The distribution of the species of Eurysternus Dalman, 1824 (Coleoptera: Scarabaeidae) in America: potential distributions and the locations of areas to be surveyed

Authors: Edgar, Camero R , and Lobo, Jorge M.

Research Article

The distribution of the species of *Eurysternus* Dalman, 1824 (Coleoptera: Scarabaeidae) in America: potential distributions and the locations of areas to be surveyed

Edgar Camero R[1] and Jorge M. Lobo[2*]

[1]*Departamento de Biología, Universidad Nacional de Colombia. P.O. Box: A.A. 14490 Bogotá, Colombia. E-mail: eecameror@unal.edu.co*

[2]*Departamento de Biodiversidad y Biología Evolutiva, Museo Nacional de Ciencias Naturales. c/ José Gutiérrez Abascal 2, 28006. Madrid. España. E-mail: mcnj117@mncn.csic.es*

*Corresponding author email: mcnj117@mncn.csic.es

Abstract

Using the distributional information from approximately 22,000 georeferenced records of the 53 currently recognized species of the genus *Eurysternus* Dalman, 1824, we explore the main macroclimatic determinants capable of explaining the distribution of these species. We also estimate the potential distribution of these species using a previously established protocol. Our results show that annual mean temperature and annual precipitation are the variables with the greatest explanatory capacity. Our results also show that species with wide climatic niches would primarily inhabit the rainiest and coldest American locations. The potential species-richness map derived from the overlap of individual potential distributions has allowed us to identify suitable areas that are not yet adequately surveyed. Future investigations must be conducted in these areas to improve the biogeographical and taxonomic knowledge of this genus.

Key words: Scarabaeidae, Neotropical region, ENFA, potential distribution, survey design.

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Introduction

Catalogues of species names and atlases of distributions are essential to describe and understand the patterns of biological diversity [1]. Unfortunately, almost-universal biases and incompleteness in the available distributional information on invertebrate species [2-4] hinder the reliability and usefulness of this information. In the case of distributional information, several methodological procedures seek to derive geographical representations of "real" or "potential" distributions from partial chorological data and different environmental predictors [5]. These so-called species distribution models (SDMs) or ecological niche models (ENM) have used the exponentially growing number of massive biological and environmental databases that are freely available on the World Wide Web [6, 7], aided by increasing computational and statistical capacity [8].The modeling procedures use different conceptual and methodological approaches. We highlight those approaches that use the available information on species occurrence to determine the environmental conditions prevailing where the species are present (the species' Grinnellian niches [9]) in order to predict the suitable region ("potential distribution" [10]). Because these potential distributions are partial geographical representations of localities with climatic conditions similar to those where the species of interest are known to occur, these simulations are useful for designing future surveys to improve biogeographical and taxonomic knowledge [11-17].

The genus *Eurysternus* Dalman, 1824 is the only genus of the tribe Eurysternini and one of the three Neotropical endemic dung beetle groups, together with the Eucraniini and Phanaeini [18]. The genus presents many morphological and ecological particularities within the subfamily Scarabaeinae. *Eurysternus* is distributed from central Mexico to southern Brazil. This genus occurs across a broad range of forest conditions and consumes a varied diet of carrion, faeces, and even leaves [19-21]. The taxonomy of the genus has recently been revised [22], increasing the number of recognized species from 31 to 53. In this study, we compile and georeference the distributional information on the *Eurysternus* species available in an exhaustive number of natural history collections and bibliographic sources. The purposes of the study are: i) to examine the general macroclimatic determinants associated with the occurrence of these species, ii) to estimate the potential distributions of each of these species for the American continent, and iii) to distinguish those climatically suitable areas that have not been adequately surveyed to pinpoint the regions that need to be explored in the future.

Methods

Information from the Musée Canadien de la Nature (CMNC) database was the primary source of distributional and taxonomic information [22]. This information was complemented by data from other museum specimen labels (see Appendix 1) and bibliographic sources (see Appendix 2). All of this information was included in the MANTIS v. 2.0 [23] database system. The resulting database currently includes approximately 22,000 records belonging to the 53 currently recognized *Eurysternus* species [22]. The locations were georeferenced using freely available gazetteers at GeoNet Names (see http://www.geonames.org/ [24]). Due to differences in the geographical precision of the information sources, a cautious approach was applied through the use of relatively high resolution (0.08° cells; approximately 100 km^2, depending on the latitude) to fit both climatic and biological information. All of these data will be freely available in www.biogeografia.org.

The potential distributions were estimated with a multidimensional envelope procedure according to the protocol recently proposed by Jiménez-Valverde *et al.* [10] and the former conceptual proposals [25, 26]. The aim of these methods is to obtain geographical representations of the set of locations with climatic

conditions similar to those where the organisms of interest are known to be present. The goal is to geographically represent the set of abiotic requirements in which a species can maintain a net positive rate of population increase without immigration (i.e. a geographical representation of the species' Grinellian niche [10]). Presence data are the unique source of information used to determine potential distributions; this implies the assumption that the environmental conditions in these presence localities constitute a partial but reliable description of the whole climatic requirements of the species.

The 19 freely available bioclimatic variables provided by WorldClim (see www.worldclim.org [27].) obtained by the interpolation of climate-station records from 1950 to 2000 (for details, see [7]) were used as predictors. As the number of used predictors may condition the obtained potential representation, most relevant predictors were selected by using Ecological Niche Factor Analysis (ENFA; see [28]), which is a method firmly rooted in the niche concept [29]. ENFA computes new uncorrelated factors by comparing climatic data in presence locations with conditions in the entire study area. This procedure serves to maximize both the marginality (the distance between the optimum recorded for the species and the average climatic conditions in the area) and the specialization values of the species (the ratio between the climatic variability in the study area and that existing at the points where the selected species occurs). The factors were retained based on their eigenvalues relative to a broken-stick distribution [28]. The original bioclimatic variables selected for each species are those that show the highest correlation values with these retained ENFA factors (absolute factor scores > 0.30). After the most relevant bioclimatic variables were selected individually for each species, we calculated the maximum and minimum scores (the extreme bioclimatic values) in all observed presence cells. All of the cells with climatic values falling within that range were selected as suitable to derive a binary potential distributional hypothesis. This procedure assumes that the recorded occurrences provide a reliable representation of the full spectrum of climatic conditions in which the species can survive and reproduce [10, 30].

Based on the ENFA analyses, the two most relevant bioclimatic variables were used to obtain further estimates. Specifically, the maximum and minimum scores for these variables in the observed presence cells were used to estimate the bioclimatic tolerance of species (maximum-minimum), as well as their averaged conditions (maximum-minimum/2 + minimum). The correlation between the tolerance and the average bioclimatic value was determined with a Spearman rank correlation coefficient (*rs*). Because the tolerance values depend on the scale measurements, both the temperature and the precipitation values were transformed to a 0-100 scale. Subsequently, minimum and maximum values in the observed localities for each one of the two previously selected variables were used to calculate the climatic area covered by each species, according to the rectangle defined by the ranges in temperature and precipitation values. These climatic-area values were used to estimate the percentage of climatic area overlapped among all possible pairwise species comparisons. Species with fewer than five 0.08º presence cells are excluded from these calculations (n = 6).

Multidimensional envelopes were obtained for each species. The potential distributions obtained from these analyses were overlaid to obtain a map of the potential species richness. This map showed a geographical picture that represented the capacity of a locality to harbor suitable climatic conditions without considering the limits imposed by contingent forces such as biotic factors or dispersal limitations. For the four species occurring in three or fewer 0.08º cells, multidimensional envelopes were constructed by increasing by 10% the minimum and maximum climatic values found at the occurrence points for the five most relevant variables (see Appendix 3). The location of the available database records was superimposed on this potential richness map to identify those potentially diverse regions that were not sufficiently surveyed. As we develop geographical representations of potential distributions, comparing the derived potential species richness map to current knowledge of realized distributions suggest that some climatically

suitable areas may be uninhabited due to dispersal limitations (as in the case of Caribbean islands or northern zones above the Isthmus of Tehuantepec). However, when the relevance of these dispersal limitations decreases, as in the case of tropical South American areas, we assume that the comparison of the obtained potential species map with the distribution survey may provide useful information on the location of unrecorded places.

Results

The bioclimatic variables that most frequently showed statistically significant correlations with the retained ENFA factors are the annual mean temperature (in 96% of the species), the annual precipitation (in 43% of the species) and the mean diurnal range of temperature (in 51% of the species). Only two other bioclimatic variables appear in at least 20% of the species: the maximum temperature of the warmest month and the annual range of temperature (Appendix 3). ENFA analyses also indicate that the different factors selected generally explain more than 97% of the total species information. The marginality values range between 0.37 and 3.30 (mean ± standard deviation; 1.17 ± 0.70) and the vast majority of species show high values of specialization (Appendix 3).

The tolerances of *Eurysternus* species for the annual mean temperature and the annual precipitation, which are the most relevant variables, are significantly correlated (rs = 0.705; n = 47; P < 0.001). Tolerance values (Fig. 1) are negatively correlated with the average annual temperature (rs = -0.731; P < 0.001) but positively correlated with the average annual precipitation (rs = 0.682; P < 0.001).
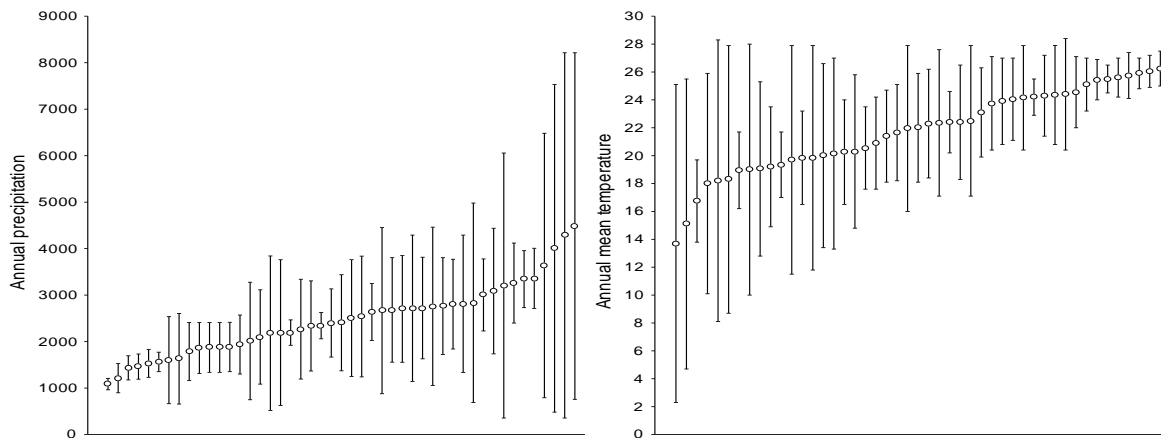
Fig. 1. Relationship between the averaged annual mean temperature and annual precipitation values of the 0.08º presence cells for each species (open circles) and the tolerance values (maximum-minimum) represented by whisker plots. Only those species with at least five occurrence cells are represented. The species (X-axes) are ordered according to their average temperature and precipitation values.

From the 1,081 possible pairwise estimates of the shared climatic area for the 47 species considered, in only 61 instances (5.6 %) does a pair of species share more than 50% of the total estimated climatic area. The average percentage of overlap was 15.4 ± 15.9% (mean ± standard deviation).

The sum of the individual potential distributions indicates that the highest values of potential species richness for *Eurysternus* species can be found in lowland areas below 1000 meters in altitude throughout the North America's east coast, South Florida, the Caribbean islands, the continent´s southern Andean highland zone and the Amazonian region (Fig. 2).
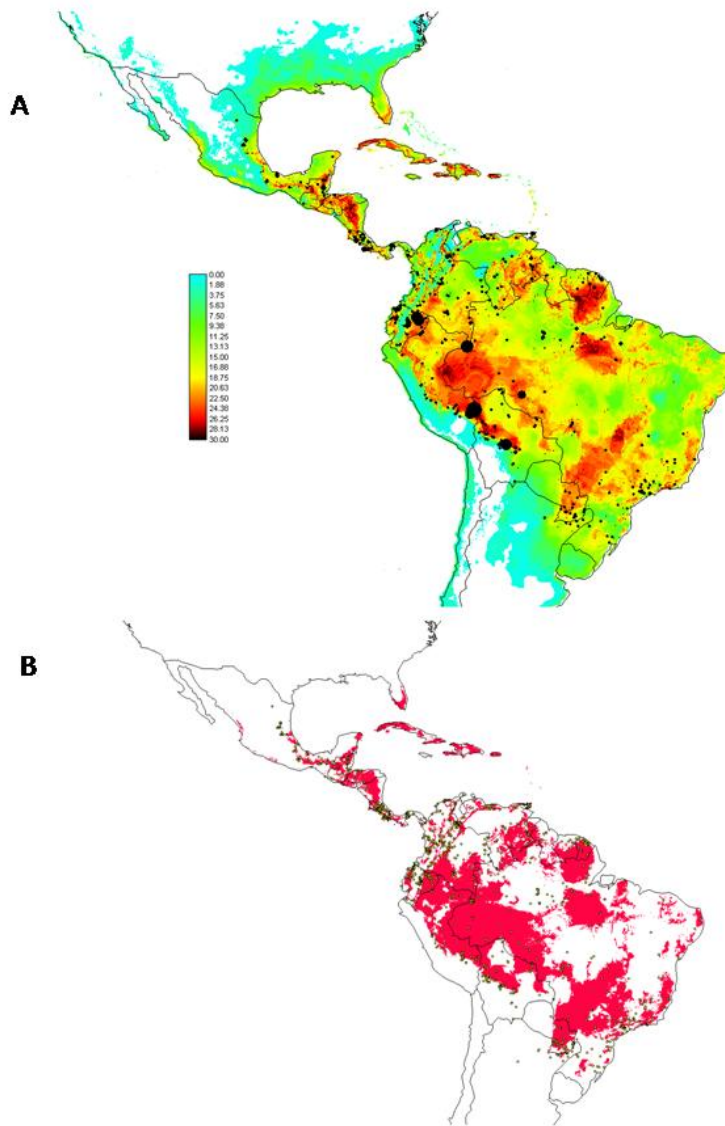
Fig. 2. (A) Potential species richness map for *Eurysternus* derived from the overlap of individual potential distributions. The records available in the database are represented by black dots with sizes corresponding linearly with the number of database records. (B) Areas with greater potential richness (upper quartile > 19 species) and location of the database records.

Discussion

Temperature-related variables appear to play the most important role in explaining American *Eurysternus* distributions. Because the marginality values range between 0 and 1 in 95% of the cases where the distribution is normal [28], approximately one-half of the species would have a climatic "optimum" similar to that of the averaged tropical American climatic conditions (marginality < 0.90); almost one-quarter would occur in climatic conditions relatively distant from the mean conditions (marginalities between 0.9 and 1.5); and one-quarter would occur under distinctive climatic conditions (marginality > 1.5).

While the derived climatic optimum of *Eurysternus* species is relatively variable, the obtained high specialization values suggest that these species generally live under highly restricted climatic conditions. In all, fifteen species show specialization values between 6 and 10, twenty-four species show values greater than 10, and seven species (*E. cavatus*, *E. cambeforti*, *E. fallaciosus*, *E. gilli*, *E. truncus*, *E. calligrammus* and *E. uniformis*) inhabit extremely specialized climatic conditions. The remaining twelve species have specialization values of approximately 5 or less, showing that they occupy a range of climatic conditions approximately five times smaller than the climatic range of the entire continent. The specialization character of *Eurysternus* species is related to low average percentage of overlap in the climatic conditions between all pairwise comparisons. Thus, although most species are typically associated with semitropical or tropical conditions, each appears to occur under relatively specific climatic conditions.

The correlation between species tolerance values for the two most important climatic variables suggests that the occurrence of these species in a broad range of temperature conditions is associated with their occurrence in a broad range of precipitation values. Therefore, we infer that a broader climatic niche in *Eurysternus* species implies at the same time a tolerance for different temperature and precipitation values. As was to be expected, the more temperature-tolerant species are those capable of living under colder conditions, whereas the most precipitation-tolerant species generally tend to occur under rainier conditions. As a consequence, the *Eurysternus* species with wider climatic niches would primarily inhabit the rainiest and coldest suitable American localities, which are mainly located in the Andean mountains (Fig. 3). Subsequent analyses should try to determine the ancestral or derived phylogenetic position of these tolerant Andean species.

As in other groups [31], dispersal constraints and historical factors seem to have played a determining role in the conformation of current American *Eurysternus* distributions, because these species are currently absent from certain *a priori* favorable climatic regions. Both the whole potential species richness map (Fig. 2) and individual predictions (Figs. 4 to 53) indicate that southern North America, Central America, the Caribbean islands and the southwestern portion of South America are frequently climatically suitable but uninhabited by many species. However, the role of dispersal limitation and historical factors should be minimized when the connectivity of the potential localities increases. Under these conditions it is more probable that the available records of *Eurysternus* species are incomplete and biased such that "real" distributions are wider than observed ones. How to detect these unsurveyed localities?
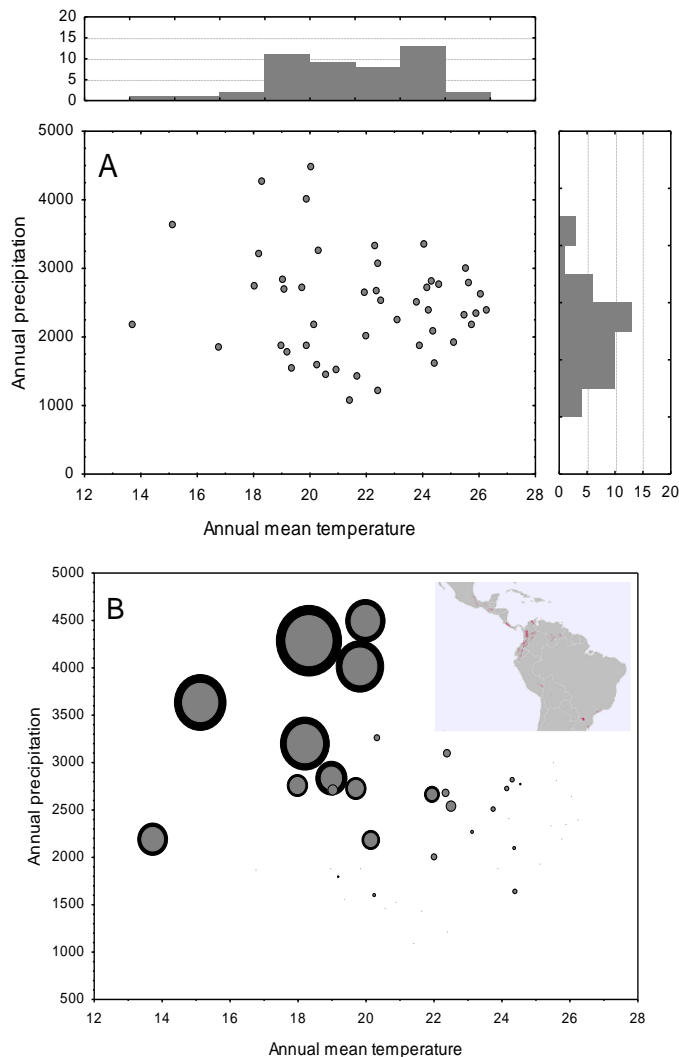
Fig. 3. (A) Relationship between the averaged annual mean temperature and annual precipitation values in the 0.08º presence cells for each species. Histograms on top and right-hand side show the frequency of these variables. **(B)** The same relationship plotted with circles whose sizes are linearly related to the climatic area covered by each species according to the range of temperature and precipitation values associated with that species. The map represents those areas suitable for any *Eurysternus* species with mean annual temperatures lower than 20ºC and annual precipitation values higher than 2000 mm.

Implications Implications for conservation

Distribution models can be applied in conservation when we are able to generate reliable predictions of realized distributions that can be coupled with reserve selection algorithms. Unfortunately, the lack of reliable absence information seriously hinders this approach [25]. When only partial representations of the potential distribution can be estimated (as in this case and in most exercises that use invertebrate data), the obtained simulations may help to delimit those areas that are potentially rich in species but not yet adequately surveyed [32]. In the future, new species may even be found in these areas [11, 12], allowing to generate more accurate distributional maps and a better taxonomical knowledge that can be subsequently used for conservation purposes.

According to our results, many of the areas with greater potential richness values (upper quartile > 19 species) are located in Central America, extending from the Yucatán Peninsula to the Panama Canal. As a substantial number of database records exist for this area, we suspect that most species that potentially inhabit this region are in fact absent due to dispersal limitation. In South America, the areas with the

greatest potential richness generally correspond to lowland zones: inter-Andean valleys, Andean lowlands, the western, central and southern regions of the Amazon and lowlands of the Guyana Shield. However, only a few of these areas have a substantial number of records: the upper Amazon at the frontier between Perú and Bolivia, the Amazon region of Leticia in the north of Perú and the south of Colombia, as well as the Andean region in northern Ecuador. The remaining climatically favorable areas include few records.

These findings suggest that future collection surveys aimed at improving the present taxonomic and biogeographical knowledge of Neotropical *Eurysternus* should be conducted in the upper Brazilian Amazon (Jurua and Rio Branco basins), the lower Amazon region between Manaus and Santarem, Amapá and the Guyanas, Mato Grosso to Paraguay, and in Central America, in Honduras and Nicaragua.

Acknowledgments

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Ap**pendix 1. Examined collections whose taxonomical and distributional information was included in the *Eurysternus* database.**

ABTS: Personal Collection. Andrew B. T. Smith, Kanata-Canada.
AFIC: Personal Collection. Adrian Forsyth, Washington D.C.-U.S.A.
BCRC: Personal Collection. Brett C. Ratcliffe, Lincoln-U.S.A.
BDGC: Personal Collection. Bruce D. Gill, Ottawa-Canada.
BMNH: Natural History Museum. London-United kingdom.
CECR: Personal Collection. Edgar Camero-R., Bogotá D.C.-Colombia.
CJAN: Personal Collection. Jorge Ari Noriega, Bogotá D.C.-Colombia.
CLCPL: Personal Collection. Luis Carlos Pardo-Locarno, Palmira-Colombia.
CMNC: Musée Canadien de la Nature, Ottawa-Canada
CMNH: Carnegie Museum of Natural History, Pittsburgh-U.S.A.
CNC: Agriculture et Agroalimentaire Canada, Ottawa-Canada.
CPALT: Personal Collection. Alejandro Lopera Toro, Bogotá D.C.-Colombia.
CPBM: Personal Collection. Betselene Murcia, Florencia-Colombia.
CPWY: Personal Collection. William Yara, Bogotá D.C.-Colombia.
DGMF: Personal Collection. David G. Marqua, Fort Davis-U.S.A.
EGRC: Personal Collection. Edward G. Riley, College Station-U.S.A.
FSCA: Museum of Entomology, Florida State Collection of Arthropods, Gainesville-U.S.A.
FVMC: Personal Collection. Fernando Z. Vaz de Mello, Cuibá-Brasil.
IAvH: Instituto de Investigación de Recursos Biológicos "Alexander von Humboldt", Villa de Leyva-Colombia.
IBSP: Colección Entomológica "Adolph Hempel", Instituto Biológico Sao Paulo, Sao Paulo-Brasil.
ICN-MHN: Instituto de Ciencias Naturales, Bogotá D.C.-Colombia.
INBio: Instituto Nacional de Biodiversidad, Santo Domingo de Heredia-Costa Rica.
MACN: Museo Argentino de Ciencias Naturales, Buenos Aires-Argentina.
MHIC: Personal Collection. Martin Hardy, Québec-Canada.
MHNG: Muséum d'Histoire Naturelle de la Ville de Genève, Genève-Switzerland.
MIZA: Museo del Instituto de Zoología Agrícola de la Universidad Central de Venezuela, Maracay-Venezuela.
MLJC: Personal Collection. Mary Liz Jameson, Lincoln-U.S.A.
MLP: Museo de Historia Natural de La Plata, La Plata-Argentina.
MNHN: Muséum National d'Histoire Naturelle, Paris-France.
MNRJ: Museu Nacional Rio de Janeiro, Rio de Janeiro-Brasil.
MTD: Staatliches Museum Für Tierkunde, Dresden-Germany.
MZSP: Museu de Zoologia Universidade de São Paulo, Sao Paulo-Brasil.
NHRS: Naturhistoriska Riksmuseet, Stockholm-Sweden.
NMPC: Národni Muzeum, Prague-Czech Republic..
OUMNH: Oxford University Museum of Natural History, Oxford-United Kingdom.
PAIC: Personal Collection. Patrick Arnaud, Saintry sur Seine-Francia.
PMOC: Personal Collection. Philippe Moretto, Toulon-Francia.
PSIC: Personal Collection. Paul Schoolmeesters, Herent-Bélgica.
QCAZ: Museo de Zoología Universidad Católica del Ecuador, Quito-Ecuador.
ROME: Royal Ontario Museum, Toronto-Canada.
SEMC: Snow Entomological Museum, Lawrence-U.S.A.
SMF: Forschungsinstitut Senckenberg, Francfort-Germany.
TAMU: Texas A & M University, College Station-U.S.A.
UASC: Museo de Historia Natural "Noel Kempff Mercado", Santa Cruz-Bolivia.
UNSM: University of Nebraska State Museum, Lincoln-U.S.A.
USNM: National Museum of Natural History, Washington D.C-U.S.A.
UVGC: Colección de la Universidad del Valle de Guatemala, Guatemala-Guatemala.
VMPC: Personal Collection. Vladislav Malý, Praga-República Checa.
WBWC: Personal Collection. William B. Warner, Phoenix-U.S.A.
WDEC: Personal Collection. W. David Edmonds, Marfa-U.S.A.
ZMHB: Museum für Naturkunde, Berlin-Germany.

Appendix 2. Examined bibliography whose taxonomical and distributional information was included in the Eurysternus database

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Appendix 3. Minimum (m) and maximum (M) altitudinal values of the 0.08° cells with observed presences for each *Eurysternus* species, as well as maximum and minimum values of the five bioclimatic variables best correlated with the significant ENFA factors (see methods). Marg is the marginality or climatic distance between the detected optimum for the species and the climatic conditions of the entire territory considered. Spec is the specialization, the ratio between the climate variability in the study area and that characterizing the presence localities of the species. DR is the number of records available in the database, and OP is the number of 0.08° cells in which each species is present. ND: not determined, due to the low number of presence localities. AMT = annual mean temperature, AP = annual precipitation, MDR = mean diurnal range of temperature, MTWM = maximum temperature of warmest month, TAR = annual range of temperature.

		Altitude		AMT		AP		MDR		MTWM		TAR					
		m	M	m	M	m	M	m	M	m	M	m	M	Marg	Spec	DR	OP
	Eurysternus spp	0	3500	2.3	28.4	355	8214	5.6	16.0	9.2	36.2	119	4958	1.40	2.29	21183	2818
1	*E. navajasi*	100	100	17.6	24.2	1231	1828	10.3	12.8	28.2	33.8	1144	3647	0.53	9.23	25	14
2	*E. hirtellus*	50	700	20.2	24.6	899	1529	7.6	11.8	27.9	31.7	1295	2234	0.62	7.82	43	14
3	*E. nanus*	800	800	25.4	25.4	1534	1534	12.4	12.4	34.2	34.2	773	773	ND	ND	6	1
4	*E. squamosus*	50	1200	21.1	27.0	2713	4007	8.8	10.6	26.7	34.1	206	986	1.94	8.55	91	36
5	*E. lanuginosus*	200	1900	18.3	26.5	1736	4437	9.4	14.1	24.4	32.2	213	1606	0.58	5.52	239	45
6	*E. strigilatus*	100	300	25.0	27.5	1667	3135	8.3	12.3	31.0	33.4	286	1065	0.84	13.91	73	19
7	*E. martinsi*	1000	1300	17.8	18.0	1604	1526	11.4	11.4	25.8	26.0	1793	1918	ND	ND	2	2
8	*E. nigovirens*	400	800	18.1	25.9	749	3277	7.7	14.4	25.6	34.7	719	3574	0.84	4.38	186	40
9	*E. aeneus*	50	500	17.6	23.5	1191	1733	10.3	13.7	28.2	33.7	2747	3832	0.81	15.12	92	18
10	*E. atrosericus*	50	500	20.8	27.9	1085	3114	8.3	12.9	29.4	35.8	286	1135	2.17	38.76	346	53
11	*E. cavatus*	0	300	24.8	27.0	2060	2626	9.3	13.2	32.4	33.5	277	423	2.16	>100	35	6
12	*E. cambeforti*	0	200	24.5	26.5	2229	3779	8.0	9.1	31.2	32.9	441	707	3.30	>100	23	11
13	*E. fallaciosus*	0	100	26.1	26.7	2120	2358	9.4	9.5	32.6	32.7	388	552	ND	ND	4	2
14	*E. cayennensis*	0	1200	11.5	27.9	1143	4291	7.7	12.8	17.7	35.6	119	1202	2.71	34.87	2743	150
15	*E. gilli*	50	200	24.0	26.9	1367	3306	8.9	13.5	30.3	33.0	286	1353	2.05	>100	326	15
16	*E. gracilis*	25	300	24.9	27.2	2025	3248	8.8	11.0	31.4	33.5	370	1069	0.73	23.63	15	10
17	*E. vastiorum*	0	1000	21.4	27.2	1337	4291	7.7	13.8	28.1	33.5	240	2097	0.77	10.07	1250	90
18	*E. ventricosus*	0	1200	17.1	27.6	1557	3805	7.1	13.1	23.5	35.7	307	895	0.86	11.43	107	35
19	*E. deplanatus*	500	1500	13.8	19.7	1313	2412	9.4	13.7	21.3	28.2	2212	2974	0.78	9.92	26	14
20	*E. parallelus*	70	1000	14.9	23.5	1161	2412	7.1	13.9	23.8	34.3	1417	4031	0.74	6.48	438	77
21	*E. inflexus*	0	1200	16.5	23.2	1339	2412	7.6	11.9	23.8	30.5	1736	2285	0.85	31.12	245	12
22	*E. wittmerorum*	0	3400	20.4	27.9	1629	3814	8.8	14.6	26.7	35.6	213	2097	1.53	5.29	546	57
23	*E. jessopi*	100	1000	18.2	25.1	1175	1695	6.6	13.4	25.9	34.2	758	3594	0.91	7.16	83	20
24	*E. foedus*	0	1300	8.7	27.9	355	8214	5.6	15.0	14.4	35.7	170	2202	1.05	3.67	1619	268
25	*E. streblus*	100	1200	13.4	26.6	756	8214	7.8	11.2	18.6	33.3	166	784	0.74	11.22	112	40
26	*E. howdeni*	200	1000	23.2	27.0	1302	2571	8.6	13.5	30.7	34.6	440	1450	0.63	11.21	42	16
27	*E. truncus*	0	2000	18.3	22.0	1824	2237	9.7	11.4	24.3	28.7	340	426	0.84	>100	6	4
28	*E. sulcifer*	0	1800	16.2	21.7	1339	2412	9.2	13.4	23.8	30.3	2077	3174	0.40	7.90	11	10

29	*E. sanbornei*	50	700	19.7	19.7	1786	1786	9.8	9.8	25.8	25.8	413	413	ND	ND	3	1
30	*E. calligrammus*	100	1500	19.9	26.3	1194	3340	7.6	12.0	28.6	32.3	539	2141	1.50	>100	28	9
31	*E. cyanescens*	100	1500	16.5	24.0	664	2537	7.0	15.0	23.8	36.2	1521	4958	0.81	6.24	193	37
32	*E. balachowskyi*	1000	1400	22.0	27.1	1724	3805	7.1	11.4	28.7	33.2	340	690	2.03	19.51	95	33
33	*E. arnaudi*	0	700	24.1	27.4	1920	2468	8.7	13.1	32.4	33.7	383	742	1.97	67.92	28	12
34	*E. velutinus*	0	1400	14.8	25.8	2399	4120	8.2	10.9	20.3	33.3	462	773	0.62	40.39	342	9
35	*E. hypocrita*	0	900	16.0	27.9	879	4452	7.7	14.8	24.2	35.7	240	2197	0.68	5.99	1470	183
36	*E. obliteratus*	50	250	12.8	25.3	1555	3851	8.0	12.6	21.8	34.3	1045	2267	0.58	4.65	67	14
37	*E. inca*	300	800	2.3	25.1	624	3762	10.1	14.8	11.9	32.8	595	2197	0.97	7.15	98	36
38	*E. uniformis*	50	2000	24.0	26.6	1367	2060	9.3	13.5	32.5	33.0	423	1353	1.50	>100	7	4
39	*E. olivaceus*	600	1000	18.4	26.2	2731	3957	9.0	9.8	24.4	32.6	538	685	1.23	9.26	11	8
40	*E. contractus*	800	2600	10.1	25.9	1054	4461	9.0	11.4	15.6	32.4	206	638	0.91	11.29	295	37
41	*E. superbus*	100	600	18.1	24.7	962	1208	10.3	11.4	24.7	31.8	436	653	0.50	12.90	92	12
42	*E. caribaeus*	300	1000	8.1	28.3	355	6057	6.9	15.0	12.9	36.0	165	4056	1.84	7.08	4610	519
43	*E. hamaticollis*	200	2300	17.1	27.9	1240	3838	8.2	13.0	23.5	35.7	298	2197	1.87	7.41	606	104
44	*E. maya*	500	1500	22.9	25.5	1371	3439	8.0	11.2	29.4	34.4	1595	2080	0.68	11.05	168	15
45	*E. cyclops*	0	1500	24.2	27.0	1841	3771	7.7	14.3	30.8	34.9	300	816	0.76	12.20	37	15
46	*E. francinae*	100	1900	17.0	21.7	1353	1771	9.2	12.2	24.9	30.3	1736	2964	0.54	6.33	66	19
47	*E. impressicollis*	0	600	20.4	28.4	656	2606	8.4	11.4	26.1	35.5	364	756	0.71	4.85	67	15
48	*E. plebejus*	0	400	11.8	27.9	482	7533	5.6	15.4	18.8	35.6	211	2610	1.04	4.33	2227	243
49	*E. angustulus*	300	1200	20.4	27.1	1248	3763	8.0	12.1	29.1	35.2	1224	2272	1.51	48.58	244	25
50	*E. magnus*	200	3400	13.3	27.0	517	3842	8.0	14.1	18.7	35.8	404	3932	0.83	5.34	245	77
51	*E. marmoreus*	200	3500	4.7	25.5	792	6482	8.2	16.0	9.2	33.0	180	2197	0.37	2.54	342	81
52	*E. mexicanus*	0	3000	10.0	28.0	687	4981	7.0	14.8	15.7	35.8	231	3923	1.33	4.56	1087	220
53	*E. harlequin*	80	600	20.8	27.0	1353	2414	9.0	13.5	29.4	33.9	298	1341	0.87	5.46	21	11

Figs. 4-53

4 *Eurysternus navajasi*

5 *Eurysternus hirtellus*

6 *Eurysternus squamosus*

7 *Eurysternus lanuginosus*

8 *Eurysternus strigilatus*

9 *Eurysternus nigrovirens*

10 *Eurysternus aeneus*

11 *Eurysternus atrosericus*

12 *Eurysternus cavatus*

239

13   *Eurysternus cambeforti*

14   *Eurysternus fallaciosus*

15   *Eurysternus cayennensis*

16   *Eurysternus gilli*

17   *Eurysternus gracilis*

18   *Eurysternus vastiorum*

19   *Eurysternus ventricosus*

20   *Eurysternus deplanatus*

21   *Eurysternus parallelus*

240

22 *Eurysternus inflexus*

23 *Eurysternus wittmerorum*

24 *Eurysternus jessopi*

25 *Eurysternus foedus*

26 *Eurysternus streblus*

27 *Eurysternus howdeni*

28 *Eurysternus truncus*

29 *Eurysternus sulcifer*

30 *Eurysternus calligrammus*

241

31 *Eurysternus cyanescens*

32 *Eurysternus balachowskyi*

33 *Eurysternus arnaudi*

34 *Eurysternus velutinus*

35 *Eurysternus hypocrita*

36 *Eurysternus obliteratus*

37 *Eurysternus inca*

38 *Eurysternus uniformis*

39 *Eurysternus olivaceus*

242

40 *Eurysternus contractus*

41 *Eurysternus superbus*

42 *Eurysternus caribaeus*

43 *Eurysternus hamaticollis*

44 *Eurysternus maya*

45 *Eurysternus cyclops*

46 *Eurysternus francinae*

47 *Eurysternus impressicollis*

48 *Eurysternus plebejus*

243

Eurysternus angustulus

49
115°

0   2000
kilometers

Eurysternus magnus

50
115°

0   2000
kilometers

Eurysternus marmoreus

51
115°

0   2000
kilometers

Eurysternus mexicanus

52
115°

0   2000
kilometers

Eurysternus harlequin

53
115°

0   2000
kilometers

244