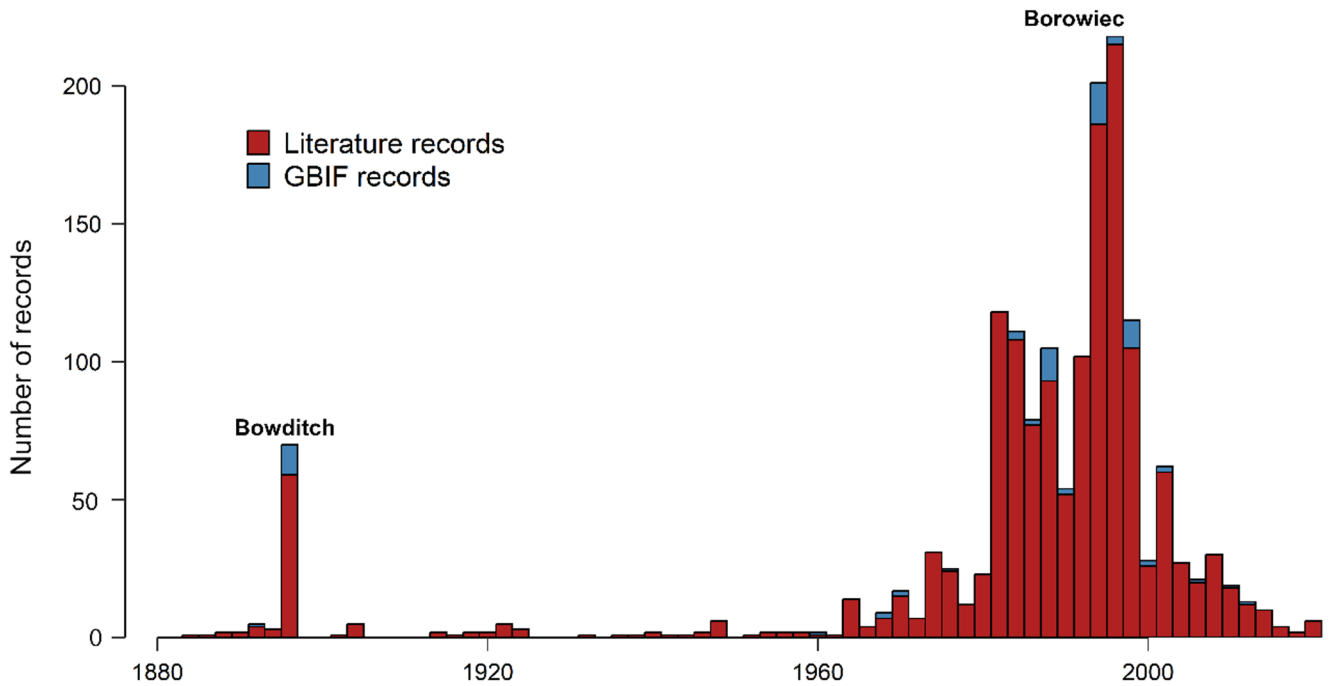
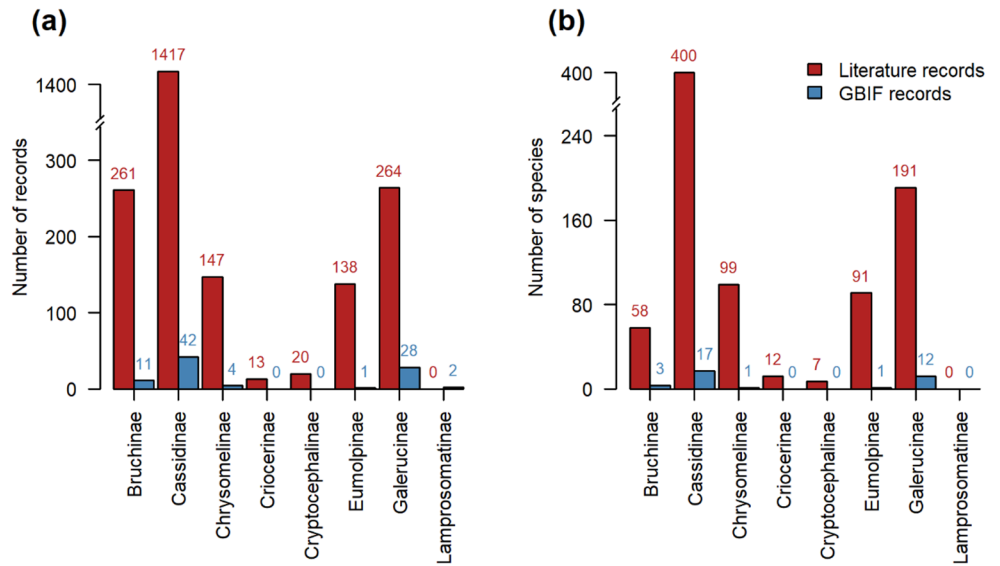


Fig. 3 Temporal bias of Chrysomelidae records obtained from the literature review and the Global Biodiversity Information Facility (GBIF) database between 1884 and 2024, highlighting the contributions from different authors

of Cryptocephalinae. Eumolpinae in Ecuador were documented through 138 literature records and one GBIF record, indicating the presence of 91 species. Galerucinae exhibited the second highest species richness in Ecuador, with 191 species compiled from 264 literature records and five additional species from 28 GBIF records. Finally, Lamprosomatinae had the fewest records, with only two records in GBIF, representing two individuals preserved at Texas A&M University Insect Collection and identified as *Oomorplus* sp.

Record biases

Out of 1,601 chrysomelid records with information on collection date, the highest number of records (1,184) corresponded to the period between 1975 and 1999, while the period between 1845 and 1870 had the fewest records (2). The 25-year time period between 1975 and 1999 had significantly greater number of chrysomelid records than expected by chance (Chi-square test; $p < 0.05$). From the year 2000 onwards, the number of leaf beetle records in Ecuador progressively decreased (Fig. 3).

Across all 25-year time periods, the nearest neighbor index was close to zero, indicating that occurrences were spatially clustered. This clustering occurred along roads, rivers, and around scientific stations and urban areas, instead of being randomly distributed throughout the study area. The highest numbers of both records and species were found in the Andean highlands region with 992 records of 371 species, while the Coastal plain region had the lowest number of records and species in mainland Ecuador, with 337 records of 152 species. The Amazon region housed 446 records of 175 leaf beetle species. Galapagos Islands was the Ecuadorian region with the fewest number of records and species, with 73 records of 10 species.

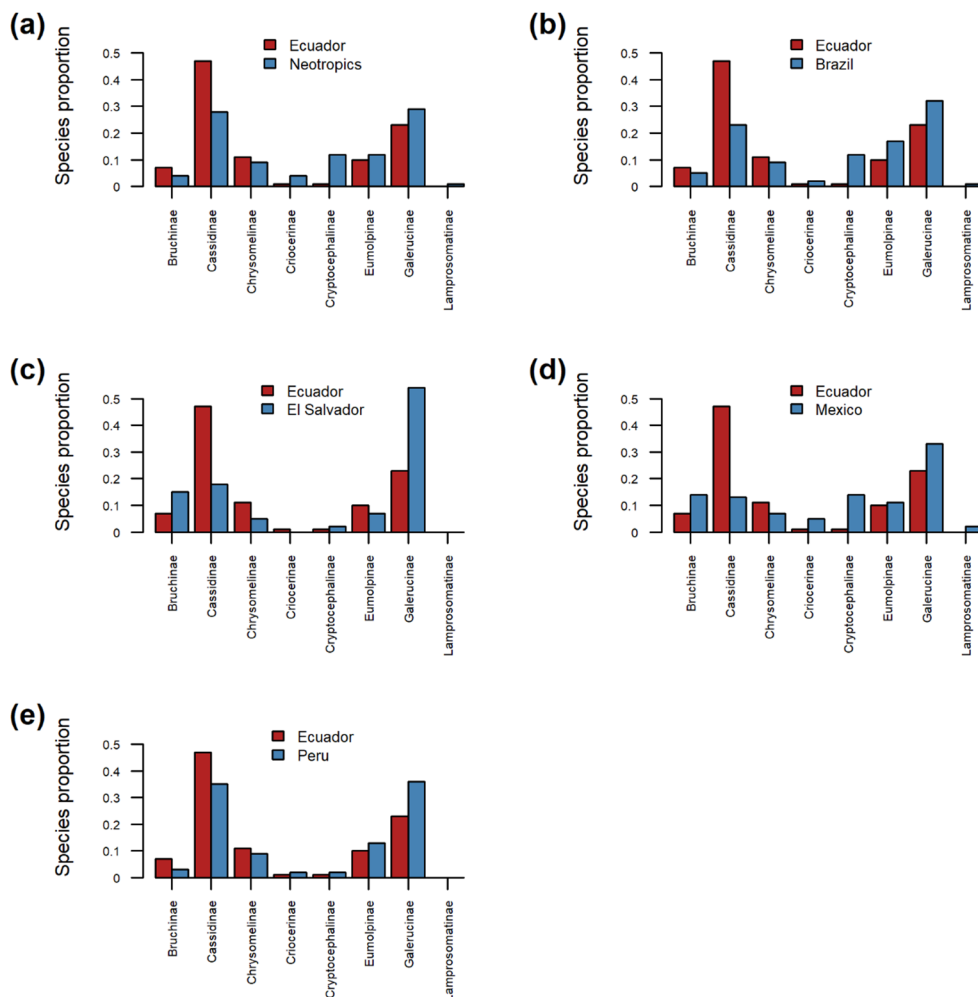
Taxonomic bias was evaluated by assessing significant differences in the proportion of species by subfamily between Ecuador and those of the entire Neotropical region, Brazil, El Salvador, Mexico, and Peru. Chi-square tests revealed that the proportions of Ecuadorian leaf beetle species differed significantly from those observed in these regions ($p < 0.05$) (Fig. 4). Additionally, pairwise comparisons of species proportions among the Neotropical region,

Brazil, El Salvador, Mexico, and Peru also showed consistent significant differences ($p < 0.05$).

Observed and potential leaf beetle richness patterns in Ecuador

Observed Chrysomelidae richness pattern analysis revealed a total of 321 10×10 km grid cells (11.22%) containing at least one species and 2,540 empty 10×10 km grid cells (88.78%) in Ecuador (Fig. 5a). The highest species richness was obtained in the Esmeraldas province near San Javier de Cachabí, with 44 chrysomelid species. Other locations with high species richness, each reporting over 30 species, included: Jatun Sacha Biological Reserve in Napo province, with 43 leaf beetle species; Macas in Morona-Santiago province, with 36 species; Tena in Napo province, with 35 species; El Reventador in the Cayambe-Coca National Park in Sucumbíos province, with 33 species; and Mera in Pastaza province, with 31 species (Fig. 5a). There was an overrepresentation of 10×10 km grid cells with the lowest species richness values, including 148 cells containing one leaf beetle and 61 cells with two species only (Fig. 5a). The

Fig. 4 Chrysomelidae species proportion by subfamily comparison between Ecuador and **a** Neotropics, **b** Brazil, **c** El Salvador, **d** Mexico, **e** Peru. Leaf beetle species proportions data was obtained from the literature review, the Global Biodiversity Information Facility (GBIF), and the leaf beetle checklists from the Neotropical region (Blackwelder 1946), Brazil (Linzmeier and Moura 2025), El Salvador (Van Roie et al. 2019), Mexico (Ordóñez-Reséndiz and López-Pérez 2021), and Peru (Chaboo 2015a, 2015b; Chaboo and Flowers 2015a, 2015b; Chaboo and Schmitt 2015; Chaboo and Schöller 2016; Chaboo and Staines 2015; Furth et al. 2015)



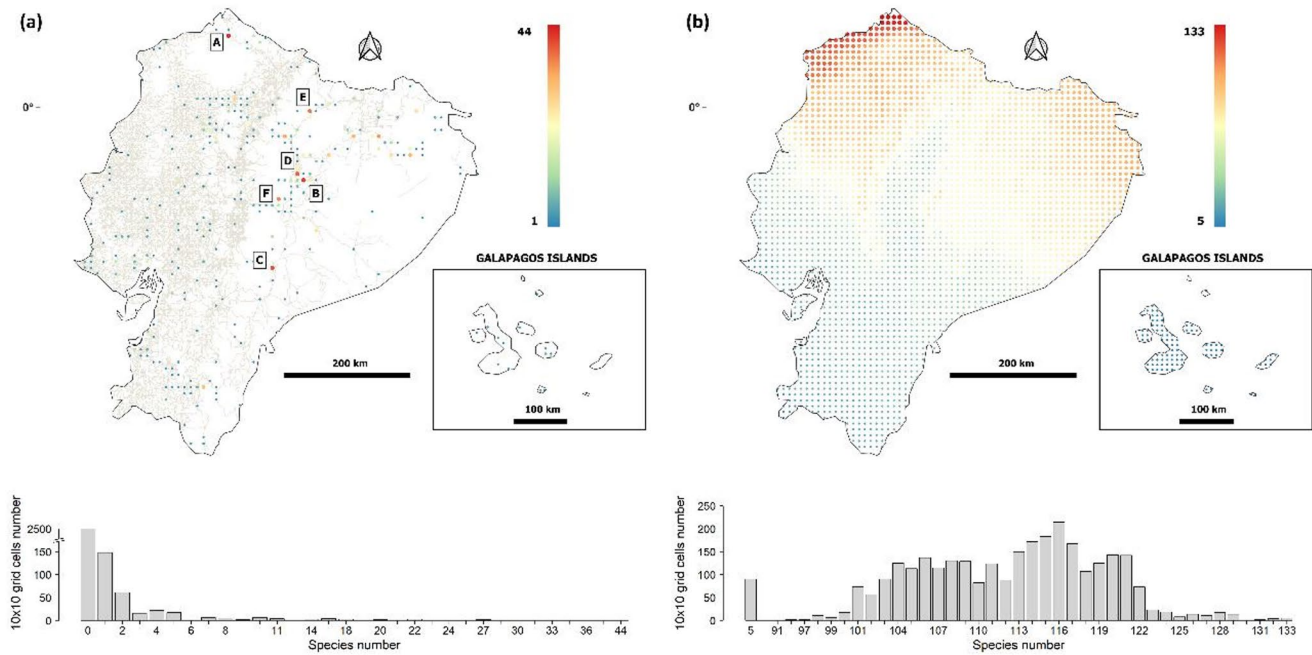


Fig. 5 **a** Observed Chrysomelidae species richness map from Ecuador. Location A: San Javier de Cachabi in Esmeraldas province, location B: Jatun Sacha Biological Reserve in Napo province, location C: Macas in Morona-Santiago province, location D: Tena in Napo province, location E: El Reventador into the Cayambe-Coca National Park in Sucumbios province and location F: Mera in Pastaza province. The

light grey lines on the map represent the Ecuadorian road network. **b** Potential Chrysomelidae species richness map from Ecuador. The figure includes the equator coordinates, the Ecuadorian physiographic regions, and two histograms indicating the number of chrysomelid species in each 10×10 km grid cells

highest number of Chrysomelidae species was found in the Andes highlands physiographic region (371 species), while the Galapagos Islands region had the lowest number of species (10 species). Amazon and Coastal plain regions housed 175 and 152 species, respectively.

Potential species richness based on distance-constrained SDM revealed a heterogeneous richness pattern across the Ecuadorian latitudinal gradient (Fig. 5b). The northernmost area in the Coastal plain physiographic region had the highest potential leaf-beetle richness values, ranging between 125 and 133 species, located in 77 10×10 km grid cells across Esmeraldas province. The lowest potential leaf-beetle richness values, ranging between 5 and 104 species, was observed in 475 10×10 km grid cells across the Galapagos Islands and in the southernmost areas of the Coastal plain and Andean highlands physiographic regions. At intermediate Ecuadorian latitudes, the Andean highlands was the physiographic region with the lowest potential leaf beetle species richness, between 105 and 114 species. SDM predicted the highest potential richness in the Coastal plain region with 138 species. Andean highlands and Amazon regions had similar potential richness values, with 128 and 124 species, respectively. The Galapagos Islands region showed the lowest predicted richness, with only five leaf beetle species.

Estimating total number of Chrysomelidae in Ecuador

Potential leaf beetle richness estimates based on SDM revealed that 144 species of chrysomelids present in other regions of the Neotropical realm had bioclimatic conditions compatible with their presence in Ecuador, including 42 species not previously recorded in the country (Fig. 6, Online Resource 3). This suggested that regional species richness might be 4.71% higher than estimates based solely on number of recorded species.

Furthermore, the analysis of proportions of leaf beetles to vascular plant species richness indicated that well-sampled tropical countries such as Brazil, El Salvador, Mexico, and Peru had one species of leaf beetle per 6 to 11 species of vascular plants. In contrast, the ratio in Ecuador was one species of leaf beetle per 23 species of vascular plants (Table 1). Based on the 19,903 species of vascular plants recorded in the country and the ratios of leaf beetle to vascular plant species richness observed in well-samples tropical countries, we estimated that there might be between 1,821 and 3,315 chrysomelid species in Ecuador.

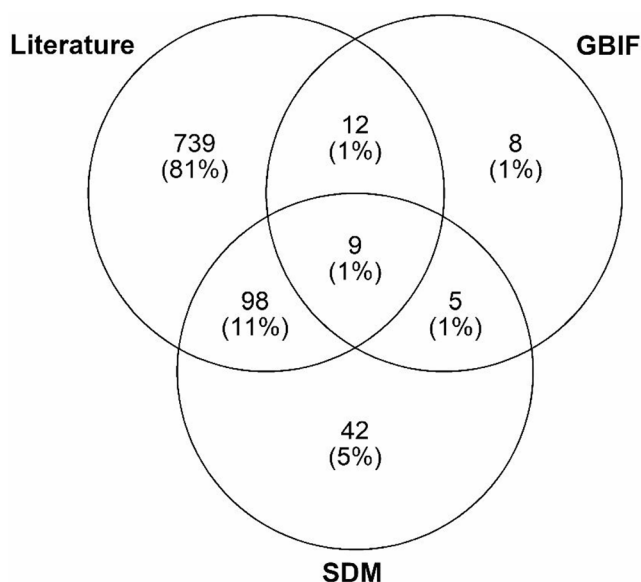


Fig. 6 Venn diagram displaying the Chrysomelidae species numbers and percentages from Ecuador sorted by source: literature review, Global Biodiversity Information Facility (GBIF) dataset, and species distribution models (SDM) across the Neotropical region

Table 1 Chrysomelidae and vascular plants species number from Ecuador, Brazil, El Salvador, Mexico, and Peru and leaf beetle-vascular plants species ratios for each tropical country. Leaf beetle species number in Brazil, El Salvador, Mexico, and Peru was compiled from Chaboo (2015a, 2015b); Chaboo and Flowers (2015a, 2015b); Chaboo and Schmitt (2015); Chaboo and Schöller (2016); Chaboo and Staines (2015); Furth et al. (2015), Linzmeier and Moura (2025), Ordóñez-Reséndiz and López-Pérez (2021), and Van Roie et al. (2019). Vascular plants species number was obtained from Flora e Funga do Brasil (2025), Ulloa Ulloa et al. (2017), Villaseñor (2016) and the Global Biodiversity Information Facility (GBIF) dataset published by the Missouri Botanical Garden

Country	Chrysomelidae species number	Vascular plants species number	Chrysomelidae-vascular plants richness ratio
Ecuador	871	19,903	1:23
Brazil	6,462	38,542	1:6
El Salvador	420	3,863	1:9
Mexico	2,505	23,314	1:9
Peru	1,767	19,147	1:11

Discussion

The Chrysomelidae species checklist generated in this study significantly increased the knowledge of leaf beetle diversity in Ecuador, expanding from 352 species in Blackwelder's catalogue (1946) to 871 species. The highest numbers of Chrysomelidae were found in the subfamilies Cassidinae and Galerucinae, representing 46.7% and 22.5% of the total species reported from Ecuador, respectively. Conversely, the subfamilies Criocerinae (1.4%), Cryptocephalinae (0.8%) and Lamprosomatinae (0%) had the lowest

documented species richness in Ecuador, with only eleven and nine published references containing Criocerinae and Cryptocephalinae species records, respectively. Lamprosomatinae records were not identified to the species level. The low representation of these subfamilies aligns with patterns observed in other tropical countries like Costa Rica, El Salvador, and Panama (Van Roie et al. 2019; Vencl et al. 2004). The limited number of informative leaf beetle records from Ecuador in the GBIF database is mainly due to two factors: most Ecuadorian records published in the literature lack georeference, and they have a high degree of taxonomic uncertainty, with many records of Chrysomelidae stored in museums and universities pending identification to species or even genus level. The underrepresentation of tropical insect groups is a pervasive issue, as less than one-third of the described insect species have occurrence data stored in electronic databases (Anderson et al. 2016; García-Roselló et al. 2015, 2023; Troudet et al. 2017). Electronic databases have not been around for too long nor has their potential been universally accepted or financially supported.

The temporal bias in Ecuadorian records of Chrysomelidae aligns with patterns observed in other tropical insect groups, showing large temporal gaps (Daru and Rodriguez 2023). Data accumulation for insect inventories requires extended periods (Fattorini 2013; Lobo and Borges 2010). Notably, there has been a progressive decrease in published chrysomelid records since 2000 which contrasts with trends observed in other insect groups over recent decades (Girardello et al. 2019; López-Bedoya et al. 2024; Rocha-Ortega et al. 2021). This decline may reflect the dwindling number of specialists focusing on this family in Neotropical areas, and perhaps a progressive lack of interest in taxonomy (Engel et al. 2021).

The collection localities and observed richness in chrysomelids (Fig. 5a) reflect a clear pattern in sampling effort, but this does not negatively affect the models (Fig. 5b), which are indeed unbiased. The main cause of the observed richness pattern is the presence of accessible areas with infrastructure that facilitates fieldwork, such as roads or facilities in national parks or biological stations (Amano and Sutherland 2013; Cayuela et al. 2009; Dennis and Thomas 2000; Girardello et al. 2019; Kadmon et al. 2004; Romo et al. 2006). Second, the majority of researchers in Ecuador (and elsewhere) are employed by institutions located in the largest cities, and thus the majority of their collections, as well as those of visiting researchers who rely on local assistance, come from nearby localities. This phenomenon seems to explain the high number of records observed in central Ecuador. Third, the sampling process often targets areas that are perceived to have high overall biodiversity. The complex topography of the Andean highlands region, combined with elevational and latitudinal environmental

gradients, results in a high habitat heterogeneity that supports remarkable biodiversity (Godoy-Bürki et al. 2017; Hole et al. 2011; Kreft and Jetz 2007; Zador et al. 2015). However, the number of collections is primarily influenced by accessibility, and the lack of infrastructure in the Amazon lowlands may explain the paucity of records from this region, despite being one of the most biodiverse places on Earth (Bass et al. 2010). Notwithstanding the importance of these three factors, the observed richness pattern suggests the influence of other underlying factors. The northeastern area of the coastal plains region, which are part of the Choco biogeographic region, are another recognized biodiversity hotspot (Myers et al. 2000; Sierra et al. 2002), and they have a well-developed road network and infrastructure, making them easily accessible for sampling. However, they have the lowest number of chrysomelid records, except for a single sampling event around San Juan de Cachabí. This pattern could be attributed to the loss of biodiversity due to high rates of deforestation and agricultural production, but the threats posed by drug trafficking, illegal logging, and mining may have led to the avoidance of biodiversity surveys in this region.

As expected, we found that the proportion of chrysomelid species in Ecuador differed from that of the entire Neotropical region. This aligns with the findings of Reid (2017), who reported that species proportions by subfamily are not consistent across regions, such as Australopapua (Australia and New Guinea). However, contrary to our expectations, the proportions of chrysomelid species by subfamily in Ecuador also differed from those in other countries where the distribution of species among subfamilies was expected to be similar, such as Brazil, El Salvador, Mexico, or Peru. These differences may be attributed to both environmental and historical factors, as the high environmental variability over short distances in Neotropical countries likely influences species distribution and promotes speciation (Hodkinson 2005; Hooghiemstra et al. 2006; Larsen et al. 2011; Price 2009). Additionally, this observed taxonomic bias may also reflect regional differences in research focus and taxonomic effort across subfamilies. Historical taxonomic research efforts on the Chrysomelidae in the Neotropics have been limited, given the enormous diversity of this beetle group in the region. Research has largely been the domain of a few taxonomists specializing in particular groups, contributing to taxonomic bias among Chrysomelidae subfamilies. Significant contributions to the characterization of the Neotropical Chrysomelidae fauna have been made by several entomologists: J. S. Baly, J. Bechyné, R. E. Blackwelder, C. H. Boheman, L. Borowiec, C. S. Chaboo, R. W. Flowers, J. Gómez-Zurita, M. Jacoby, C. D. Johnson, A. Konstantinov, M. Pic, V. Sabini, L. Sekerka, F. Spaeth, C. L. Staines, E. Uhmman, and M. J. Viana. Their research focused on

subfamilies such as Bruchinae, Cassidinae, Chrysomelinae, Eumolpinae, and Galerucinae, which are distributed throughout Central and South America. However, Criocerinae, Cryptocephalinae, and Lamprosomatinae still remain poorly studied in the Neotropics (Chaboo and Schöller 2016; Van Roie et al. 2019), with some exceptions in Brasil (Linzmeier and Moura 2025), Mexico (Jacoby 1880–1892; Moldenke 1970, 1981; Ordóñez-Reséndiz and López-Pérez 2021), and Argentina (Agrain et al. 2017).

Observed and predicted species richness patterns of Chrysomelidae from Ecuador show similarities and discrepancies. Both patterns agree that the highest richness values occur in the Chocó biogeographic region in northwestern Ecuador. The greatest discrepancy between the two patterns occurs in the Andean highlands physiographic region. The observed richness pattern indicates that the Andean highlands region has higher species richness than the coastal plain and Amazon regions, whereas the predicted richness pattern shows the opposite trend. In addition to the differences in sampling effort discussed above, these discrepancies in leaf beetle richness may be explained by the fact that SDM predict higher species richness in Ecuadorian regions with greater annual mean temperature and precipitation. These abiotic factors positively influence beetle species richness, as they affect the seasonal activity of beetle species (Fremlin and Fremlin 2010; Lachat et al. 2012), and drive ecosystem productivity, thereby increasing food availability for phytophagous beetles (Linzmeier and Ribeiro-Costa 2008, 2013). Overall, these differences likely reflect undersampling in ecologically rich but poorly surveyed regions of Ecuador.

Species distribution models based on GBIF records predicted the potential presence in Ecuador of 42 leaf beetle species currently known from Mexico to Paraguay and not yet recorded in the country. Adding these data to the observed species richness in Ecuador would increase the potential richness to 913 species. Based on richness ratios for Chrysomelidae and vascular plants found in well-sampled tropical countries, we estimated that the total number of chrysomelids in Ecuador would potentially be between 1,821 and 3,315, which is between 109 and 280% greater than the number of recorded species and between 99 and 263% greater than the number of recorded species plus the number of species predicted by SDM. These estimates of potential chrysomelid richness are consistent with the findings of Kuschel (1963) and Peck and Kukalová-Peck (1990) for the Galápagos Islands, who used vascular plant richness to suggest that between 184 and 634 species of phytophagous beetles had not yet been reported from the islands. However, the proportion of unrecorded species in Ecuador may be even higher for two main reasons. First, estimates of the “Linnean shortfall” (i.e. knowledge gaps for species

taxonomy; Brown and Lomolino 1998) suggest that the number of insect species worldwide is three to six times greater than the number currently described (Lin et al. 2022; Stork 2018). Second, in some tropical regions, the ratio of beetle species—particularly within certain groups—to plant species may surpass the ratios observed in our study. This suggests that the actual number of Chrysomelidae species in Ecuador could be up to an order of magnitude higher than currently recorded.

Conservation prospects

Comprehensive species checklists and detailed species distribution information are crucial for advancing ecological, evolutionary and conservation research (Lagomarsino and Frost 2020; Mace 2004; Yañez-Arenas et al. 2014). The limited scope of basic biological research, often due to a lack of expertise and resources, as well as various shortfalls identified by the scientific community, hinder the development and implementation of effective conservation strategies for tropical insect species (Cardoso et al. 2011; New 1997). Addressing these shortfalls is essential for the effective conservation of these species.

Enhancing taxonomic and distributional knowledge of tropical insect communities is critical for several reasons. First, it helps to reduce the Linnean (Brown and Lomolino 1998), Wallacean (knowledge gaps for species distribution) (Lomolino 2004), Prestonian (knowledge gaps for species abundance) and Hutchinsonian (knowledge gaps for abiotic tolerances of species) shortfalls (Cardoso et al. 2011). Second, it provides a better understanding of biodiversity patterns, which is fundamental to identifying areas of high conservation priority (Funk and Richardson 2002; Jones et al. 2009; McNeely 2002). Finally, it helps to elucidate the evolutionary processes that generate and maintain biodiversity (Lagomarsino and Frost 2020), providing insights into how species adapt to their environments and the potential impacts of environmental change.

In the context of Ecuador, improving our understanding of the taxonomy and distribution of chrysomelids will have significant conservation implications. Comprehensive data will allow the identification of key habitats and the formulation of targeted conservation strategies (McNeely 2002; Nagy et al. 2023). This is particularly important in a country known for its rich biodiversity and high levels of endemism (Castro and Espinosa 2015; Espinoza and Noriega 2018; Thormann et al. 2018). Moreover, improved taxonomic and distributional data can increase the effectiveness of biodiversity monitoring programs. By providing baseline data, these programs can track changes in species populations over time, thereby informing adaptive management strategies that can respond to emerging threats such as habitat

loss, climate change, and invasive species (Mace 2004; Sanitha and Madeswaran 2020). Improved taxonomic data on leaf beetles will also provide a stronger foundation for future research aimed at collecting detailed information on plant-insect associations, as well as interactions between insects and their predators, parasites, and symbionts. Such data are essential for advancing our understanding of ecological interactions and the natural history of Ecuadorian ecosystems, ultimately contributing to more informed conservation and management strategies.

In conclusion, the future of conservation in Ecuador depends heavily on strengthening our knowledge of the taxonomy and distribution of tropical insects, especially in those groups with high species diversity such as the Chrysomelidae. This endeavor will not only contribute to global biodiversity conservation efforts, but will also ensure the preservation of Ecuador's unique and diverse biological heritage.

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Data availability Data is provided within the manuscript or supplementary information files.

Declarations

Competing interests The authors declare no competing interests.

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