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Bioclimatic profile and potential distribution of the Mesopotamian harvestman *Discocyrtus testudineus* (Holmberg, 1876) (Opiliones, Gonyleptidae)

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Abstract

The geographic range of the Neotropical harvestman *Discocyrtus testudineus* (Holmberg, 1876) (Gonyleptidae) is addressed by determining the species' bioclimatic profile and modeling its potential distribution. Analysis was performed on a record set of 71 localities, including literature records and 34 new localities reported here. The bioclimatic profile was characterized through extreme, median and dispersion features of the values of 19 bioclimatic variables across the record set. Predictive models were built with the presence-only methods MAXENT and, secondarily, BIOCLIM. *Discocyrtus testudineus* is a typical Mesopotamian harvestman, spreading across a wide region along the middle and lower Paraná River in subtropical / temperate Argentina, and extending, more or less continuously, up to the central province of Córdoba. Apparently diverging records (Paso de los Libres, on the Uruguay River, and Quilmes, on the southern coast of Rio de la Plata) proved to be predictable, even if suppressed from the dataset. Comparisons of cumulative frequencies curves and dispersion features (box-plots) were made with *Discocyrtus dilatatus* Sørensen, 1884 and *Gryne orensis* (Sørensen, 1884), other Mesopotamian species for which bioclimatic data are available. The relative importance of the bioclimatic variables used for modeling was also estimated.

Key words: Neotropical Region, Mesopotamia, bioclimatic profile, species distribution modeling, MAXENT, BIOCLIM

Introduction

The gonyleptid *Discocyrtus testudineus* (Holmberg, 1876) is one of the most characteristic harvestmen inhabiting the so-called "Mesopotamian *sensu stricto*" opiliogeographical area in Argentina (Acosta 2002). It is also one of the earliest species described in the region: it was named by Holmberg (1876) from a single specimen collected in Puerto Obligado, about 170 km NW of Buenos Aires. While originally assigned to the "repository" genus *Gonyleptes* Kirby, 1818, Holmberg then erected for this species the monotypic genus *Discocyrtus* Holmberg, 1878. With the passing of time and continued contributions of several authors, *Discocyrtus* has become nearly the largest gonyleptid genus, containing about 80 nominal species, most concentrated in the Brazilian states of Rio de Janeiro, São Paulo, Minas Gerais, Paraná, Santa Catarina and Rio Grande do Sul (Soares & Soares 1954; Kury 2003). In such an extensive genus range, the type species, *D. testudineus*, and two Mesopotamian congeners—*D. prospicuus* (Holmberg, 1876) and *D. dilatatus* Sørensen, 1884—are the southern- and westernmost representatives (Acosta 1995, 2002). The current taxonomical concept of *D. testudineus* relies on Ringuelet (1956, 1959), who recognized the intraspecific variation, thereby determining that *Discocyrtus laevis* Mello-Leitão, 1931 and *Microgoniosoma fuscum* Mello-Leitão, 1930 (successively placed in Gonyleptinae and Goniosomatinae: Mello-Leitão 1930, 1935) are its junior synonyms. Among Argentinean gonyleptids, *D. testudineus* can be easily identified by the paired acute apophyses arming the scutal area III, and for males, by the curved femora that give this species its typical "knock-kneed" habitus (Fig. 1). Ringuelet (1959) based his redescription on external features alone, but several depictions of the male genital morphology of this species are scattered in the literature (Hansen & Sørensen 1904: plate VI, figs. 28–31; Pinto-da-Rocha & Giribet 2007: 200; Macías-Ordóñez *et al.* 2010: 296).

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FIGURE 1. Male *Discocyrtus testudineus* from the Province of Misiones, Argentina. Photo: Dardo Martí.

Although the distribution of *D. testudineus* was roughly known through records reported by Holmberg (1878), Sørensen (1884, 1895) and Roewer (1913), Ringuelet (1959) was the first author to provide a comprehensive account of the species range. According to localities given by Ringuelet (1959), *D. testudineus* extends from Paraguay and the Argentinean province of Misiones up to northern province of Buenos Aires, with records spread along the lower and middle course of Paraná River. Thereafter, Acosta (1995) added some occurrences along the Ctalamochita River (a tributary of Paraná River) in the province of Córdoba. Aside those reliable citations, there are some nebulous references given by Mello-Leitão (1932, 1939). Without specifying details, Mello-Leitão (1932) stated that *D. testudineus* occurred in "Republica Argentina, Paraguay, Matto Grosso [Brazil]". Using the same telegraphic style and with no explanation, Mello-Leitão (1939) added: "Brèsil, Uruguay, Paraguay, Prov. Buenos Aires, Chaco". These doubtful citations for Uruguay and Brazil were not even mentioned nor discussed by Soares and Soares (1954), Ringuelet (1955, 1963) or Kury (2003); only Capocasale (1968) explicitly set aside the reference for Uruguay because of its unconfirmed status. The species range has a broad overlap with other Mesopotamian harvestmen, like the cosmetid *Gryne orensis* (Sørensen, 1884) (particularly along the Paraná basin) and the congener *Discocyrtus dilatatus*, which also extends into the province of Córdoba (Acosta 2002; Acosta & Vergara 2013; Vergara & Acosta, in prep.). Both of the latter species have frequently been collected in association with *D. testudineus* (Valentinis de Martínez 1974; Acosta 1995; Acosta & Vergara 2013).

Decaying logs or litter in gallery forests are typical places where to look for *D. testudineus* (*"unter gefällten Bäumen häufig"*, says Roewer 1913:102); at times it has also been collected under fallen trunks in open grasslands, though it appears more dependent on shade than *D. dilatatus* (Acosta 1995). There is also a record from a small erosion cave on the Paraná River cliffs (Cueva de los Murciélagos, in northern province of Buenos Aires; Lipps *et al.* 2006), most likely representing just an occasional refuge for this epygean species. Some kind of distributional exclusion was suspected with a "marginal" *Discocyrtus* species, *D. prospicuus*, since, except for a few localities where they cohabit, the latter seems to avoid most areas occupied by *D. testudineus*, even if distributional models have indicated them as suitable (Acosta & Guerrero 2011).

This paper aims to characterize the geographical distribution of *D. testudineus* using a bioclimatic modeling approach. To accomplish this, 34 new records were available, duplicating the number of localities previously documented (Table 1). Most new records filled in the range known so far, *i.e.*, they complete the distributional knowledge in blank areas easily predicted to have the species. Besides several records bordering the Paraná River, the new materials add meaningful points in the interior of province of Entre Ríos (Rosario del Tala; several sites along the northern border of the Paraná delta; Fig. 2). In province of Córdoba they provide more density along Ctalamochita River and incorporate two westernmost records on the upper course of Xanaes River (Despeñaderos, Anizacate-La Bolsa: Fig. 2). A couple of records worth mentioning are exceptions to easily predictable localities and deserved special attention. First, the collection of *D. testudineus* in a locality by the Uruguay River (Paso de los Libres, province of Corrientes) was unexpected, for it clearly diverges from the implied "Paraná River pattern" (Fig. 2: k). Second, the recent finding (recorded by Guerrero *et al.* 2013) in a locality along the Rio de la Plata (Fig. 2: f) surpasses by about 80 km southwards the distributional limit hypothesized by Acosta and Guerrero (2011) for this species. Along with the calibration of distributional models, this contribution is oriented to get a complete descriptive insight of factors presumed to determine the distribution of this wide-ranged harvestman. For that purpose, bioclimatic variables are carefully analyzed below, including the inspection of variability and frequencies in the record set of *D. testudineus*, along with the first comparative overview with other Mesopotamian harvestmen.

Methods

Data acquisition. The dataset consisted of all records previously published for *D. testudineus*, together with localities of newly collected specimens (Table 1). References from the literature were evaluated, so that unrecognizable or imprecise localities were removed before modeling; but, if a closer description of the collecting site was available, an effort was made to get its approximate location. The full dataset comprised 71 unique points (Table 1, Fig. 2). Published localities were geo-referenced with help of printed road maps, gazetteers and Google Earth© (presumable imprecision was considered negligible, taking into account the aims of this paper and the scale used: Acosta 2008). Most new materials were geo-referenced using a Garmin® GPS, otherwise estimated with Google Earth©. As stated above, species identification was based on Ringuelet (1959).

Acronyms. CDA: Cátedra de Diversidad Animal I, Facultad de Ciencias Exactas, Físicas y Naturales, Universidad Nacional de Córdoba (conventional collection is indicated with a 000.xxx accession number; freezer collection denoted as "–F"); I.F.S.C.: Instituto Fitotécnico de Santa Catalina, Universidad Nacional de La Plata, Llavallol; LEA: Luis E. Acosta collection; MACN: Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Buenos Aires.

Climate layers. All GIS operations, including preparation of digital layers and dataset files for modeling, display of results, and area calculations, were accomplished with the free software DIVA-GIS, version 7.1.6.2. (http://www.diva-gis.org/). Climate data were extracted from the WorldClim 1.4. dataset (Hijmans *et al.* 2005), which contains values for 19 bioclimatic (bc) variables—listed in Table 2—averaging the period 1950–2000, at a resolution of 30 arc second (0.71 to 0.76 km^2 / grid cell at the latitudes involved). For use in MAXENT, raster layers were extracted in DIVA-GIS grid format. In the case of MAXENT, to prevent the inclusion of highly correlated variables (Pearson>0.75), pairwise correlation analyses were made separately for temperature and precipitation variables (Rissler & Apodaca 2007; Kozak *et al.* 2008). Correlation was calculated on values of 770 points over the study region (central and northern Argentina, Paraguay, Uruguay and southern Brazil), keeping one variable in a correlated pair (Acosta & Guerrero 2011). Since variables selection cannot be based on biological knowledge (lacking for *D. testudineus*), the choice in a highly correlated pair was defined by its percent contribution and permutation importance in preliminary models, run with all 19 variables, to avoid discarding an *a priori* presumable relevant predictor. As a result, 11 bc variables were selected for use in MAXENT (Tables 2 and 3).

Bioclimatic profile. The bioclimatic profile consists of a descriptive account of values for all 19 climatic variables extracted by BIOCLIM (available as an inbuilt module in DIVA-GIS) and summarized in Table 2. This profile relies on the envelope concept, *i.e.*, the orthogonal multi-dimensional hyper-space (each variable representing one dimension) that delimits the climatic preferences of the modeled species. Frequency features of the variables were interpreted through cumulative frequencies and histogram tools available in the Modeling tab of DIVA-GIS. Frequency was characterized and denoted as follows (Table 2): (1) normal (N), if a bell shaped curve was recoverable over the histogram, even if slightly shifted to one side (>N or N<); (2) skewed to higher or lower

TABLE 1. Record set of *Discocyrtus testudineus*, with locality names, geographical coordinates and sources for each record. Latitude and longitude are in decimal degrees. Coordinates of asterisked localities (**) are approximate; extreme geographical points of the range are underlined. Localities representing lowest, median or highest values for bioclimatic (bc) variables are indicated with numbers as in Table 2. New records are indicated as NR, along with collection data. References for Brazil and Uruguay (Mello-Leitão 1932, 1939) are considered unreliable and thereby not included in the dataset.

Province or Department	Locality	Latitude (S)	Longitude (W)	bc lowest	bc median	bc highest	Source
ARGENTINA							
Misiones [1]	Posadas (University Campus)	-27.4338	-55.8883	15	-	-	**NR:** 4♂, 7 ♀, 1 juv. (CDA-F), 5–xi–2006 (D. Martí)
Misiones	Candelaria	-27.4667	-55.7500	-	-	12, 13, 14, 16, 17, 19	Ringuelet, 1959
Formosa	San Francisco de Laishi	-26.2384	-58.6255	-	7, 15	5	**NR:** 1 juv. (CDA-F), 3–xii–2011 (J. Vergara, R. González-Ittig, L. Vaschetto)
Chaco [2]	Resistencia	-27.4517	-58.9917	-	-	-	Sørensen, 1895
Chaco	Bridge at Colonia Benítez	-27.3352	-58.9661	-	-	-	**NR:** 1♂, 1 ♀ (CDA-F), 2–xii–2011 (J. Vergara, R. González-Ittig, L. Vaschetto)
Chaco	Río Tragadero (flooding forest) **	-27.4300	-58.8707	-	-	-	**NR:** 1♂, 1 ♀ (LEA 000.343), v–2003 (M. Chatellánez)
Chaco	10 km from Puerto Antequera, to Isla del Cerrito	-27.3873	-58.8004	-	-	-	**NR:** 3♂ (CDA 000.852), 24–ii–2005 (L. Acosta, G. Rubio, P. Olivero, M. Garcia)
Chaco	7 km from Puerto Antequera	-27.3996	-58.8176	-	-	-	**NR:** 9♂, 4 ♀ (CDA-F), 2–xii–2011 (J. Vergara, R. González-Ittig, L. Vaschetto)
Chaco	Colonia Castelli	-25.9510	-60.6235	-	-	3, 5, 8	Ringuelet, 1959
Chaco	Riacho de Oro, mouth ** [3]	-27.0390	-58.5678	-	-	-	Sørensen, 1884
Corrientes	San Cosme	-27.3727	-58.5112	-	-	-	Ringuelet, 1959
Corrientes	El Perichón	-27.4077	-58.7457	-	-	-	**NR:** 1♂ (CDA-F), 23–ii–2005 (L. Acosta, G. Abalos)
Corrientes	Rio Empedrado, by National High road 12 bridge	-27.8634	-58.7638	-	-	-	**NR:** 2♂ (CDA-F), 2–iv–2012 (J. Vergara, L.Vaschetto, C. Argañaraz)

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TABLE 1. (Continued)

Province or Department	Locality	Latitude (S)	Longitude (W)	bc lowest	bc median	bc highest	Source
Corrientes	Cabañas Empedrado	-27.9501	-58.8101	-	-	-	**NR:** 1♂ (CDA-F), 1–iv–2012 (J. Vergara, L.Vaschetto, C. Argañaraz)
Corrientes	Santa Lucía	-28.9857	-59.0947	-	8, 18	-	**NR:** 4 ♀ (CDA 000.851), 25–ii–2005 (L. Acosta, P. Olivero, M. García)
Corrientes	Esquina	-30.0088	-59.5330	-	-	-	**NR:** 1♂, 6 ♀ (CDA 000.853), 26–ii–2005 (L. Acosta, P. Olivero, M. García)
Corrientes	Paso de los Libres	-29.7227	-57.0880	-	-	-	**NR:** 2♂, 4 ♀ (CDA-F), 27–ii–2012 (L. Acosta, R. Gonzalez-Ittig, L. Vaschetto)
Entre Ríos	La Paz	-30.7563	-59.6553	-	-	-	**NR:** 2♂, 2 ♀ (CDA-F), 24–i–2012 (L. Acosta, L.M. Acosta)
Entre Ríos	"Colonia Berduc" (near La Picada) **	-31.7333	-60.3293	-	-	-	Ringuelet, 1959
Entre Ríos	Strobel	-32.0507	-60.6160	-	5, 7, 9	-	**NR:** 8♂, 19 ♀ (LEA 000.358), 24–iii–2006 (L. Acosta, M. Garcia)
Entre Ríos	1 km National Park Predelta	-32.1100	-60.6318	-	1, 6, 7, 10, 11	-	**NR:** 2♂, 4 ♀ (LEA 000.359), 24–iii–2006 (L. Acosta, M. Garcia)
Entre Ríos	La Azotea	-32.0997	-60.6452	-	2, 6, 7	-	**NR:** 1♂ (LEA 000.361), 24–iii–2006 (L. Acosta, M. Garcia)
Entre Ríos	Diamante	-32.0622	-60.6472	-	1, 6, 7, 11	-	Ringuelet, 1959
Entre Ríos	Paraná	-31.7188	-60.5333	-	7	-	Ringuelet, 1959
Entre Ríos	Arroyo El Brete (Paraná) **	-31.7280	-60.5003	-	-	-	Ringuelet, 1959
Entre Ríos	Rosario del Tala	-32.3167	-59.0833	-	-	-	**NR:** 13♂, 13 ♀ (LEA 000.363), 25–iii–2006 (L. Acosta, M. Garcia)
Entre Ríos	Gualeguay	-33.1528	-59.2933	-	-	-	**NR:** 4♂, 2 ♀ (CDA-F), 25–xi–2006 (L. Acosta, M. García)
Entre Ríos	"Colonia Carbó" [Enrique Carbó]	-33.1472	-59.2092	-	13, 16	-	Ringuelet, 1959

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TABLE 1. (Continued)

Province or Department	Locality	Latitude (S)	Longitude (W)	bc lowest	bc median	bc highest	Source
Entre Ríos	Rincón de Nogoyá Sur	-32.8500	-59.8600	-	6	-	**NR:** 5♂, 7 ♀, 2 juv. (CDA 000.855), 25–xi–2006 (L. Acosta, M. García)
Entre Ríos	“Island in Department Victoria” ** [4]	-33.1167	-60.4833	-	14	-	Ringuelet, 1959
Entre Ríos	Victoria	-32.6167	-60.1667	-	14	-	**NR:** 1 ♀ (MACN), iii–1983 (J.D. Anghilante)
Entre Ríos	Near Baradero ** [5]	-33.7533	-59.2300	-	-	-	Sørensen, 1884
Entre Ríos	Puerto Constanza	-33.8307	-59.0315	-	-	-	Ringuelet, 1959
Entre Ríos	Near Ibicuy	-33.8789	-58.9102	-	4, 7	-	E. L. Guerrero (pers. comm.), I.F.S.C. A020, A022, A024
Entre Ríos	Río Paranacito (mistakenly assigned to Buenos Aires)	-33.6957	-58.9173	-	-	-	Ringuelet, 1959
Santa Fe	Puerto Reconquista, 5 km to Arroyo Correntoso	-29.2623	-59.5993	-	-	-	**NR:** 2♂ (CDA-F), 24–xii–2007 (R. Gonzalez-Ittig)
Santa Fe	La Invernada (Dept. Reconquista) **	-29.0338	-59.4527	-	-	-	Ringuelet, 1959
Santa Fe	Lehmann	-31.1250	-61.4428	-	-	-	**NR:** 1 ♀ (CDA-F), 12–iv–2011 (J. Vergara, C. Argañaraz, L. Paoloni)
Santa Fe	Laguna Paiva	-31.2880	-60.6250	-	16	-	**NR:** 1 ♀ (LEA 000.372), 15–viii-1994 (L. Burroni)
Santa Fe	Near Villa Hernandarias ** [6]	-31.2500	-60.0300	-	-	-	Sørensen, 1884
Santa Fe	Santa Fe (locus typicus of *Discocyrtus laevis*)	-31.6262	-60.6810	-	2, 7, 13	-	Ringuelet, 1956
Santa Fe	Madrejón "Don Felipe", Depto La Capital	-31.6500	-60.6008	-	7	-	Valentinis de Martinez, 1974
Santa Fe	Colonia Mascías (Dept. Garay)	-30.7950	-59.9917	-	17, 18, 19	-	Ringuelet, 1959
Santa Fe	Colastiné Sur	-31.6648	-60.6073	-	7	-	Ringuelet, 1959
Santa Fe	Between Maciel and Coronda **	-32.2333	-60.9667	-	-	-	Ringuelet, 1959

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TABLE 1. (Continued)

Province or Department	Locality	Latitude (S)	Longitude (W)	bc lowest	bc median	bc highest	Source
Santa Fe	San José de la Esquina	-33.1070	-61.6978	-	-	-	Ringuelet, 1959
Santa Fe	Rosario	-33.0053	-60.6241	-	14	-	Ringuelet, 1959
Santa Fe	Villa Constitución, Isla del Sol	-33.2165	-60.3257	-	-	-	**NR:** 1♂, 1 ♀ (CDA 000.850), 2–iii–2007 (L. Acosta, M. García)
Santa Fe	Villa del Medio, left bank of Arroyo del Medio	-33.2840	-60.2683	-	-	-	**NR:** 2♂, 8 ♀ (CDA 000.849), 2–iii-2007 (L. Acosta, M. García)
Buenos Aires	San Nicolás	-33.3223	-60.2250	-	3	-	Sørensen, 1884
Buenos Aires	Ramallo	-33.4783	-60.0000	-	-	-	Ringuelet, 1959
Buenos Aires	Puerto Obligado (locus typicus) [7]	-33.5950	-59.8133	-	-	-	Holmberg, 1876
Buenos Aires	Baradero [8]	-33.8000	-59.5000	-	-	-	Holmberg, 1878
Buenos Aires	Lima, gallery forest	-33.9742	-59.1781	-	-	-	Guerrero, 2011
Buenos Aires	Quilmes, riparian forest	-34.6900	-58.2617	2, 3, 5	-	-	Guerrero *et al.*, 2013
Buenos Aires	Zárate (locus typicus of *Microgoniosoma fuscum*)	-34.0881	-59.0274	8	12	-	Ringuelet, 1959
Buenos Aires	Otamendi	-34.1850	-58.8717	1, 10	-	-	Guerrero, 2011
Buenos Aires	Martin Garcia island	-34.1833	-58.2550	-	-	-	Ringuelet, 1959
Buenos Aires	Paraná Guazú **	-33.9500	-58.8500	18	7	-	Ringuelet, 1959
Córdoba	Pampayasta Sur	-32.2477	-63.6472	-	18	-	Acosta, 1995
Córdoba	Villa Nueva (riverside, near Yellow bridge)	-32.4223	-63.2427	-	-	-	Acosta, 1995
Córdoba	Villa Nueva (gallery forest near dam)	-32.4225	-63.2620	-	-	-	**NR:** 5♂, 1 ♀ (CDA-F), 14–ii–2008 (L. Acosta, M. García, G. Rubio)

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TABLE 1. (Continued)

Province or Department	Locality	Latitude (S)	Longitude (W)	bc lowest	bc median	bc highest	Source
Córdoba	Villa María (bridge over Ctalamochita river, Highway 158)	-32.4198	-63.3027	-	-	-	**NR:** 1 ♀ (LEA 000.411), 8–xii–1992 (L. Acosta)
Córdoba	Estancia Yucat	-32.3514	-63.4408	-	-	-	**NR:** 7♂, 4 ♀ (CDA-F), 21–xii–2011 (L. Acosta, L. Vaschetto)
Córdoba	Ramón J. Cárcano	-32.5122	-63.1125	-	-	-	**NR:** 3♂, 2 ♀ (CDA-F), 28–ii–2007 (L. Acosta, M. García)
Córdoba	Ballesteros Sur (riverside)	-32.5830	-63.0193	-	-	-	**NR:** 2♂, 2 ♀ (CDA-F), 28–ii–2007 (L. Acosta, M. García)
Córdoba	Morrison (abandoned bridge)	-32.6120	-62.8411	9, 11	-	4	**NR:** 2♂ (CDA-F), 28–ii–2007 (L. Acosta, M. García)
Córdoba	Despeñaderos (close to railway bridge)	-31.8040	-64.2950	6, 14	-	7, 15	**NR:** 6♂, 2 ♀ (CDA-F), 18–xii–2008 (L. Acosta, M. García, G. Rubio, J. Vergara)
Córdoba	Between Anizacate and La Bolsa	-31.7217	-64.4208	12, 13, 16, 17, 19	-	2, 7	**NR:** 4♂, 2 ♀ (LEA 000.403), 14–iii–1994 (L. Acosta, L. Burroni)
PARAGUAY							
Central	Asunción	-25.2833	-57.6333	4, 7	-	1, 5, 6, 9, 10, 11, 18	Sørensen, 1895
Ñeembucú	Monte Rita ** [9]	-26.8850	-58.3715	-	-	-	Sørensen, 1884

[1] Holmberg (1878) refers to specimens from "Misiones" without further detail.

[2] The imprecise reference of Roewer (1913) for "Argentinien (Grao Chaco)" was disregarded.

[3] Coordinates placed at the mouth of the river, following Sørensen (1884: *ad ostium amnis "Riacho del Oro"*).

[4] The complete reference, with same collector and almost same date, is given by Ringuelet (1959: 233) for *Holmbergiana weyenberghii* (Holmberg, 1876): "Island in Department Victoria, in front of Arroyo Seco, Prov. Santa Fe". The place is recognized as "Isla del Paraguayo", on Paraná river, belonging to province of Entre Ríos.

[5] "*E provincia Entre-Ríos erga coloniam Baradero*" (Sørensen 1884), *i.e.*, 'towards colonia Baradero'. Estimated on the Entre Ríos side on Paraná river.

[6] "*Provincia Santa Fe, haud procul a vico Villa Hernandaria*" (Sørensen 1884), *i.e.*, not far from Villa Hernandarias. This locality belongs to the adjacent province of Entre Ríos, so the site is estimated on the Santa Fe side on Paraná river.

[7] This point also corresponds to the citation by Lipps *et al.* (2006) for "Vuelta de Obligado, Cueva de los Murciélagos".

[8] Baradero is mistakenly mentioned by Roewer (1913) as type locality.

[9] According to Sørensen (1884: 637), this Paraguayan locality is situated towards the mouth of Bermejo River (*"in loco quodam 'Monte Rita' appellato, erga ostium fluminis Rio Bermejo sito"*).

values (Sk+ or Sk-), when distribution is strongly concentrated on one side, *i.e.*, the largest peak was identified on the first or second bar, from there descending gradually; (3) bimodal (B), with two peaks; and (4) multimodal (M), actually tri-modal in all cases. For characterizations 3 and 4, if one peak is larger its position is marked with a circumflex (^). Additionally, box-plots were also inspected to determine dispersion, using the InfoStat package (Di Rienzo *et al.* 2013); in box-plots, values over 1.5xIQR (inter-quartile range) are considered "outliers"; beyond 3xIQR (outer fence) they are labeled as "extreme outliers". Both frequency and dispersion were compared with two sympatric Mesopotamian harvestmen, *D. dilatatus* (n=85) and *G. orensis* (n=45), for which similar data are so far available (Acosta & Vergara 2013; Vergara & Acosta, in prep.). Graph layouts were obtained with InfoStat.

TABLE 2. Bioclimatic profile of *Discocyrtus testudineus* (n=71) (BIOCLIM): basic statistics of the 19 bioclimatic variables, along with features of the frequency distribution (freq.). Temperature in Celsius degrees (ºC), precipitation in mm. Abbreviations of bioclimatic variables (bc x) as in text and Table 3. The 11 variables employed for modeling with MAXENT are asterisked. Frequency distributions are primarily characterized as normal (N), skewed towards the lower (Sk–) or upper end (Sk+), bimodal (B) and multimodal (M); additional notation was added to indicate normal curve slightly shifted to the left (N<) or the right (>N), or highly concentrated (>N<), or bimodal or multimodal with highest peak at the right (B^) or the left (^B, ^M). The number of extreme low (left) and high (right) outliers in the curves are provided; if extreme outliers exist (*i.e.*, beyond the outer fence), they are in square brackets.

Bioclimatic variables	Median	Min–Max	range	SD	freq.	outliers
bc 1—annual mean temperature	18.11	16.38–23.42	7.04	1.94	Sk–	0–0
bc 2—mean monthly T° range	12.10	9.35–13.96	4.61	0.90	>N	2–0
bc 3—isothermality (2/7 x 100) *	48.53	42.12–54.71	12.59	2.14	>N<	2–5
bc 4—T° seasonality (STD x 100) *	480.52	372.99–508.11	135.11	32.27	Sk+	3–0
bc 5—max T° of warmest month *	31.90	29.00–34.40	5.40	1.18	N	0–0
bc 6—min T° of coldest month *	6.50	3.30–12.90	9.60	2.49	^B	0–0
bc 7—T° annual range (5–6) *	25.30	21.50–27.60	6.10	1.65	B^	0–0
bc 8—mean T° wettest quarter *	23.47	19.63–26.70	7.07	1.44	>N	0–0
bc 9—mean T° driest quarter *	12.35	10.45–18.78	8.33	2.28	Sk–	0–0
bc 10—mean T° warmest quarter	24.13	22.50–27.92	5.42	1.57	Sk–	0–0
bc 11—mean T° coldest quarter	12.25	10.45–18.78	8.33	2.29	Sk–	0–0
bc 12—annual precipitation	990	657–1702	1045	199.12	N<	1–2 [+1]
bc 13—precipitation wettest month	140	103–198	95	20.67	^M	0–0
bc 14—precipitation driest month *	36	11–98	87	15.81	N<	0–[2]
bc 15—precipitation seasonality (CV) *	41.61	16.83–69.15	52.31	12.46	M	0–2
bc 16—precipitation wettest quarter *	358	285–478	193	53.24	^M	0–0
bc 17—precipitation driest quarter	128	34–343	309	55.04	N<	0–2
bc 18—precipitation warmest quarter *	325	256–448	192	52.37	^B	0–2
bc 19—precipitation coldest quarter	128	34–349	315	55.28	N<	0–2

Models calibration and accuracy. Models were built using the presence-only method MAXENT (Maximum Entropy Modeling of Species Geographic Distributions, thoroughly explained in Phillips *et al.* 2006; Phillips & Dudík 2008; Elith *et al.* 2011). Version 3.3.3k of the free software MAXENT (http://www.cs.princeton.edu/~schapire/maxent) was employed to produce the models. Most settings were kept in their default (recommended) values, except for "maximal number of background points" (raised to 20000), and "maximum iterations" (set to 2500). Features selection was made automatically by the software ("auto" option activated), and the logistic output was selected for the resulting maps. This output expresses continuous probabilities from 0 to 1 across the whole grid, so that a threshold must be set to define a boundary between "suitable" and "not suitable" predictions. Unless otherwise indicated, in this paper the "equal training sensitivity plus specificity" threshold was applied for binary maps, following Liu *et al.* (2005), Acosta and Guerrero (2011) and Acosta and Vergara (2013). When relevant, a second recommended threshold ("maximum training sensitivity plus specificity") is displayed too. Unlike my previous work, in which default models were built in a single run with the full dataset, the best calibration of MAXENT models was obtained from 30 runs using the "subsample" replicate type, and random test percentage set in 10 (with "random seed" selected). By this procedure, 30 binary maps were obtained (built with 64 training and 7 test points, randomly split for each run). The final binary model (Fig. 2) is made of the overlay of all 30 single runs, retaining as "suitable" any cell shared by 60% of the maps. Whenever suitability levels are shown (Figs. 5–7), the average grid (available as summary file of the replicate runs in the MAXENT output) was employed, displaying average thresholds yielded by the software. Accuracy of results was evaluated through the AUC (Area Under Curve) assessment, incorporated in MAXENT; AUC values over 0.8 are considered a "good" model performance; above 0.9 the accuracy is considered "high" (Luoto *et al.* 2005). A second modeling method, BIOCLIM (Acosta 2008, and references therein) was accessorily employed. Aside for the extraction of values of the species' profile and curves of cumulative frequencies, BIOCLIM was used to obtain a predictive map, to contrast MAXENT results. Such a map is the projection of the species envelope (see above), where "suitable" grid cells are those matching the multi-dimensional envelope values. Only a binary map is shown for BIOCLIM (overlaid to MAXENT model in Fig. 2), displaying the full suitability range ("True/False", 0–100 percentiles).

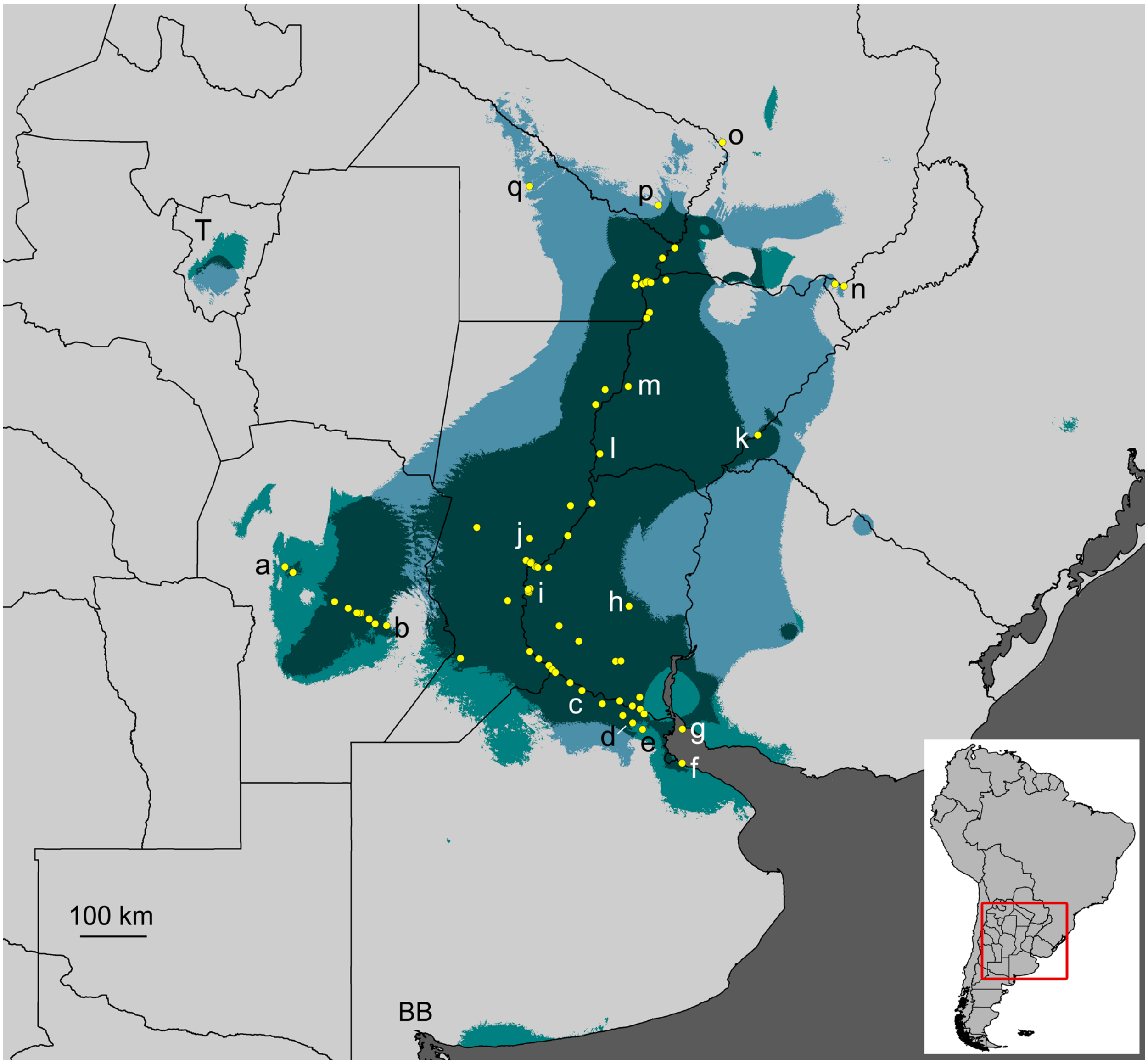


FIGURE 2. Locality records (yellow dots) and binary distribution models of *Discocyrtus testudineus* built with the full dataset (n=71). Map displays the overlay of models obtained with MAXENT (light green; sum of 30 binary replicates, binary map retains as suitable grid cells shared by 60% of the replicates or more) and BIOCLIM (light blue; true-false, full extension); overlapping areas in dark green. Selected localities: a. Anizacate/La Bolsa (West)—Despeñaderos (East), b. Morrison, c. Puerto Obligado (type locality), d. Zárate, e. Otamendi, f. Quilmes, g. Martín García island, h. Rosario del Tala, i. Diamante—Predelta National Park, j. Laguna Paiva, k. Paso de los Libres, l. Esquina, m. Santa Lucía, n. Candelaria (East)—Posadas (West), o. Asunción, p. San Francisco de Laishi, q. Colonia Castelli. T: province of Tucumán; BB: Bahía Blanca. Inset: location of the depicted area in South America.

Importance of variables. Four estimators, available in MAXENT (Phillips *et al.* 2011), were employed to assess the relative importance of each variable in the final models: (a) the percent contribution, which computes the increase in regularized gain added to the contribution of a given variable, in each iteration of the training algorithm; (b) the permutation importance, in which values of each variable on training presence and background data are permuted at random, then the model reevaluated on the permuted data; the resulting drop in training AUC is then normalized to percentages; (c) the jackknife analysis, calculating the training gain with one variable omitted at a time (the bc that decreases gain the most when omitted is deemed to contain the most information not present in other variables); and (d) the jackknife analysis run with one variable alone (the variable with the highest gain has the most useful information by itself). Since variables ranked differently for each estimator, an "overall scoring" (a+b-c+d) was calculated for the final ranking (Table 3).

TABLE 3. Relative importance of the 11 bc variables used to build the MAXENT model of *Discocyrtus testudineus.* Estimators include: percent contribution of each variable to the whole model; permutation importance; jackknife analysis, training gain with each variable set aside at a time; and jackknife, training gain with each variable run in isolation. In each column, the five highest scores are underlined, and the highest one is in bold. Variables are ordered according to an overall scoring (last column), computing all four estimators.

Variable	Percent bc contribution	Permutation importance	Training gain without	Training gain with only	Score
bc4—temperature seasonality	**33.073**	6.846	2.170	**1.172**	38.92
bc3—isothermality	3.067	**32.612**	**2.166**	0.842	34.35
bc14—precipitation driest month	23.588	4.655	2.188	0.807	26.86
bc9—mean T° driest quarter	7.257	9.310	2.204	0.758	15.12
bc6—min T° of coldest month	1.815	14.942	2.202	0.470	15.03
bc5—max T° warmest month	2.941	13.613	2.166	0.464	14.85
bc18—precipitation warmest quarter	12.014	0.906	2.216	0.630	11.33
bc7—T° annual range	7.808	3.492	2.193	0.741	9.85
bc15—precipitation seasonality	4.991	5.929	2.191	0.630	9.36
bc8—mean T° wettest quarter	2.907	6.360	2.196	0.589	7.66
bc16—precipitation wettest quarter	0.539	1.337	2.216	0.692	0.35

Input variants. To determine if records from Paso de los Libres and Quilmes (both suspected to be a step outside the species distribution pattern) are necessary to predict the local portion of models embracing them, two alternative datasets were made, deleting each locality one at a time (n=70). For each variant, 10 replicates were run using the same settings as above, obtaining the average grid to show suitability levels and two different thresholds ("equal training sensitivity plus specificity" and "maximum training sensitivity plus specificity"). The aim was to evaluate if the removed localities are really outsiders, through the ability of climatic information of the remaining records to predict those areas as suitable (or not).

Results

Bioclimatic profile. Climatic values obtained from the presence records of *D. testudineus* are summarized in Table 2. According to those values, preferences of the species correspond to a temperate or subtropical humid climate, the mean annual temperature ranging between 16.4°C and 23.4°C, and the annual precipitation between 650 and 1700 mm. The temperature of the warmest month can be as high as 34.4°C, and the coldest records do not fall below 0°C. With respect to frequency distributions, almost the half of variables adopts a normal (or almost normal) shape, although no common pattern is evident from those features: they include both absolute values (like bc5-maximal temperature of the warmest month or bc12-annual precipitation) and variables describing climatic stability (*e.g.*, bc3-isothermality, highly concentrated around median values). It is to be noted that all variables classed as skewed (bc1 and bc9–11 towards the lower end; bc4 towards the upper end) show an additional small peak on the opposite end. The number of outliers is in general very low (none in many cases; Table 2). Temperature seasonality (bc4), the only variable with a frequency shifted to the right, has the highest number of low-valued outliers (3); just two precipitation variables (bc12, bc14) have extreme outliers.

With respect to localities that held extreme climatic values, they are in general consistent with their geographical position (Table 1; Fig. 2). Asunción, for example, the northernmost point, has many of the warmest records (bc1, bc5–6, bc9–11); as a subtropical locality, it shows also the lowest temperature seasonality (bc4) and annual range (bc7), and is among five outliers for isothermality (bc3). On the opposite end, lowest temperature records are scattered in a chain of southern localities, such as Otamendi (bc1, bc10), Zárate (bc8), Morrison (bc9, bc11) and Despeñaderos (bc6); the southernmost site (Quilmes) is the lowest only for bc5 and two relative measures (bc2, bc3). The highest value for maximal temperature of the warmest month (bc5) is shared by Colonia Castelli, San Francisco de Laishi and Asunción; the former two placed near the borders of the xeric Chaco. Candelaria (province of Misiones), the easternmost place, is also the wettest, as revealed by many precipitation variables at their highest end (bc12–14, bc16–17, bc19). Its neighboring site, Posadas, shares with Candelaria being outlier for many of the mentioned variables, while having the lowest precipitation seasonality (bc15) as well. The highest precipitation seasonality corresponds to Despeñaderos and Anizacate-La Bolsa (both localities are outliers for bc15, the former having the end value of the distribution); they are placed on the westernmost margin of the species range in a region with a marked decrease in rainfall during winter. Values of all localities near the dry Chaco are far from this lowest bc15, indicating this variable is not a limiting factor there. Although seemingly marginal to the known distribution, Paso de los Libres, the only site on the Uruguay River (Fig. 2: k), did not give evidence of any divergence nor extreme condition with respect to the bulk of bioclimatic data. The area around Diamante and the Predelta National Park (Fig. 2: i), together with some sites nearby in province of Entre Ríos, concentrates most median values for temperature variables; precipitation median values are more scattered, though with some density in province of Santa Fe (Colonia Mascías, Santa Fe, Laguna Paiva).

Comparisons. Comparing *D. testudineus* with *D. dilatatus*, which are sympatric in large portions of their ranges, the overall picture is of similarity in the distribution of most variables, with much less dispersion in the former. Plotted for cumulative frequency (Fig. 3), curves of many variables run close and interlock, denoting similar values. This applies for all absolute temperature variables (bc1, bc5, bc6, bc8–bc11) and for some precipitation variables (bc12, bc13). In all of them, curves of *D. testudineus* start at slightly higher values than *D. dilatatus*, but they cross, and the former terminates at lower values (Fig. 3: bc1, bc5); in other words, slope of *D. testudineus* is in average higher, making the variables ranges concentrate. In all such variables, curves of another sympatric species, *Gryne orensis,* are more separated from those of *D. dilatatus* and *D. testudineus*, and clearly denote preferences for warmer climate. Worth mentioning is the case of bc5, which describes the highest extreme temperatures. Despite values ranges which are different (*D. dilatatus* the largest, *D. testudineus* in middle, *G. orensis* the shortest), with the bulk of the data most similar between the two former, all three have almost the same highest extreme values (34.40°C for *D. dilatatus* and *D. testudineus*; 34.60°C for *G. orensis*) (Fig. 3, Fig. 4).

Dissimilarities between *D. testudineus* and *D. dilatatus* are found mostly in relative temperature variables. Isothermality (bc3) in *D. testudineus* has the lowest values for all three species, while *D. dilatatus* and *G. orensis* closely overlap on higher values (Fig. 3). Complementarily, bc4-temperature seasonality is the highest in *D. testudineus*, although in this case crossing *D. dilatatus* curve at high values (Fig. 3). With respect to precipitation variables, those reflecting decrease during dry/cold periods (bc14, bc17, bc19) and their correlation on seasonality (bc15) are more similar between *D. testudineus* and *G. orensis* around more humid monthly/quarterly values and lower seasonality than *D. dilatatus* (Fig. 3). Finally, bc16 and bc18 curves are more or less equidistant, in a gradient from less to more humidity (*D. testudineus, D. dilatatus, G. orensis*, respectively). Overall, considering not only extreme values but especially the inter-quartile range in box-plots (Fig. 4), variables show the largest span in *D. dilatatus*, followed in most cases by *D. testudineus*, then by *G. orensis*. Ranges of *D. testudineus* almost equal those of *G. orensis* in bc2, bc6, bc16, and are the smallest in bc3, bc4, bc7 and bc12. For *D. testudineus* variation concentrates narrowly at low values for bc3-isothermality and at high values for bc4-temperature seasonality (in a lesser extent, also for bc7-temperature annual range), suggesting the need of varying temperatures along the year. Similar narrowness is shown by bc12 (annual precipitation), although this is not repeated in monthly or quarterly values. Precipitation seasonality (bc15) concentrates narrowly around low values, both for *D. testudineus*, and even more for *G. orensis* (Fig. 4).

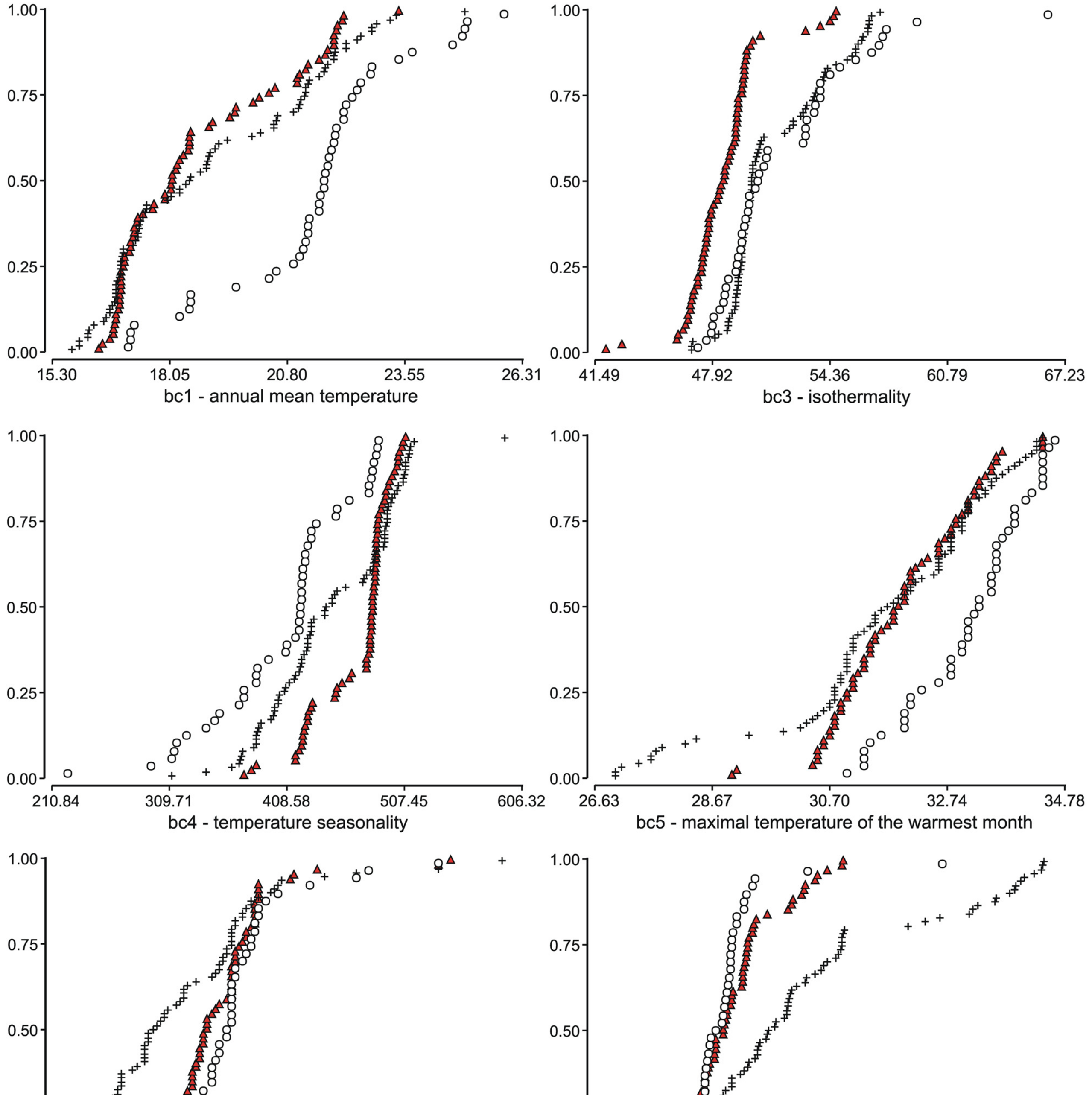


FIGURE 3. Cumulative frequency plots of selected bc variables, comparing *Discocyrtus testudineus* (triangles, n=71), *Discocyrtus dilatatus* (crosses, n=85) and *Gryne orensis* (circles, n=45).

Potential range. Models obtained with MAXENT identified a broad suitable area for *D. testudineus* along the Paraná River, from the region of confluence with Paraguay River up to the mouth in Rio de la Plata (Fig. 2), and within this were two large sectors of high suitability (Fig. 5). In southern province of Corrientes the dominant N–S Paraná pattern has an eastwards expansion, to comprise the sole locality on Uruguay River (Paso de los Libres, Fig. 2: k). In accordance to the "Mesopotamian *s.s.* area" (Acosta 2002), the model also extends suitable conditions across province of Santa Fe, towards the central province of Córdoba, widely embracing records there (Fig. 2). Results display this extension with lower suitability than the core range (Fig. 5); in addition, it appears fuzzily interrupted near the inter-provincial boundary (Figs. 2, 5). Medium to high suitability fringes run southwards along left and right banks of Rio de la Plata (Fig. 5), but records only exist on the Argentinean side (Quilmes) and on an island (Martin García). Moreover, two isolated areas are predicted in all runs: one spot in the province of Tucumán and a strip bordering the southern coast near Bahia Blanca. Performance of models was high in all cases: AUC ranged from 0.9695 to 0.9768 in the 30-replicates run (average=0.9724, SD=0.0020). The adopted MAXENT model predicts a suitable area of approximately 345.000 km^2. It leaves outside some northern records, namely Asunción (a remarkable outlier in the bioclimatic profile), Colonia Castelli and San Francisco de Laishi, the two latter "at the gates" of the xeric Chaco (Fig. 2). Also Posadas and Candelaria (Misiones), with highest values for precipitation, are left outside the suitable area with the threshold used.

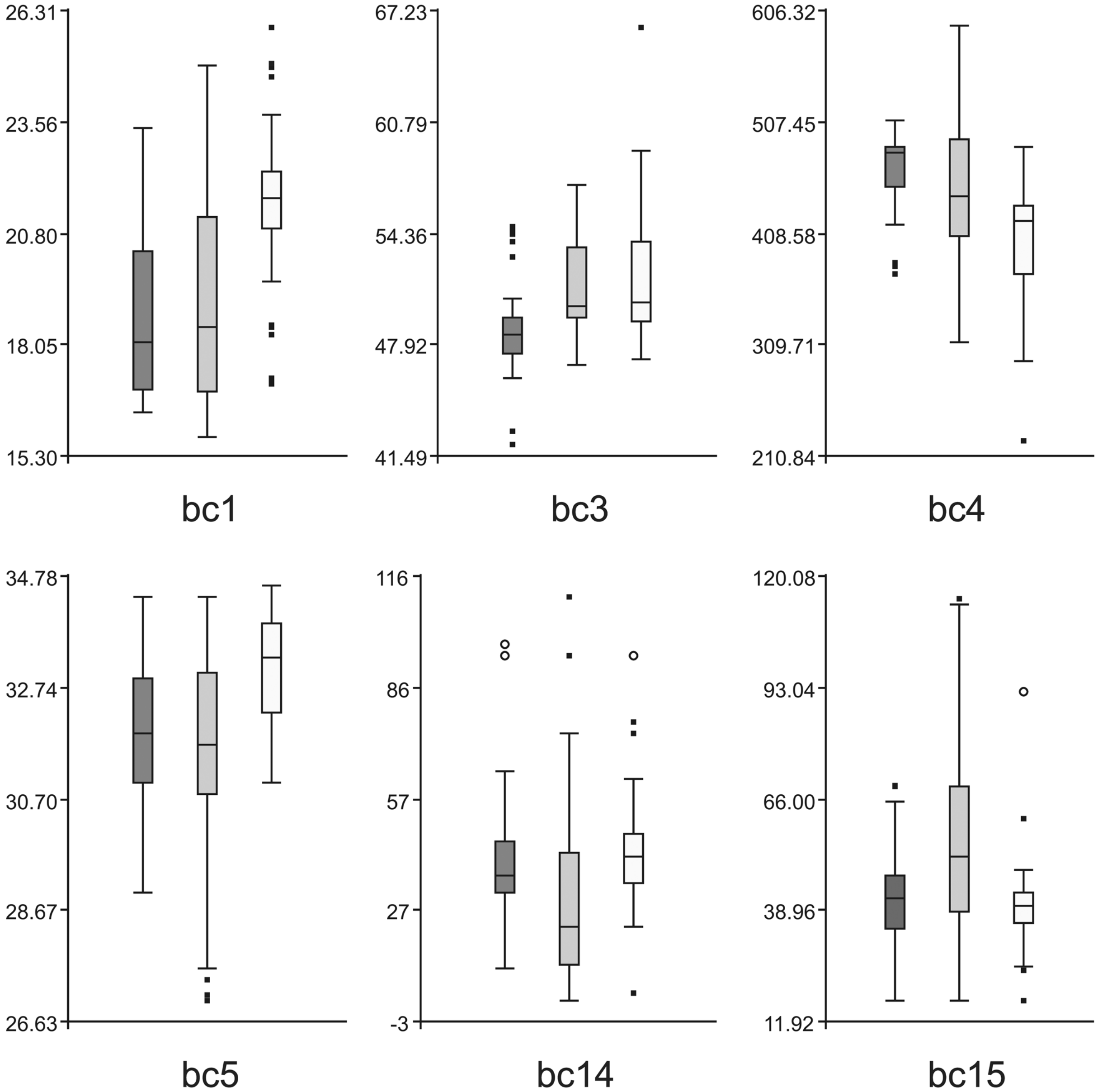


FIGURE 4. Box-plots of the same selected bc variables depicted for cumulative frequency in Fig. 3, showing outliers (black squares) and extreme outliers (white dots). References: *Discocyrtus testudineus* (dark grey, first position), *Discocyrtus dilatatus* (light grey, second position) and *Gryne orensis* (white, third position).

In comparison, the binary model built by BIOCLIM yielded a more permissive prediction, about 35% larger than MAXENT, principally overflowing the core range to both sides (Fig. 2). The BIOCLIM model adds a suitable strip on the West, with a remarkable digitation along Bermejo River (clearly driven by the record at Colonia

Castelli). To the East, BIOCLIM covers the gaps left by MAXENT in provinces of Entre Ríos and Corrientes, further including almost one quarter of the Uruguayan territory and a small nearby portion in southern Brazil. Interestingly, suitability in Tucumán is predicted with BIOCLIM too, though only partially matching the spot obtained with MAXENT (Fig. 2). Most of the MAXENT prediction on the Rio de la Plata is trimmed by BIOCLIM, except for narrow "threads" connecting the extreme records. Potential range in province of Córdoba is narrower than MAXENT, though continuously connected to the core area. Asunción and Candelaria-Posadas still represent marginal localities with BIOCLIM. Almost 80% of the area predicted by MAXENT, but only 59% of that modeled by BIOCLIM, consists of grid cells shared by the two models.

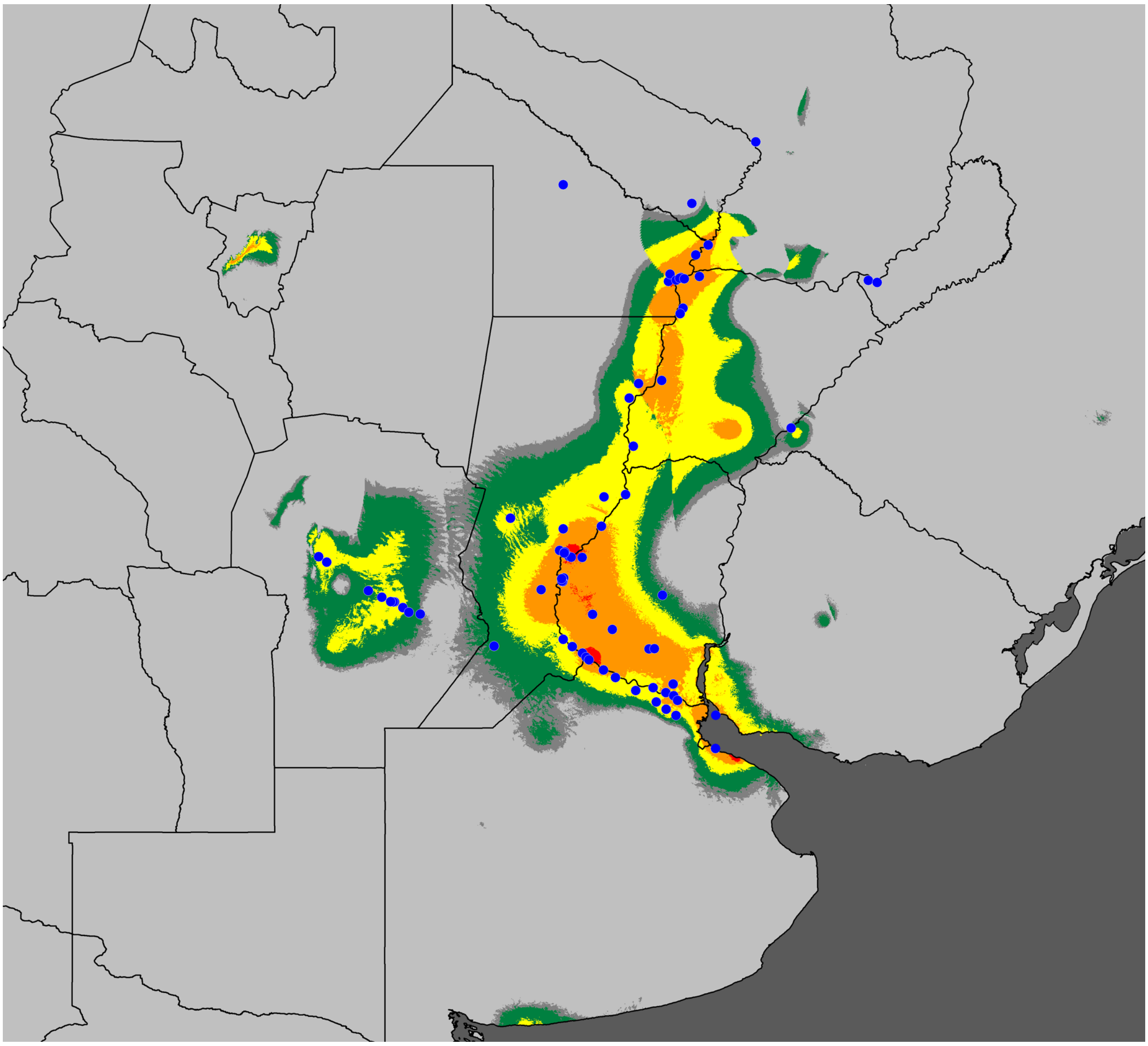
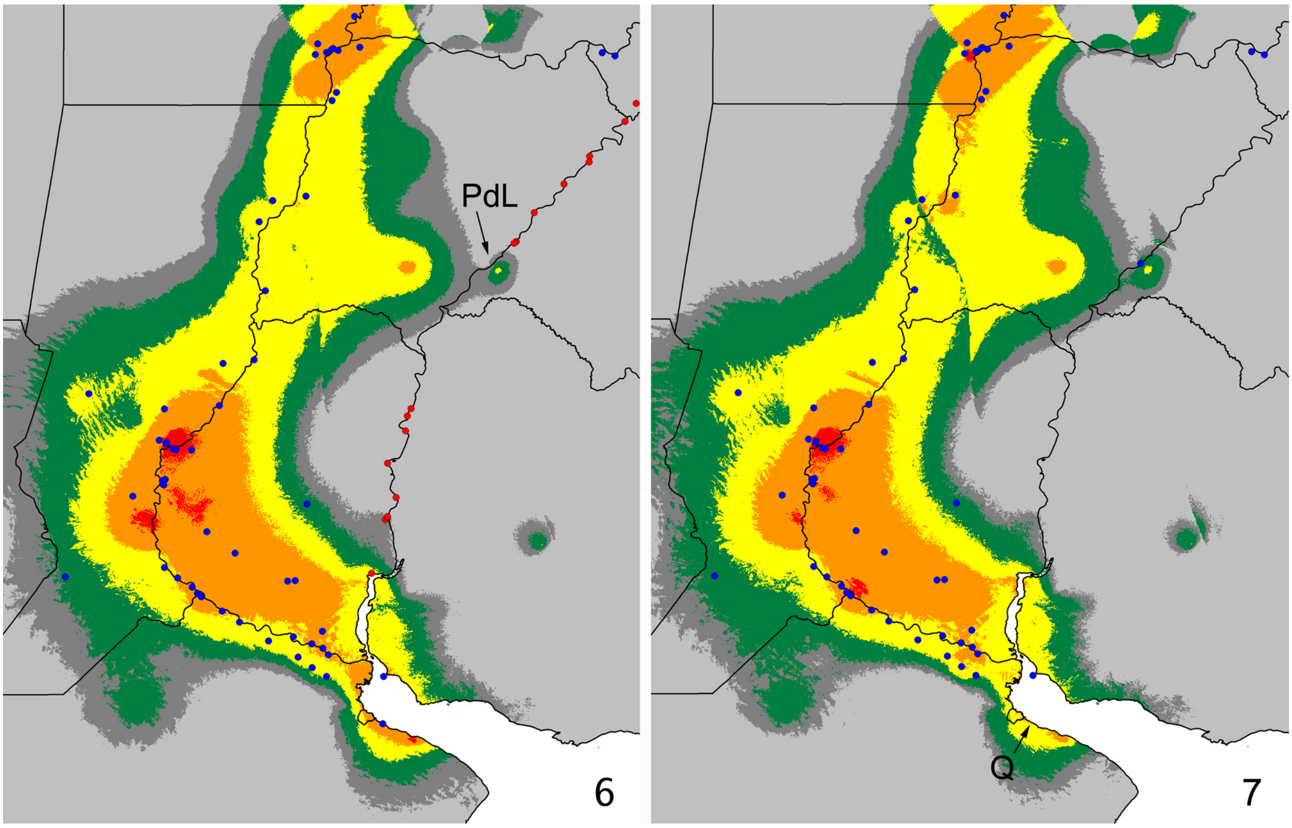


FIGURE 5. Potential distribution of *Discocyrtus testudineus*: average values of the 30-replicates run with MAXENT (default dataset, random test percentage 10%); thresholds displayed are the average of the 30 replicates (average training AUC 0.9724). Suitability levels: dark grey: 0.279–0.332 (the latter value is the "maximum training sensitivity plus specificity" threshold); green: 0.332–0.500; yellow: 0.500–0.680; orange: 0.680–0.820; red: above 0.820. Light grey: areas below the default threshold (equal training sensitivity plus specificity). Dots: training records.



FIGURES 6–7. Potential distribution models of *Discocyrtus testudineus*: detail in the Mesopotamian region, showing effects of deleting one selected point in the record set. **Fig. 6:** Paso de los Libres (PdL) removed, **Fig. 7:** Quilmes (Q) removed. Models display the average grid of the 10-replicates run with MAXENT, using average thresholds. Suitability levels: dark grey: 0.244–0.339 (Fig. 6), 0.268–0.331 (Fig. 7) (the second value is the “maximum training sensitivity plus specificity” threshold); green: 0.334–0.500 (Fig. 6), 0.331–0.500 (Fig. 7); yellow: 0.500–0.680; orange: 0.680–0.820; red: above 0.820. Light grey: areas below the default threshold (equal training sensitivity plus specificity). Blue dots: training records; red dots in Fig. 6: localities surveyed on the Uruguay river, with negative samplings for *D. testudineus*.

Importance of variables. As stated, variables were scored for overall rating, considering all four estimators of relative importance (Table 3). The two most important variables describe temperature stability during the year, *i.e.*, bc4-temperature seasonality and bc3-isothermality. Together they monopolize the top values for all four estimators. Both give a picture of a species preferring greater seasonal differences than the sympatric *D. dilatatus* and *G. orensis*. These two variables are also remarkable because of their low dispersion, suggesting a quite narrow constraint for the species. On a second level, bc14-precipitation of the driest month and bc9-mean temperature of the driest quarter ranked high for at least three estimators, probably indicating some critical influence of climate in driest periods. In middle of the ranking, bc5-maximal temperature of the warmest month showed considerable influence, as expected for a variable that is deemed to be limiting towards the dry Chaco (Acosta & Vergara 2013). Not all variables related to climatic variations ranked high, however: bc7-temperature annual range and bc15-precipitation seasonality placed almost at the bottom. The very lowest places were occupied by bc8-mean temperature of the wettest quarter and bc16-precipitation of the wettest quarter, suggesting little weight of those variables related to wet periods (*i.e.*, humidity seems not critical in those time-lapses). Absolute annual values for temperature (bc1) or precipitation (bc12) are not ranked here, since they were not selected for modeling (in preliminary runs they scored very low).

Influence of diverging records. Neither the suppression of Paso de los Libres nor Quilmes from the dataset significantly affected the final models. Changes driven by the absence of Paso de los Libres are negligible, even considering suitability degree (Fig. 6). That is, MAXENT was able to recover the same eastwards projection with the rest of the records, thereby indicating that the presence around Paso de los Libres was predictable, through suitable conditions that reach the Uruguay River in that restricted site alone. This assertion appears empirically sustained by detailed samplings I carried out in 14 localities along the whole Argentinean portion of Uruguay River (*ca.* 650 km; Fig. 6), in which *D. testudineus* was never collected, but other Mesopotamian species instead (*D. prospicuus* in the first place; Acosta & Guerrero 2011). The second dataset variant excluded Quilmes, the southernmost record; MAXENT was able to predict the area as well, with just some slight differences concerning suitability degree (a little lower) and extent (slightly smaller) when that record is removed (Fig. 7).

Discussion

As stressed in previous papers (Acosta 2008; Acosta & Guerrero 2011), current knowledge on the ecological and distributional requirements of Neotropical harvestmen is extremely poor. Habitats of most species have hitherto been characterized through a kind of "intuitive extrapolation" from the few data available, the ecoregional assignment of the recorded localities, and scattered field notes on sampled materials (Valentinis de Martínez 1974, Acosta 1995, Guerrero 2011). Although not intended to substitute specific research, distribution models (also known as "ecological niche models") clearly provide a first concrete approach to the species environmental preferences and help us understand the climatic constraints underlying distributions. The value of this initial approach is emphasized when species records and biological knowledge are scarce (Pearce & Boyce 2006), as is the case for *D. testudineus*.

Range modeled with MAXENT fulfilled the previous assumptions for *D. testudineus* based on, say, a "non-analytical, expert-based" assessment well (*e.g.*, Acosta 2002). This species was expected to spread across the Mesopotamian *s.s.* opiliological area, as defined by Acosta (2002), and MAXENT models succeeded to match this expectation very closely. As a "typical" Mesopotamian harvestman, like *D. dilatatus* or *G. orensis*, *D. testudineus* appears to primarily occupy the plains along the Paraguay-Paraná course (Figs. 2, 5). Its presence in the province of Córdoba (a feature met only by a subset of Mesopotamian species—of the aforementioned, only *D. testudineus* and *D. dilatatus*) seems a secondary extension of its core range; moreover, as MAXENT models suggest, the connection between the core range and the Córdoba portion seems diffuse. This might reflect the fact that records are not widespread in Córdoba but principally restricted along the Ctalamochita River, even when MAXENT predicts a generous extension in that province. BIOCLIM, which recognizes a much narrower suitable area, appears a little more realistic in this particular sector, although still predicting an elongated strip not fully supported by actual data (Fig. 2). Records in Córdoba, together with other localities in province of Buenos Aires (Zárate, Otamendi, Quilmes; Fig. 2), represent a southernmost front for the species range in which extreme values for variables are scattered (not concentrated on one single site). Some northern localities, like Asunción and Candelaria-Posadas, stand for strong outsiders, by holding many extreme variables values; they all are marginal for BIOCLIM and are left outside of the suitable area with the current threshold by MAXENT (Fig. 2).

The results of the analysis of the relevance of variables (Table 3) show that six temperature predictors ranked on top, suggesting that temperature has more influence than precipitation for *D. testudineus*. As stated in previous papers, temperature seasonality (bc4) revealed again a remarkable importance, ranking first in *D. testudineus*, *D. dilatatus* and *G. orensis*, and second in *D. prospicuus* (Acosta & Guerrero 2011; Acosta & Vergara 2013; Vergara & Acosta in prep.). Other variables do not seem to follow such a homogeneous pattern across different species. For example, the second relevant variable for *D. testudineus*, isothermality (bc3), ranked almost at the bottom for *D. dilatatus* or *G. orensis* but was first in *D. prospicuus* (Acosta & Guerrero 2011; Acosta & Vergara 2013; Vergara & Acosta in prep.). Precipitation of the driest month (bc14) was highly relevant for *D. testudineus* (3rd place) and *G. orensis* (2nd place) but not for *D. dilatatus* (least relevant). Regarding bc15-precipitation seasonality, it consistently occupied an intermediate to low place of importance in all species, and a similar ranking is shown by bc5-maximal temperature of the warmest month. Although not decisive in its overall influence onto the models, bc5 probably matters more locally, near the xeric Chaco borders, where it might represent the most limiting variable while moving westwards (Acosta & Vergara 2013). As seen, highest values for bc5 are almost the same for *D. testudineus*, *D. dilatatus* and *G. orensis*, as if there were an abrupt boundary of maximal temperature (Fig. 4) not crossed by typical Mesopotamian species. As indicated, *D. testudineus*, *D. dilatatus* and *G. orensis* are sympatric in large regions and are very often collected together, even sharing the same hideaways; the association *D. testudineus* + *D. dilatatus* is very frequent in provinces of Córdoba and Santa Fe; *D. testudineus* + *G. orensis* more often in sites close to Paraná River; *D. dilatatus* + *G. orensis* in provinces of Corrientes, Chaco and Formosa (Valentinis de Martínez 1974; Acosta 1995; Acosta & Vergara 2013). Profile and curves comparisons (Figs. 3–4) showed that *D. testudineus* and *G. orensis* (with little dispersion for bc15-precipitation seasonality) are more dependent to humidity than *D. dilatatus*, matching well the field observations revealing large populations in shady sites and the closeness to rivers of most collecting sites (Valentinis de Martínez 1974; Acosta 1995; Guerrero 2011; Guerrero *et al.* 2013; Acosta & Vergara 2013). Both *D. testudineus* and *G. orensis* seem adapted to intermittent flooding. In contrast, *D. dilatatus* can be collected in any suited spot throughout the whole region, near rivers or not (Acosta 1995). This amplitude is readily recognizable in the wider span of variables values (Figs. 3–4) and in being the only species of the three having an extensive range in the Yungas ecoregion as well (Acosta 2007; Vergara & Acosta in prep.). Like other modeled Mesopotamian species (Acosta & Guerrero 2011, Acosta & Vergara 2013, Vergara & Acosta in prep.), *D. testudineus* seems able to tolerate some anthropic influence, but probably to a lesser degree than *D. prospicuus* or *D. dilatatus.*

Interestingly, both MAXENT and BIOCLIM project for *D. testudineus* a suitable sector in province of Tucumán (Figs. 2, 5), insinuating at least the potential —not hitherto supported by records— for a Mesopotamian-Yungas disjunct pattern. It is worth mentioning that this sector has been recognized as suitable for other "pure" (*i.e.*, not disjunct) Mesopotamian harvestmen (Acosta 2007), and also for some disjunct species when records from the Yungas are removed (Acosta & Guerrero 2011, Vergara & Acosta in prep.), suggesting a close climatic similarity. In addition, MAXENT (but not BIOCLIM) predicts a small portion on the southern coast of province of Buenos Aires, near Bahia Blanca (Figs. 2, 5). Suggestively, Ringuelet (1959) repeatedly mentions this locality as a kind of presumed retreat for "Brazilian" harvestmen, as insinuated by the curious citations of Roewer (1912, 1913, 1915, 1916, 1929) for a dozen subtropical species. In Ringuelet´s view, if those citations are right, they might support the notion of a "refuge" for subtropical harvestmen which has remained after the last paleo-environmental expansion-retraction pulse (Ringuelet 1959:152). One might be tempted to see the southern prediction of *D. testudineus* as agreeing with that scenario, but so far this seems pure speculation; none of all those bizarre records have yet been confirmed, and they are currently considered either mistaken or highly suspect (Ringuelet 1959; Acosta 1995, 2002).

MAXENT results proved a remarkable precision when predicting presence at Paso de los Libres. The finding of *D. testudineus* in that locality was unexpected, considering that previous samples seemed to limit the species to the Paraná River influence, while the well surveyed Uruguay River was apparently the realm of other Mesopotamian harvestmen. As seen, even with Paso de los Libres deleted models predicted that range extension, which reaches the Uruguay River and appears to disrupt the pure "Uruguayan" character at that point (Fig. 6). Nores *et al.* (2005) previously described an interruption of gallery forest at Monte Caseros, province of Corrientes (about 80 km S of Paso de los Libres), it being replaced there by xerophytic woodland. The same pattern, with thorny shrublands of the Espinal ecoregion reaching the Uruguay River in that sector alone, is displayed in the ecoregional proposal by Brown *et al.* (2006). By predicting that intromission and leaving as unsuitable the rest of the Uruguay River (where "absence" of *D. testudineus* is well supported), MAXENT was much more precise than BIOCLIM, which broadly classed as suitable the whole river coastal region and far beyond (Fig. 2).

Presence on the Rio de la Plata coast (recorded at Quilmes) is another successful MAXENT prediction (Fig. 7), not paralleled by BIOCLIM. Already Acosta and Guerrero (2011) stressed that the range of *D. testudineus* probably ended at Otamendi, around 80 km NW of Quilmes. The assertion was based not only on own results, but especially considered the "historical sampling pressure" in the area. In fact, because of their proximity to museums in Buenos Aires and La Plata, localities between the Paraná delta and the Argentinean side of the Rio de la Plata are the most densely represented in local collections, like those available to Ringuelet (1959). Therefore, little was expected to change the picture in this sector, at least for such a conspicuous and easy-to-collect harvestman. As Guerrero *et al.* (2013) explain, settlement of *D. testudineus* in Quilmes might be a recent event, which accompanied the evolution of the coastal biota in the last few decades. The southern coast of Rio de la Plata receives the continuous faunistic and floristic input of Mesopotamian species, brought by the tributary rivers Uruguay and Paraná. The rich harvestman fauna on Martín García island (Ringuelet 1959) might well have arrived there in the same way. Guerrero *et al.* (2013) detected in Quilmes several plants and arachnids of Paranian origin, which occur more northerly and might have surpassed their previous distributional limit (the lower delta), revealing a presumable recent (maybe still ongoing) colonization. Of course, if *D. testudineus* is an active invader, it is not known which factors will determine if settlement is successful or not. Similar range predictions are projected for the Uruguayan coast (Figs. 2, 5, 7), but for the moment the nearest actual record (known from long ago) is from Martin García island. In any case, as for Quilmes, MAXENT models suggest that the bioclimatic potential for such an establishment exists.

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