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A predictive modeling approach to test distributional uniformity of Uruguayan harvestmen (Arachnida: Opiliones)

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Abstract

Background: Harvestmen are a good taxon for biogeographic studies due to their low vagility and their dependence on environmental conditions which make most of them live in humid and shaded habitats. Current knowledge of the geographical distribution of Uruguayan opilofauna suggests that no evident zoogeographic areas are present, mainly because of the apparent uniformity of the landscape of this country. Recent biogeographic studies indicate that Uruguay represents a biogeographical crossroad between three South American provinces, and the aim of this study is focused on determining if this fact is reflected in the distribution of the Uruguayan opilofauna. To test this presumption, we used the species distribution model methodology. Distribution data about four harvestmen species from Uruguay and neighboring countries were analyzed. We used the maximum entropy principle to perform a distribution model for each species.

Results: We recognized *Acanthopachylus aculeatus* and *Pachyloides thorellii* as two Pampasic representatives of the Uruguayan opilofauna. The other species studied, *Discocyrtus prospicuus* and *Metalibitia paraguayensis*, reflect Mesopotamian and Paranaense influences in the Uruguayan territory. Isothermality was the climatic variable with the best contribution in the models of the four species, reflecting constrained latitudinal ranges.

Conclusions: Results of the present study suggest that two roughly different opiliological areas for Uruguay can be recognized, based on climatic variables.

Keywords: Opilofauna; Potential distribution; Biogeographic patterns; South America; Neotropical

Background

Present knowledge on the diversity of Uruguayan harvestmen is mainly based on the contributions made by Ringuelet (1955, 1963) and Capocasale (1968, 1993, 2003). The latter paper (Capocasale 2003) consists of a catalogue, in which a total of 25 species belonging to 5 families were cited for the country. In his contributions, Capocasale (1968, 2003) also provided a coarse reference to the species distributions, either indicating the occurrence localities on a map (Capocasale 1968) or merely assigning them to the administrative divisions (departments) (Capocasale 2003). Indeed, this author explicitly avoided

recognizing zoogeographic areas since he considered that harvestmen species were distributed quite uniformly throughout the country (i.e., distributional patterns were not apparent for him). Following a similar rationale, Kury (2003) stressed that the opilofauna of Uruguay was the poorest in South America, allegedly due to the environmental uniformity of the landscape of this country as assessed by most 'classical' biogeographic approaches, like Cabrera and Willink (1973) and Morrone (2002). Besides this, such a low species richness of the Uruguayan opilofauna associated to the small size of the territory might seem an obvious correlation.

As a fact, the Uruguayan territory is extensively dominated by grasslands, which results in a recognizable landscape uniformity (Evia and Gudynas 2000). In their revised map of the ecoregions of the world, Olson et al. (2001) place Uruguay, together with the southern portion of the Brazilian state Rio Grande do Sul, in an ecoregion thereby

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named 'Uruguayan savanna'. Morrone (2002) locates Uruguay in the 'Pampa province', which also comprises eastern Argentina (provinces of Buenos Aires and Entre Ríos) and southern Brazil, as mentioned above. The Pampas are characterized by savannas covered by 1-m-high temperate grasslands and shrubs. This homogeneous picture, however, might be a 'thick-brush' oversimplification that hides some patterns. At least for harvestmen, distributions in Uruguay still remain poorly surveyed in large parts of the country, so the alleged uniformity might reflect lack of knowledge. More importantly, Uruguayan environments were actually shown to be more diverse than it seems in a quick glance. Grela (2004) demonstrated that the Uruguayan dendroflora is represented by two quite distinct areas: the Oriental one, mainly influenced by the Paranaense Forest, together with a small intromission of Cerrado, and the Occidental area, where two provinces converge: Chaco and Paranaense Forest, *sensu* Morrone (2002). The biogeographical affinities between the Pampean Province in Argentina and Uruguay were already indicated for varied taxonomic groups, like Asteraceae (Crisci et al. 2001), Pleistocene mammals (Carlini et al. 2004), as well as harvestmen (Acosta 2002) and scorpions (Acosta 1993; Mattoni and Acosta 1997; Acosta et al. 2008). Furthermore, this area is a part of the 'peripampasic arc', a biogeographical track that comprises ancient mountain systems with biotic connections, where a high biodiversity and endemic species converge (Acosta 1993; Acosta and Maury 1998a, b; Acosta et al. 2008; Ferretti et al. 2012). Ferretti et al. (2012) recognized a mygalomorph spider track connecting part of Argentina, Uruguay, and southern Brazil. Recently, Laborda et al. (2012) reported the southernmost record in lower Uruguay River of a spider species associated to subtropical forests from Northeastern Argentina. This record represents new evidence that supports the proposal that this river acts as a biological corridor that allows the intromission of the Paranaense Forest and Chaco Provinces in Uruguay, as proposed by Grela (2004).

The scarcity of records, together with their evident geographical bias around the capital city, Montevideo (see, e.g., Capocasale 1968), might be considered a concrete hindrance to get a valid overview of range patterns. To overcome this problem, we used the benefits of building models of potential distribution, using an ecological niche modeling approach, based on bioclimatic suitability for selected species. Range modeling is considered a good way to predict a species distribution when presence points are deemed to be incomplete, and at the same time, it provides accurate results and biologically meaningful fit between species occurrence and environment variables (Van Der Wal et al. 2009; Peterson et al. 2011). In this sense, we take advantage of one property that makes harvestmen a good taxon for biogeographic studies: their

apparent dependence on environmental conditions, like temperature and humidity (Acosta 2002, 2008; Acosta and Guerrero 2011; Pinto da Rocha et al. 2005, 2007).

The present study was focused to test whether the alleged uniformity of the Uruguayan landscape applies for the opilofauna, or, instead, the country congregates different opilological components as a result of a biogeographic crossroad. Our aim is to verify if modeled ranges of selected species are able to properly depict different biogeographical affinities for harvestmen. In any case, distribution models will represent a first step to study the regional biogeographic influence on the distribution of Uruguayan harvestmen species.

Methods

Species and occurrence data

For this study, we selected four species of Uruguayan harvestmen: the gonyleptids *Acanthopachylus aculeatus* (Kirby 1818), *Discocyrtus prospicius* (Holmberg 1876), and *Pachylodes thorellii* Holmberg 1878, and the cosmetid *Metalibitia paraguayensis* (Sørensen 1884). These species were selected because of the availability of enough point records (not less than 60), not only from Uruguay but also from their whole range, i.e., also comprising Argentina, Brazil, and Paraguay. A part of the records originated in the literature (Sørensen 1884; Soares and Soares 1986; Ringuelet 1959, 1963; Capocasale 1968; Capocasale and Gudynas 1993; Acosta 1989, 1992, 1999, 2002; Kury 2003; Toscano-Gadea and Simó 2004; Guerrero 2011; Acosta and Guerrero 2011); in those cases, the easy identification of the mentioned species assured our confidence in their taxonomical accuracy. Many additional records were obtained from Uruguayan arachnological collections: Museo Nacional de Historia Natural, Montevideo (MNHN) and Sección Entomología, Facultad de Ciencias, Universidad de la República (FCE-Op). Localities were georeferenced using Gazzetter Diva GIS (<http://www.diva-gis.org/gData>), Google Earth (<http://earth.google.es/>), and Map Planet (<http://www.mapplanet.com/>). Imprecise or doubtful records were not considered in this study. The database used for modeling consisted of 129 unique locality records for *A. aculeatus*, 68 for *P. thorellii*, and 65 for *M. paraguayensis*. Dataset of *D. prospicius* comprises all 80 point records reported by Acosta and Guerrero (2011). The complete record set for Uruguay, including the new records for all four species, is detailed in Table 1.

Environmental variables

Bioclimatic variables were obtained from the WorldClim database (<http://www.worldclim.org/>), at a resolution of 30 arc sec, i.e., about 1 × 1 km (Hijmans et al. 2005a, b). It comprises 19 bioclimatic variables derived from maximum, minimum, and averages of temperature and

Table 1 Complete record set for Uruguay of *Discocyrtus prospicius*, *Pachyoides thorellii*, *Acanthopachylus aculeatus*, and *Metalibitia paraguayensis*, with geographical coordinates

Department	Locality	Longitude (W)	Latitude (S)	Source
<i>Discocyrtus prospicius</i>				
Artigas	Isla Rica	-57.8840	-30.5311	Capocasale (1968)
Artigas	Isla Zapallo	-57.8737	-30.4989	Acosta and Guerrero (2011)
Canelones	Villa Argentina	-55.7793	-34.7708	Acosta and Guerrero (2011)
Colonia	Barra de Rosario	-57.3506	-34.4368	NR: 1 ♂, 2 ♀ (FCE-Op 318), 12-vi-1960 (L. C. de Zolessi)
Colonia	Barrancas de San Pedro	-57.9077	-34.3614	Acosta and Guerrero (2011)
Colonia	Colonia	-57.8656	-34.4371	Acosta and Guerrero (2011)
Colonia	Nueva Palmira	-58.4136	-33.8662	Acosta and Guerrero (2011)
Colonia	Punta Arroyo Limetas	-58.1053	-34.1728	Capocasale (1968)
Colonia	Punta Gorda	-58.4175	-33.9117	Capocasale (1968)
Lavalleja	Parque Sierra Minas	-55.1973	-34.4260	Acosta and Guerrero (2011)
Paysandú	Paysandú	-58.0889	-32.3005	Acosta and Guerrero (2011)
Río Negro	Fray Bentos	-58.2500	-33.1133	Acosta and Guerrero (2011)
Salto	Isla Redonda	-57.9154	-31.1673	Acosta and Guerrero (2011)
San José	Arazatí	-56.9992	-34.5577	Capocasale (1968)
<i>Pachyoides thorellii</i>				
Canelones	Canelones	-56.2833	-34.5333	NR: 3 ♂, 1 ♀ (MNHN 259), 08-vi-1970 (J. E. García)
Canelones	Marindia	-55.8261	-34.7805	Toscano-Gadea and Simó (2004)
				NR: 1 ♀ (FCE-Op 158), 1 immature (FCE-Op 159), 1-vii-2004 (C. Toscano-Gadea); 4 ♂ (FCE-Op 181), 1-vii-2002 (C. Toscano-Gadea)
Canelones	San José de Carrasco	-55.9820	-34.8518	NR: 2 ♂ (FC-Op 190), 9-viii-2002 (C. Toscano-Gadea)
Canelones	Santa Lucía del Este	-56.4859	-34.7440	Capocasale (1968)
Canelones	Villa Argentina	-55.7773	-34.7703	Capocasale (1968)
Cerro Largo	Río Tacuarí	-54.0100	-32.6262	NR: 1 ♀ (MNHN 1129), 13-iv-1965 (F. Achaval)
Colonia	Arroyo Cufre	-57.3333	-34.4333	Capocasale (1968)
Colonia	Colonia Suiza	-57.2166	-34.3166	NR: 1 ♂ (MNHN 217), 10-i-1971 (E. Corbella and R. Gutiérrez)
Florida	Florida	-56.2159	-34.1095	Kury (2003)
Lavalleja	Arequita	-55.2833	-34.2500	Capocasale (1968)
Lavalleja	Gruta Arequita	-55.2673	-34.2889	Kury (2003)
Lavalleja	Cerro de los Cuervos	-55.2585	-34.2846	NR: 1 ♂ (FCE-Op 108), 23-ix-1997 (M. Simó and G. Useta); 1 ♂ (FCE-Op 114), 17-x-1998 (M. Simó and G. Useta); 1 immature (FCE-Op 126), 15-viii-1998 (M. Simó)
Lavalleja	Cerro de las Chivas	-54.6791	-33.8898	NR: 1 ♀ (FCE-Op 79), 06-ix-1959
Maldonado	Abra de Perdomo	-54.9666	-34.7333	NR: 2 ♂ (MNHN 260), 17-v-1970 (A. Romero and J. E. García)
Maldonado	Barra Arroyo Maldonado	-54.8666	-34.8666	NR: 2 ♂ (MNHN 1106), 1 ♂ (MNHN 1151), 22-xi-1963 (M. Klappenbach)
Maldonado	Sierra de las Ánimas	-55.3166	-34.7666	Capocasale (1968); Capocasale and Gudynas (1993)
Maldonado	Grutas de Salamanca	-54.5666	-34.0333	Capocasale (1968)
Maldonado	Isla de Lobos	-54.8845	-35.0267	Capocasale (1968)
Maldonado	Laguna de Maldonado	-55.0300	-34.8472	NR: 1 ♂ (FCE-Op 94), 27-i-2001
Maldonado	Pan de Azúcar	-55.3936	-34.7426	Capocasale (1968)
Maldonado	Punta Ballena	-55.0285	-34.8976	Capocasale (1968)
Maldonado	Punta del Este	-54.9146	-34.9428	NR: 1 ♀ (MNHN 255), 23-vi-1970 (J. E. García)
Montevideo	Buceo	-56.1333	-34.9000	Capocasale (1968)
Montevideo	Camino Las Tropas	-56.2543	-34.8435	Capocasale (1968)

Table 1 Complete record set for Uruguay of *Discocyrtus prospicuus*, *Pachyloides thorellii*, *Acanthopachylus aculeatus*, and *Metalibitia paraguayensis*, with geographical coordinates (Continued)

Montevideo	Campo de Golf	-56.1635	-34.9250	Capocasale (1968)
Montevideo	Malvín	-56.1152	-34.8973	Capocasale (1968)
Montevideo	Malvín Norte	-56.1130	-34.8741	NR: 1 ♂ (FCE-Op 119), 22-xi-2004 (H. Coitiño)
Montevideo	Melilla	-56.2500	-34.7833	NR: 1 ♂ (FCE-Op 6), 08-iii-1998 (F. Costa)
Montevideo	Parque Rodó	-56.1668	-34.9132	Kury (2003)
Montevideo	Parque Zorrilla	-56.1536	-34.9207	Capocasale (1968)
Montevideo	Prado	-56.1966	-34.8663	NR: 1 ♂ (MNHN 215), 13-i-1971 (E. Goberna)
Montevideo	Puerto Buceo	-56.1326	-34.9105	Capocasale (1968)
Montevideo	Punta Carretas	-34.9000	-56.0666	Capocasale (1968)
Montevideo	Sayago	-56.2333	-34.8333	Capocasale (1968)
Paysandú	Paysandú	-58.0755	-32.3213	NR: 5 immatures (FCE-Op 139), 09-viii-2005
Rocha	Palmares de San Luis	-53.7166	-33.6166	NR: 1 ♀ (MNHN 315), 13-i-1957 (C. Carbonell)
Rocha	La Coronilla	-53.8500	-33.5666	NR: 1 ♂ (MNHN 225), 26-ii-1970 (L. A. de Gambardella)
Rocha	Potrero Grande	-53.7287	-33.8999	NR: 1 immature (FCE-Op 116), 23-iii-1995; 4 immatures (FCE-Op 145), 28-iv-1995; 1 ♂ (FCE-Op 165), 1 ♂ (FCE-Op 196) 18-xii-2000; 1 ♂ (FCE-Op 175), 04-iv-2001; 2 ♂ (FCE-Op 176), 1 ♂ (FCE-Op 180) 24-ii-1995; 1 ♂ (FCE-Op 178), 23-xi-2000; 1 ♂ (FCE-Op 197), 28-iv-1995; 1 ♂ (FCE-Op 199), 03-iii-2001; 1 ♂, 3 ♀ (FCE-Op 200), 25-v-1995; 1 ♂ (FCE-Op 235), 23-iii-1995 (All collected by C. Toscano-Gadea); 3 ♂ (FCE-Op 240), 19-i-1995 (M. Simó and C. Toscano-Gadea); 1 ♂ (FCE-Op 241), 25-viii-1994 (Pérez and Toscano-Gadea); 1 ♂ (FCE-Op 242) 28-iv-1995 (Toscano-Gadea and Mignone)
Rocha	Bocas del Sarandí	-54.1928	-34.1959	NR: 1 ♂ (FCE-Op 164), 25-ii-1995; 21 ♂ (FCE-Op 238), 4-iii-1995 (G. Useta and F. Pérez-Miles)
Rocha	Sarandí del Consejo	-53.9990	-34.3015	NR: 1 ♂ (FCE-Op 201), 29-iv-1995
San José	Sierra Mahoma	-56.9333	-34.0833	NR: 2 ♂, 1 ♀ (MNHN 1262), 29-viii-1965 (F. Achaval)
Treinta y Tres	Río Olimar	-54.8000	-32.9166	NR: 1 immature (MNHN 1091), 22-ix-1963
Treinta y Tres	Cerro Chato	-55.1166	-33.0833	NR: 1 ♂ (MNHN 1234), 26-iii-1964 (R. Capocasale and Bruno)
<i>Acanthopachylus aculeatus</i>				
Canelones	Canelón Grande	-56.4000	-34.5000	Capocasale (1968)
Canelones	Estación la Pedrera	-55.8166	-34.6166	NR: 1 ♀ (FCE-Op 239), 16-x-2002 (F. Costa)
Canelones	Marindia	-56.1000	-34.8166	Toscano-Gadea and Simó (2004). NR: 7 ♂, 20 ♀ (FCE-Op 92), 16-i-1977 (G. Olivera); 1 ♀, 1 immature (FCE-Op 193), 1-vii-2002 (C. Toscano-Gadea)
Canelones	Los Titanes	-55.5452	-34.7861	Capocasale (1968)
Canelones	Piedras de Afilar	-55.5333	-34.7166	NR: 1 ♂ (FCE-Op 174), 05-vii-2004 (A. Aisenberg and G. Useta)
Canelones	San José de Carrasco	-55.9820	-34.8518	1 ♂, 7 ♀ (FCE-Op 172), 08-ix-2002 (C. Toscano-Gadea); 1 immature (FCE-Op 194), 09-viii-2002 (C. Toscano-Gadea)
Canelones	Santa Lucía del Este	-56.4859	-34.7440	Capocasale (1968)
Canelones	Villa Argentina	-55.7773	-34.7703	Capocasale (1968). NR: 1 ♀ (FCE-Op 90), viii-2002 (F. Costa)
Cerro Largo	Camino Las Cuentas	-54.5971	-32.6197	Capocasale (1968)
Cerro Largo	Cerro de las Cuentas	-54.6000	-32.6166	Capocasale (1968)
Cerro Largo	Sarandí del Quebracho	-54.6333	-32.6833	Capocasale (1968)
Cerro Largo	Sierras de Aceguá	-54.4166	-31.9000	Capocasale (1968)
Cerro Largo	Ruta 8. Río Tacuarí	-54.0100	-32.6262	NR: 1 ♂ (MNHN Z042/1217) 15-iv-1965 (F. Achaval)
Colonia	Barra del Rosario	-57.3500	-34.4333	Capocasale (1968)
Colonia	Carmelo	-58.2958	-33.9936	Ringuelet (1963)
Colonia	Punta Gorda	-58.4000	-33.9333	Capocasale (1968)
Durazno	Arroyo Las Cañas	-55.6833	-32.7666	NR: 1 ♀, 4 immatures (MNHN 262) 15-viii-1970 (J. E. García)

Table 1 Complete record set for Uruguay of *Discocyrtus prospicius*, *Pachylodes thorellii*, *Acanthopachylus aculeatus*, and *Metalibitia paraguayensis*, with geographical coordinates (Continued)

Durazno	Cerro Chato	-55.1166	-33.0833	Capocasale (1968)
Lavalleja	Aguas Blancas	-55.4492	-34.5172	Capocasale (1968)
Lavalleja	Cerro Arequita	-55.2833	-34.2500	Ringuelet (1963). NR: 1♂ (FCE-Op 103), 04-iv-1998; 1♀ (FCE-Op 105), 17-v-1998 (M. Simó); 1♂, 1♀ (FCE-Op 115), 17-x-1998 (Simó, Useta and Vázquez); 2♀ (FCE-Op 117), 23-i-1998 (Simó, Useta and Vázquez); 1♀ (FCE-Op 121), 16-vii-1998 (Simó, Useta and Vázquez)
Lavalleja	Cerro de los Cuervos	-55.2585	-34.2846	NR: 1♂, 2♀ (FCE-Op 107), 23-ix-1997 (M. Simó and G. Useta); 1♀ (FCE-Op120), 22-iii-2004 (C. Toscano-Gadea)
Lavalleja	Cerro de las Chivas	-54.6791	-33.8898	NR: 5 ♂, 5 ♀, 12 immatures (FCE-Op 273), 06-ix-1959
Lavalleja	Solís de Mataojo	-55.0666	-34.1000	Capocasale (1968)
Lavalleja	Cerro del Penitente	-55.1666	-34.3500	Capocasale (1968)
Lavalleja	Sierra de Minas	-55.3333	-34.5000	Capocasale (1968)
Maldonado	Abra de Perdomo	-54.9666	-34.7333	NR: 4♀ (MNHN 261), 17-v-1970 (A. Romero and J. E. García); 1♂, 1 ♀ (MNHN 263), 7-vi-1960 (A. Romero and C. Barlocco)
Maldonado	Arroyo Maldonado	-54.8666	-34.8666	NR: 7♂, 27♀ (MNHN P54), 22-xi-1963 (M. Klappenbach)
Maldonado	Balneario Solís	-55.3666	-34.8000	NR: 1♂ (MNHN P30), 27-x-1963 (R. Praderi)
Maldonado	Cerro Catedral	-54.6833	-34.3333	NR: 1♂, 10♀ (FCE-Op 229), 07-v-2002. (F. Costa)
Maldonado	Cerro de las Ánimas	-55.3166	-34.7666	Ringuelet (1963), Capocasale (1968)
Maldonado	Sierra de las Ánimas	-55.3166	-34.7000	NR: 1♀ (FCE-Op 106), 03-iv-1987 (A. Brady)
Maldonado	Cerro del Toro	-55.2666	-34.8666	NR: 1♂ (MNHN P59), 29-xi-1953
Maldonado	Cerro Pan de Azúcar	-55.2666	-34.8333	Capocasale (1968)
Maldonado	Punta Ballena	-55.0285	-34.8976	Capocasale (1968)
Maldonado	Punta del Este	-54.9146	-34.9428	NR: 1♀ (MNHN 254), 23-vi-1970 (J. E. García)
Maldonado	San Carlos	-54.9166	-34.8000	Capocasale (1968)
Montevideo	Buceo	-56.1333	-34.9000	Capocasale (1968)
Montevideo	Buceo, Puerto	-56.1326	-34.9105	Capocasale (1968)
Montevideo	Campo de Golf	-56.1635	-34.9250	Capocasale (1968)
Montevideo	Cañada de las Yeguas	-56.3066	-34.8942	NR: 1♀ (FCE-Op 112), 30-ix-1995
Montevideo	Cerro (1)	-56.2666	-34.8500	Capocasale (1968)
Montevideo	Cerro (2)	-56.2114	-34.8298	NR: 2♀ (FCE-Op 202), v-1980
Montevideo	Colón	-56.2333	-34.8000	Capocasale (1968)
Montevideo	Manga	-56.1000	-34.8166	Capocasale (1968)
Montevideo	Melilla	-56.2500	-34.7833	NR: 1♂, 1♀ (FCE-Op 167), 10-i-1998 (C. Toscano-Gadea); 1♂ (FCE-Op 170), 13-i-1999 (C. Toscano-Gadea); 1♂ (FCE-Op 177), 07-ix-1998 (C. Toscano-Gadea); 1♀ (FCE-Op 179), 07-ii-1998 (C. Toscano-Gadea)
Montevideo	Parque Lecocq	-56.3306	-34.7892	Capocasale (1968)
Montevideo	Parque Rodó	-56.1701	-34.9097	Capocasale (1968)
Montevideo	Parque Rodó, Canteras	-56.1700	-34.9090	Capocasale (1968)
Montevideo	Parque Zorrilla	-56.1536	-34.9207	Capocasale (1968)
Montevideo	Paso de la Arena	-56.2666	-34.8333	Capocasale (1968)
Montevideo	Punta Carretas	-56.0666	-34.9000	Capocasale (1968)
Montevideo	Punta Espinillo	-56.4161	-34.8308	Capocasale (1968)
Montevideo	Punta Gorda	-56.0815	-34.8992	NR: 7 immatures (FCE-Op 100), 10-vii-2003
Montevideo	Rambla Naciones Unidas	-56.1375	-34.9103	Capocasale (1968)
Montevideo	Sayago	-56.2333	-34.8333	Capocasale (1968)
Paysandú	Pueblo Constanca	-58.0000	-32.2000	NR: 1♂, 2♀ (FCE-Op 101), 04-i-2004

Table 1 Complete record set for Uruguay of *Discocyrtus prospicius*, *Pachyloides thorellii*, *Acanthopachylus aculeatus*, and *Metalibitia paraguayensis*, with geographical coordinates (Continued)

Paysandú	Ruta 3. km 420	-57.8465	-32.0359	Capocasale (1968)
Río Negro	Arroyo Salsipuedes	-56.6166	-32.5500	NR: 5♂, 9♀, 39 immatures (MNHN 200), 1♀ (MNHN 265), 22- viii-1970 (E. García)
Rivera	Arroyo Lunarejo	-55.8333	-31.2500	NR: 3♂, 3♀ (FCE-Op 137), 1995
Rocha	Bocas del Sarandí	-54.1928	-34.1959	NR: 1♀ (FCE-Op 185), 25-ii-1995 (C. Toscano-Gadea)
Rocha	Cabo Polonio	-53.7833	-34.4000	Capocasale (1968). NR: 1♂, 1♀ (FCE-Op 186), 18-iii-2004 (F. Achaval)
Rocha	Colonia Don Bosco	-53.7481	-34.0743	NR: 1♂ (FCE-Op 110), 29-vi-2001
Rocha	La Coronilla	-53.8500	-33.5666	NR: 1♀ (MNHN 208), 26-ii-1970 (L. A. de Gambardella)
Rocha	Santa Teresa	-53.5333	-33.9833	NR: 1♀ (MNHN 207), 09-ii-1970 (H. Bonino)
Rocha	San Luis	-53.7166	-33.6166	Capocasale (1968)
San José	Playa Pascual	-56.5833	-34.7500	Capocasale (1968)
San José	Sierra de Mahoma	-56.9333	-34.0833	Capocasale (1968)
Tacuarembó	Paso Borracho	-55.4666	-31.9000	Capocasale (1968)
Tacuarembó	Puntas Arroyo Laureles	-56.1500	-32.6000	Capocasale (1968)
Treinta y Tres	Quebrada de los Cuervos	-54.4500	-33.1666	Ringuelet (1963)
Treinta y Tres	Santa Clara de Olimar	-54.9666	-32.9166	Capocasale (1968)
<i>Metalibitia paraguayensis</i>				
Artigas	Arroyo Cuaró	-56.5000	-30.6833	Capocasale (1968)
Artigas	Arroyo de la Invernada	-56.0166	-30.8000	Capocasale (1968)
Artigas	Pedregal	-57.7133	-30.7138	NR: 1 ♂, 2 ♀ (FCE-Op 98), 10-x-1978 (Zolesi, Morelli and Rodríguez)
Artigas	Ruta 30	-56.8040	-30.4398	Capocasale (1968)
Cerro Largo	Sarandí del Quebracho	-54.6333	-32.6833	NR: 1 ♂ (FCE-Op 75), 18-vi-1954
Cerro Largo	Sierra de Aceguá	-54.4166	-31.9000	NR: 2 ♂, 1 ♀ (FCE-Op 124), 22-iii-2004 (Pérez-Miles and Toscano-Gadea); 1 ♀ (FCE-Op 111), 23-iii-2004
Maldonado	Cerro de las Ánimas	-55.3166	-34.7666	Capocasale (1968)
Maldonado	Grutas de Salamanca	-54.5666	-34.0333	Capocasale (1968)
Montevideo	Cañada de las Yeguas	-56.3066	-34.8942	NR: 1 ♀ (FCE-Op 113), 30-ix-1995
Rivera	Arroyo Carpintería	-54.4833	-31.8000	Capocasale (1968)
Rivera	Arroyo Lunarejo	-55.8333	-31.2500	Capocasale (1968)
Rivera	Ruta 5. Cerro Chivos	-55.8261	-31.3718	NR: 2 ♂, 1 ♀ (MNHN 1450), 03-vi-1962 (P. San Martín)
Rivera	Subida de Pena (1)	-55.9278	-31.1086	Capocasale (1968)
Rivera	Subida de Pena (2)	-56.8040	-30.4398	Capocasale (1968)
Rivera	Sierra de la Aurora	-55.7166	-31.0500	Capocasale (1968)
Salto	Arapey	-33.0833	-55.1166	NR: 6 ♂ (FCE – Op 59), 13-iii-1972 (L. A. González)
Salto	Salto Grande	-57.9166	-31.2333	Capocasale (1968)
San José	Sierra de Mahoma	-56.9333	-34.0833	Capocasale (1968)
Tacuarembó	Arroyo Laureles	-55.1166	-33.0833	Capocasale (1968)
Tacuarembó	Chamberlain	-32.6166	-56.4833	NR: 2 ♂, 1 immature (FCE – Op 203), 05-xii-1966 (Carbonell, Moné and San Martín)
Tacuarembó	Pozo Hondo	-56.2232	-31.8433	Capocasale (1968)
Tacuarembó	Rincón de Vassoura	-31.3833	-55.8664	NR: 2 ♀, 19 immatures (MNHN 1402/Z156), 15-xii-1965

NR, new records (with collection data).

precipitation in the period between years 1950 and 2000. Size of the climatic coverages used to build the models (between -73.525° W/-48.017° W, and -17.575°

S/-41.692° S) was aimed to embrace not only all distribution points of the selected species (within and outside Uruguay) but also a large adjacent region in southern

South America, covering Paraguay, Uruguay, southern Brazil, and all Argentina and Chile north of Patagonia. In any case, model maps displayed in Figures 1, 2, 3, and 4 are limited to the Uruguayan portion of our results. To avoid using highly correlated variables, these were selected following criteria applied by Acosta and Guerrero (2011). On the basis of 770 points from the entire study area, we analyzed the correlation of the variable values through a pairwise correlation test, separately for temperature and precipitation variables (Pearson >0.75). The choice of a variable in a correlated pair (or trio) was primarily evaluated in a preliminary run of the model with all variables, retaining those with the best contribution percentage and/or better rank in the jackknife test. This procedure was performed separately for each species, leading us to select 10 variables for *A. aculeatus* and *P. thorellii*, and 9 for *M. paraguayensis* (all detailed in Table 2); as previously stated (Acosta and Guerrero 2011), models of *D. prospicius* were calibrated with 11 variables.

Modeling procedure

Predictive distributional models were built with MaxEnt (Phillips et al. 2004, 2006), using the version 3.3.3 k of the software (<http://www.cs.princeton.edu/~schapire/maxent/>). This is a presence/background method that proved better performance than others, like presence-only methods (Peterson et al. 2011). MaxEnt is a maximum entropy algorithm that estimates the probability distribution for a species' occurrence based on the actual occurrence points and the defined environmental constraints (Elith et al. 2006, 2011; Phillips and Dudík 2008; Franklin 2010). Entropy is defined by Shannon (1948) as the choice that is involved in the selection of an event, so maximum

entropy refers to maximum choice and closest to uniform (Phillips et al. 2004). The output of the MaxEnt model is a map showing continuous probabilities of presence, so a threshold must be set to define the predicted presence or absence of a species; in our case, we selected 'equal training sensitivity and specificity'. In any case, we preferred to show probability maps (instead of binary ones) to emphasize local differences of the probabilities, more than the boundaries themselves. We set the run to 2,500 maximum iterations, allowing the logistic output format to remove the duplicates from the same grid cell. Maps were displayed by importing models into the free software DIVA-GIS, version 7.1.7 (Hijmans et al. 2005a, b).

Evaluation and relative importance of variables

MaxEnt evaluates the model's performance using the receiver operating characteristic (ROC) (Hanley and McNeil 1982), frequently used in the evaluation of distribution models based on presence-absence algorithms (Benito de Pando and Peñas de Giles 2007; Peterson et al. 2011). We set the random training data as 75% of the sample (25% of the sample as test data). Area under the curve (AUC) is an unbiased measure of discrimination accuracy calculated from the ROC and represents the average sensitivity over all possible specificities (Lobo et al. 2008; Zhonglin et al. 2009). The program automatically calculates the statistical significance of the prediction, using a binomial test of omission that can be used to evaluate the usefulness of the model (Baldwin 2009). An AUC equal to 1.0 represents an ideal diagnostic test because it achieves both 100% sensitivity and 100% specificity. If AUC is 0.5, it indicates that the test has 50% sensitivity and 50% specificity rates, suggesting high omission and commission errors, and a model not

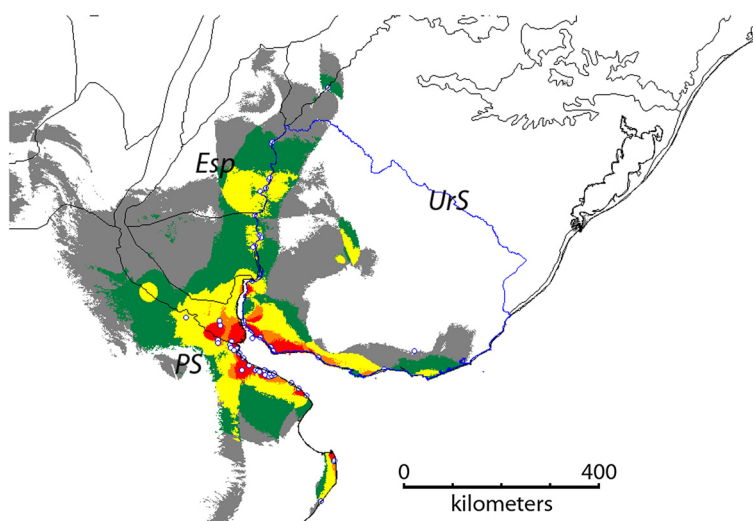


Figure 1 Predictive distributional model obtained with MaxEnt for *Discocyrtus prospicius* (training AUC, 0.993). The model shows the probability steps (grey, 0.130; green, 0.279; yellow, 0.48; orange, 0.75; red, 0.82; white, all areas below the selected threshold, equal training sensitivity plus specificity). White circles denote records. Ecoregions: PS, Humid Pampas; UrS, Uruguayan Savanna; Esp, Espinal.

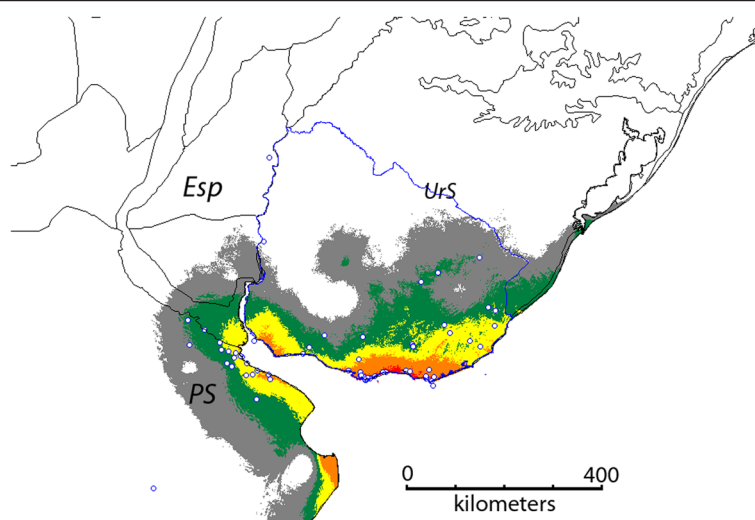


Figure 2 Predictive distributional model obtained with MaxEnt for *Pachyloides thorellii* (training AUC, 0.982). The model shows the probability steps (grey, 0.186; green, 0.348; yellow, 0.511; orange, 0.674; red, 0.837; white, all areas below the selected threshold, equal training sensitivity plus specificity). White circles denote records. Ecoregions: PS, Humid Pampas; UrS, Uruguayan Savanna; Esp, Espinal.

better than random (Cantor et al. 1999; Saatchi et al. 2008; Peterson et al. 2011; Jiménez-Valverde 2012). To estimate the variables with major incidence in the model, we performed a jackknife analysis to measure variable importance. This method evaluates the importance of each variable and compares it with the other altogether (Peterson et al. 2011).

Results

Discocyrtus prospicius

The distribution of this species in Uruguay is restricted to a narrow corridor along the riparian forest

of the coast of Uruguay and Río de la Plata rivers, showing a low probability of occurrence at the center of the country (Figure 1). This species inhabits the islands of Uruguay River, which present subtropical vegetation. Some records were obtained in sites with high synanthropic influence, such as the coast in Villa Argentina in Canelones, and Parque de Vacaciones, UTE in Lavalleja (Figure 1). Two temperature variables presented the highest contribution to the model: isothermality (bc3) and temperature seasonality (bc4) (Table 2). The jackknife analysis indicates that bc3 (isothermality) presented the most information considering all the variables, so that it decreases the

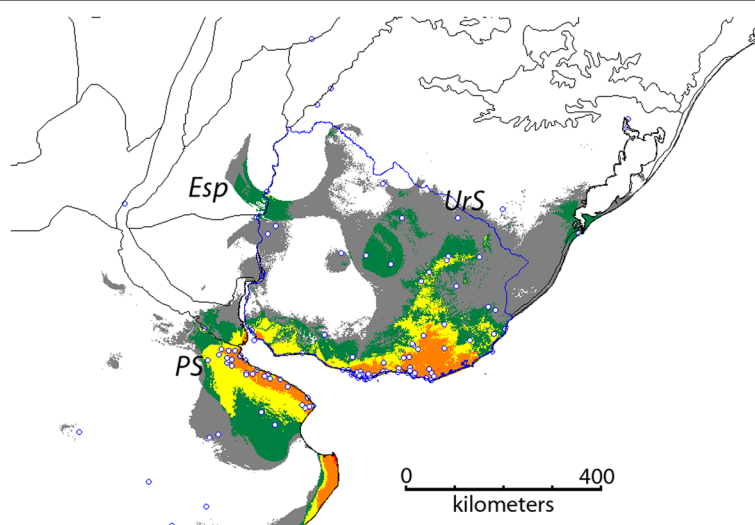


Figure 3 Predictive distributional model obtained with MaxEnt for *Acanthopachylus aculeatus* (training AUC, 0.980). The model shows the probability steps (grey, 0.177; green, 0.342; yellow, 0.506; orange, 0.671; red, 0.835; white, all areas below the selected threshold, equal training sensitivity plus specificity). White circles denote records. Ecoregions: PS, Humid Pampas; UrS, Uruguayan Savanna; Esp, Espinal.

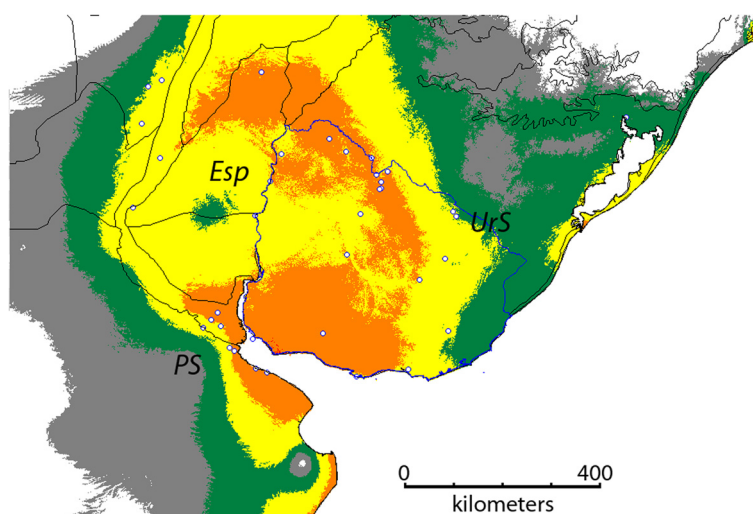


Figure 4 Predictive distributional model obtained with MaxEnt for *Metalibitia paraguayensis* (training AUC, 0.922). The model shows the probability steps (grey, 0.170; green, 0.336; yellow, 0.502; orange, 0.668; red, 0.834; white, all areas below the selected threshold, equal training sensitivity plus specificity). White circles denote records. Ecoregions: PS, Humid Pampas; UrS, Uruguayan Savanna; Esp, Espinal.

models' gain the most when indicated that omitted (Acosta and Guerrero 2011).

Pachyoides thorellii

In our analysis, 49 presence records were used for training, 16 for testing, and 10,049 points as background for

estimating MaxEnt distribution. The model indicates that this species comprises a Pampasian range along the Rio de la Plata River, with the most suitable area situated at the Uruguayan southeastern coast (Figure 2). This species was recorded in some wetlands, such as Bocas del Sarandí and Potrero Grande in the southeast of the

Table 2 Relative contributions of the environmental variables to the MaxEnt model for the species studied

Variable	<i>Acanthopachylus aculeatus</i>			<i>Discocyrtus prospicius</i>			<i>Metalibitia paraguayensis</i>			<i>Pachyoides thorellii</i>		
	% VC	TGW	TGWO	% VC	TGW	TGWO	% VC	TGW	TGWO	% VC	TGW	TGWO
bc1 - annual mean temperature	6.059	2.698	1.165	-	-	-	-	-	-	14.368	2.871	1.257
bc2 - mean diurnal range mean of monthly (max temp – min temp)	5.472	2.728	0.966	0.232	2.983	0.522	-	-	-	3.066	2.934	1.080
bc3 - isothermality (BIO2/BIO7) (×100)	31.424	2.734	1.683	25.563	2.986	1.469	28.389	1.128	0.506	33.439	2.918	1.848
bc4 - temperature seasonality (standard deviation × 100)	5.152	2.699	0.96	19.478	2.877	1.334	17.503	1.137	0.668	3.271	2.923	0.894
bc5 - max temp of warmest month	-	-	-	0.252	2.98	0.614	-	-	-	-	-	-
bc6 - min temperature of coldest month	-	-	-	-	-	-	2.388	1.09	0.371	-	-	-
bc7 - temperature annual range (BIO5-BIO6)	-	-	-	-	-	-	14.547	1.139	0.413	-	-	-
bc8 - mean temp of wettest quarter	2.5	2.701	0.747	5.23	2.948	0.912	3.187	1.102	0.227	0.009	2.934	0.552
bc9 - mean temp of driest quarter	0.289	2.727	0.408	0.744	2.983	1.204	-	-	-	0.01	2.933	0.235
bc11 - mean temp of coldest quarter	-	-	-	18.791	2.937	1.457	-	-	-	-	-	-
bc13 - precipitation of wettest month	8.68	2.7	0.964	-	-	-	-	-	-	-	-	-
bc14 - precipitation of driest month	6.784	2.727	1.349	-	-	-	13.412	1.15	0.401	33.549	2.922	1.383
bc15 - precipitation seasonality (coefficient of variation)	17.845	2.72	1.31	2.958	2.899	0.736	0.04	1.153	0.291	8.004	2.903	1.349
bc16 - precipitation of wettest quarter	-	-	-	9.864	2.971	0.973	-	-	-	-	-	-
bc17 - precipitation of driest quarter	15.795	2.723	1.324	-	-	-	-	-	-	3.607	2.913	1.382
bc18 - precipitation of warmest quarter	-	-	-	7.723	2.976	0.976	18.948	1.119	0.512	0.677	2.920	1.237
bc19 - precipitation of coldest quarter	-	-	-	9.163	2.295	0.967	1.588	1.141	0.256	-	-	-

%VC, variable percentage contribution; TGW, training gain without; TGWO, training gain with only. Data of *Discocyrtus prospicius* are from Acosta and Guerrero (2011). For each species, variables without values were those not selected to build the MaxEnt model. In each column, the highest values are denoted with italics.

country. Other records were located in forests of hilly systems such as Sierra de Ánimas and Sierra de Minas, where it lives in humid habitats, under stones or litter. Along the coast of Río de la Plata and the Atlantic Ocean, the species was found in patches dominated by hydrophytic vegetation and also in suburban areas, confirming its synanthropic habits (*cf.* Acosta 1999). The two variables with the highest contribution were precipitation of the driest month (bc14, 33.5%) and isothermality (bc3, 33.4%), both with similar values (Table 2). The jackknife analysis indicates that bc3 is the variable with highest gain when used in isolation. Furthermore, bc2 (mean diurnal range mean of monthly, 3.07%) and bc8 (mean temp of wettest quarter, 0.01%) have the most information that is not present in the other variables (Table 2).

Acanthopachylus aculeatus

The analysis was performed on 95 presence records for training, 31 for testing, and 10,095 points to determine the MaxEnt distribution. The distribution model resembles that of *P. thorellii* because both species show a Pampasian distribution along the Río de la Plata River and the best suitable area is situated at the Uruguayan southeastern coast (Figure 3). Furthermore, *A. aculeatus* extends the high distribution probabilities to Buenos Aires coast. It is also distributed in other parts of the Uruguayan territory, especially the eastern hills of this country. This species is the most frequently collected in the country, and it was recorded in the same kind of habitats indicated for *P. thorellii*. The two variables with the best contribution were isothermality (bc3, 31.4%) and precipitation seasonality (bc15, 17.8%) (Table 2). The jackknife analysis indicates that bc3 is the variable with highest gain when used in isolation and also it has the most information that is not present in the other variables (Table 2).

Metalibitia paraguayensis

For the analysis, 47 presence records were used for training, 15 for testing, and 10,047 points for the MaxEnt distribution. In contrast to *A. aculeatus* and *P. thorellii*, *M. paraguayensis* extends the best prediction from southwest to the north of Uruguay, showing a Pampean and Chacoan distribution (Figure 4). The species was recorded in natural environments under trunks or stones in riparian forest and hilly systems of Sierra de las Ánimas, Sierra de Aceguá, Sierra de Mahoma, and Cuchilla Negra. The two variables with the best contribution were isothermality (bc3, 28.4%) and precipitation of warmest quarter (bc18, 18.9%) (Table 2). The jackknife analysis indicates that temperature seasonality (bc4, 17.5%) is the variable with highest gain when used in isolation and precipitation

seasonality (bc15, 0.04%) has the most information that is not present in the other variables (Table 2).

Discussion

Species distribution models

At a first glance, predictive maps obtained for three (out of four) representative species of harvestmen seem to support the idea of a uniform distribution pattern. The only species clearly occupying a defined sector in the Uruguayan map is *D. prospicius*, which has been considered a representative of the 'Mesopotamian' harvestmen-fauna in Argentina (Acosta 2002). As Acosta and Guerrero (2011) showed, range of this species is not typically Mesopotamian since it tends to be limited to the borders of rivers Uruguay and Río de la Plata, together with some other separate areas. This marginal pattern is clearly reflected in the Uruguayan portion of the species range, following the relationship through the Uruguay River at the west of this country, up to the Río de la Plata banks (Figure 1). A presumed Paranaense lineage of *D. prospicius* is supported by the preference of this species for inhabiting riparian forests and its taxonomic closeness to *Discocyrtus bucki* (Mello-Leitão 1935) from Misiones, Argentina (Acosta and Guerrero 2011). Like in Argentina, this species was observed in riparian forests in western Uruguay. It was also found in sandy habitats of the coast of the Río de la Plata River and Atlantic Ocean (Toscano-Gadea and Simó 2004). This coast was occupied by psammophile forests in the past. Today, the original habitat was dramatically reduced and fragmented by anthropic activities, and the original vegetation was substituted by exotic plants, only small patches of the original habitat being preserved (Costa et al. 2006). Considering the drastic reduction of native habitat, *D. prospicius* might be considered as a locally threatened species in southern Uruguay; however, it is not known whether its synanthropic habits may counterbalance such a negative pressure, as suggested for other parts of its range, like the Sierras of Córdoba (Acosta and Guerrero 2011). In this regard, Simó et al. (2000) reported the presence of the spiders *Parabatinga brevipes* (Keyserling 1891) and *Asthenoctenus borellii* Simon, 1897 (Ctenidae) in this Uruguayan coastal environment as a result of a positive anthropogenic influence that expanded the range of both species from their natural habitats. Taking all this into account, the predictive distribution model here obtained could be useful for future environmental studies and conservation plans in the southern coast of Uruguay.

As for the remaining species, predictions cover much larger portions of the country. Although presence records of *M. paraguayensis* in Uruguay concentrate mostly at the north and the center of the country, models predict an extensive range in most of the country and beyond, into Argentina and Brazil. Highest probabilities, indeed, cover only the western half of the country, probably reflecting

the influence of the neighboring Mesopotamian area *sensu stricto* (Acosta 2002). In contrast with the other studied species, records of *M. paraguayensis* in Uruguay came only from natural environments, which suggests that it has low tolerance to anthropic influence. In Argentina, however, some records originated in moderately disturbed areas (Acosta 1989).

The two species most frequently represented in arachnological collections are the Pachylinae *A. aculeatus* and *P. thorellii*; no doubt that this overrepresentation originates in the sampling bias around Montevideo (where both are very common), as already emphasized. Nevertheless, distribution models for these species look closely alike, indicating the highest presence probability in southern Uruguay, along the Río de la Plata borders. This condition is mirrored by a similar pattern on the Argentinean side (Figure 1). In both cases, high probabilities spread far into the country, but only (or mostly) covering the eastern half. These patterns suggest a rough match with the Oriental dendrofloristic hotspot along the hilly systems of Sierra de las Ánimas and Sierra de Aceguá *sensu* Grela (2004). Acosta (2002) proposed *A. aculeatus* and *P. thorellii* as representatives of the Pampean area in Argentina. Sharing of these species by Buenos Aires Province and southern Uruguay clearly reflects the biogeographic influence of the Pampean Province in most of the Uruguayan landscape. As already mentioned by Ringuelet (1959) and Acosta (2002), these two species could be benefited from the anthropic activities, expanding their distribution range.

Environmental contribution to the models

The discrimination capacity of the models was always excellent, taking into account the values obtained of the training AUC for the four species studied (all scoring above 0.9). Isothermality is the temperature variable with the highest contribution to the models of the four species. It is a quantification of the oscillation between monthly diurnal and year temperature, which suggests that these species are sensitive to temperature oscillations. Accordingly, the most suitable conditions are represented in a constrained latitudinal range (from -29.41° S to -35.49° S), which comprises Uruguay, southern Brazil, and eastern Argentina. A similar distribution pattern was recently reported for the spider *Latonigena auricomis* Simon, 1893 (Gnaphosidae), for which isothermality was the variable with highest contribution (Jorge et al. 2013). Future studies could be focused on testing if other arachnid species distributions in this latitudinal range could reflect the influence of this climatic variable.

It is worth noting that *P. thorellii* was the only species studied where a precipitation variable (precipitation in the driest month, bc14) had the highest contribution to the model, with a value almost equaling isothermality.

Overall biogeographic pattern

Sites with a 'biogeographic crossroads' character are considered of high species richness and beta diversity, where evolutionary processes such as speciation and coevolution may be preserved, so they appear to be areas of high conservation priority (Spector 2002). Our results agree with the dendrofloristic distribution proposed by Grela (2004) for Uruguay in the sense that the opiliofauna of Uruguay should be considered as a mosaic showing influence of neighboring biogeographic regions. Geographic similarities between southern Uruguay and Buenos Aires Province, based on geological and zoological studies, indicate the influence of the Pampean Province. Although expectations about the distribution of the opiliofauna in Uruguay were in correlation to the apparent uniformity of the Uruguayan landscape mentioned in previous studies (Capocasale 1968), we consider that at least two roughly different opilological areas for Uruguay could be proposed, based on climatic variables and reflecting respectively the Pampean and the Mesopotamian/Paranaense influences. The noteworthy prediction of *Discocyrtus testudineus* (Holmberg 1876) on a narrow fringe along the Uruguayan side of lower Uruguay River (Acosta 2014), even when this species has hitherto no record in the country, may strengthen the mentioned affinity of the west of the country with the Mesopotamian pattern type. Further studies should focus on including other species of Uruguayan harvestmen, additional environmental variables such as vegetation, and new records, especially at the center of the country where a transitional area between the regions is presumed.

Conclusions

This study recognized at least two different opilological areas for Uruguay based on climatic variables: a Pampean region that comprises most of the Uruguayan territory and a Mesopotamian/Paranaense region observed in the west and north of the country.

Competing interests

The authors declare that they have no competing interests.

Authors' contributions

The paper was originally conceived by MS and LEA. MS, LEA, and JCG analyzed the data. JCG made the figures and tables with MS. LG and IC identified and elaborated a database of the specimens of the Uruguayan arachnological collection. MS, JCG, and LEA finalized the manuscript. All authors read and approved the final manuscript.

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