Article

Geographical distribution of *Discocyrtus prospicuus* (Arachnida: Opiliones: Gonyleptidae): Is there a pattern?

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Abstract

The environmental constraints determining the distribution of the harvestman *Discocyrtus prospicuus* in Argentina and Uruguay are addressed. Habitat observations across the entire range (Río de la Plata-Atlantic coast area; Córdoba sierras; northwestern Argentina) are provided. Previous published localities (verified for accuracy), new records and bioclimatic predictors were used to characterize the species bioclimatic profile and to build predictive distributional models with BIO-CLIM and MAXENT algorithms. Relative importance of each bioclimatic variable in the final models is assessed. It was determined that *D. prospicuus* is primarily a gallery forest dweller, with preferred climate temperate to temperate-cold; variables related to thermic uniformity rank among the most influential. Results consistently support the alleged yungas-Mesopotamian disjunction; but the link between the Río de la Plata and Córdoba sierras areas shows disagreement between methods (predicted continuous with BIOCLIM, separate with MAXENT). It is suggested that the need for constant air humidity (favored in the core area by its proximity to large rivers and the seacoast) and competitive exclusion with congener *D. testudineus* may represent additional limiting factors. Some observations on the species tolerance to human activity are also given.

Key words: Neotropical Region, disjunction, habitat, ecological niche modeling, bioclimatic variables, MAXENT, BIO-CLIM

Introduction

Much too often, knowledge on geographical distribution arises as a mere collection of point records (Peterson 2006), normally as systematic revisions and cataloging accumulate. In spite of being an important aspect of the study of biodiversity, distributional knowledge resulting from such an incidental approach cannot be regarded as other than provisory. Although this is the case for Neotropical harvestmen, most species having low number of records available (Kury 2003), this taxon has been since long appreciated for demonstrating zoogeographical patterns, frequently matching vegetation-based ecoregions (Ringuelet 1959; Acosta 2002; Pinto-da-Rocha *et al.* 2005). One remarkable feature of harvestmen distribution is the striking degree of endemicity shown by many species in some areas (Pinto-da-Rocha *et al.* 2005), which might reveal their close dependence on environmental conditions, as generally assumed, and the historical factors involved (Giribet & Kury 2007). However, as noted elsewhere, not all harvestmen are narrowly distributed endemics, as some species spread over thousands of square kilometers, provided the suitable environment is large enough (Acosta 2008).

Large distributions are typical for harvestmen assigned to the "Mesopotamian area" in Argentina (Acosta 2002). In this country, the Mesopotamia is strictly the geographical region between two large rivers, Paraná and Uruguay. As an opiliofaunistic concept, the region extends further westwards: some 150–200 kilometers into the Chaco ecoregion in the North, and up to the central Sierras in the South (Acosta 2002). Three species of *Discocyrtus* Holmberg, 1878 (Gonyleptidae) have been considered to be emblematic examples of this region (Acosta 1995, 2002): *D. dilatatus* Sørensen, 1884, *D. testudineus* (Holmberg, 1876) and *D. prospicuus* (Holmberg, 1876). While the two former species have quite similar ranges, fairly covering the Mesopotamian area (Ringuelet 1959; Acosta

1995), the distribution pattern of the latter is indeed more difficult to define. According to published evidence (Ringuelet 1959; Capocasale 1968; Acosta 1995, 2002), records of *D. prospicuus* concentrate in at least four sectors (Fig. 1): (1) a presumable "core area" surrounding the Río de la Plata estuary (RLP from now on), the lower delta of Paraná River and the lowest part of Uruguay River, both on the Argentinean and the Uruguayan sides; (2) a "secondary" separate area in northwestern Argentina (provinces of Tucumán, Salta and Jujuy), corresponding to the yungas (montane rainforests) ecoregion; (3) further records in the central Argentinean province of Córdoba, both in the sierras and in the plains, which have been thought to be continuous with the core area (Acosta 2002); and (4) records from the subtropical province of Misiones, northeastern Argentina, with no evidence of continuity with the RLP core area. In other words, contrary to the other Mesopotamian *Discocyrtus* species, localities of *D. prospicuus* suggest a patchy, and to some extent marginal, range. In fact, most records from the core area appear to be primarily related to gallery forests. As an additional point of interest, together with *D. dilatatus* and *Geraeocormobius sylvarum* Holmberg, 1887, *D. prospicuus* is one of three Mesopotamian gonyleptids with a disjunct pattern, its range including the Mesopotamia and the yungas (Acosta 1995, 2002, 2008; Acosta *et al*. 2007). This fact was ascribed to a more general hypothetical framework—presumable Pleistocene range expansions and retractions (Acosta 2002, following Nores 1992)—, which in the first place needs accurate knowledge of the actual distribution patterns of the species involved. A defined range pattern, at least one clearly associated to one or more biogeographical areas, is difficult to discover for *D. prospicuus* (Fig. 1).

In order to understand the distribution constraints of this species, a two-sided approach was conducted in this paper. On one hand, intensive sampling effort and examination of existing collections were applied to improve the documentary basis. This task was combined with a critical revision of published records, to check one by one their taxonomic accuracy. The set of all confirmed records was used to perform the second and main part of the work: to examine the species' bioclimatic profile and to model its potential distribution, using two widely accepted methods, BIOCLIM and MAXENT.

Ecological niche modeling represents a valid strategy to understand the distribution constraints of a species, when previous knowledge is limited (Peterson 2006; Pearce & Boyce 2006; Gibson *et al.* 2007; Pearson 2007; Pearson *et al.* 2007; Acosta 2008). The elementary data used by all modeling methods are the occurrence records, which are analyzed in combination with different types of environmental predictors (in this paper, climatic), in the form of digital coverages. This two-way input yields a predictive map displaying potential or suitable areas where the presence of a species is expected, even if unrecorded (Guisan & Zimmermann 2000; Hernández *et al.* 2006). Most methods work in association with a Geographic Information System (GIS), and many are based on the concept of bioclimatic envelope: the initial aim is to find the bioclimatic profile of a species, *i.e.*, the set of climatic conditions that bounds together all existing records, which are deemed to reflect primary requirements that ensure the populations' maintenance (Pearson 2007). The bioclimatic profile is then a partial representation of the niche of the species, providing an analytical approach to tackle one particular set of (but not all) factors determining distribution (Araújo & Guisan 2006). The methods used in this paper, BIOCLIM and MAXENT, agree in that they are presence-only algorithms, *i.e.*, they do not require verified absence records (Pearce & Boyce 2006); presumable negative records, however, were available to us for some areas, and were used for post-modeling considerations. Both methods are of proven performance, though MAXENT is computationally more complex and in general outperforms all other available algorithms (Hernández *et al.* 2006; Sangermano & Eastman 2007).

The main objectives of this paper are to model the potential distribution of *D. prospicuus* and to characterize its bioclimatic profile, for obtaining general insights into the climatic tolerance limits of this species. We thereby aim to test if bioclimatic models are able to depict the seemingly unpredictable species range, and if the presumed disjunct pattern, Mesopotamia-yungas, is supported by the models. Modeling results were contrasted with direct habitat observations gathered during field work, to obtain a preliminary picture of the environmental factors that determine the distribution of *D. prospicuus*.

Methods

Data acquisition. All records for *D. prospicuus* available in the literature were considered and analyzed (Holmberg 1876; Ringuelet 1959; Capocasale 1966, 1968, Acosta 1995, 1999, 2002). Localities that remained unrecognizable or imprecise were set aside. Taxonomic criteria for species recognition relied on Ringuelet (1959), Capocasale (1966) and Acosta (1999). Historical records were checked for taxonomic reliability by direct inspec-

tion of most voucher specimens; some localities were validated through newly collected material. Records were completed with the new localities obtained in this survey, together with unpublished records from Uruguay, facilitated by M. Simó, L. Giuliani and I. Castellano. Fieldwork mainly targeted areas with no records but where the species was deemed to be potentially present, following both Acosta (2002) and preliminary runs of the models. Despite many collecting failures in some regions with expected presence, new material collected almost doubled the hitherto known records. Harvestmen were searched and hand collected (Acosta *et al.* 2007) under bark or fallen objects, like tree trunks and piles of abandoned bricks. Capture effort was not quantified, but sites where other species (not *D. prospicuus*) were collected during the intensive surveys were deemed to represent "presumable negatives" for *D. prospicuus*. The full dataset consisted of 80 unique point localities (Fig. 1 and Table 1). Localities were identified and geo-referenced using printed road maps and digital gazetteers (NGA GEOnet Names Server [GNS], United States Board on Geographic Names; Google Earth ©), in all cases crosschecked to ensure coordinates' accuracy. Information provided in the labels (or personal consultation with collectors, when available) was used to define locations as precisely as possible. As localities might represent just the nearest reference to the actual collecting point, an undetermined degree of imprecision is to be expected in some cases. As explained in Acosta (2008), this fact is considered not to represent a severe problem in the wide-scale context employed here.
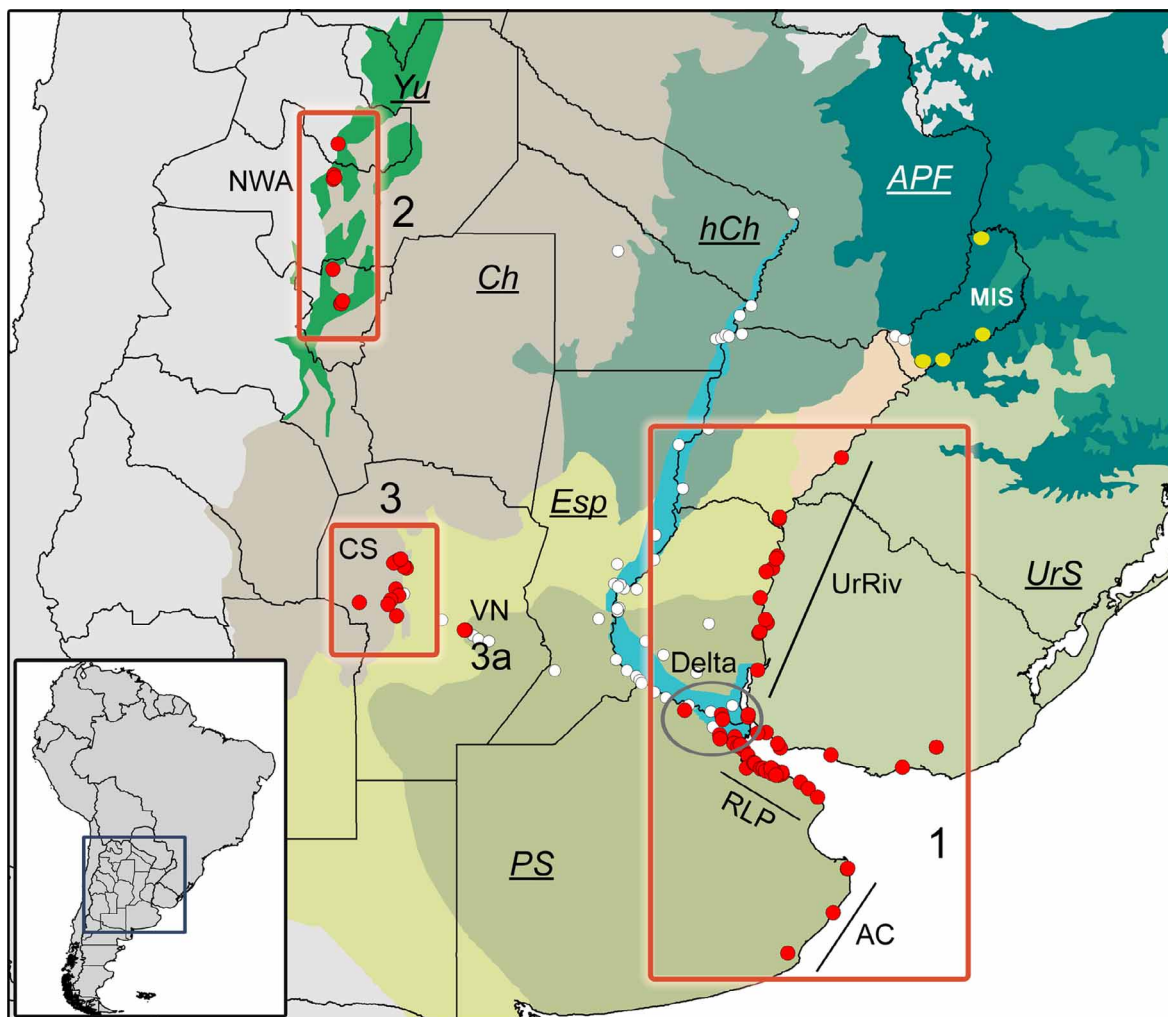

FIGURE 1. Locality records of *Discocyrtus prospicuus* (red dots), displayed over selected ecoregions in central-northern Argentina and Uruguay. Rectangles indicate the main portions of the species range: 1. Core area, including: lower Uruguay River banks (UrRiv), lower Paraná delta (ellipse), RLP (Rio de la Plata banks), Atlantic coast (AC); 2. Northwestern Argentina (NWA), comprising provinces of Jujuy, Salta and Tucumán; 3. Central sierras (CS) in province of Córdoba; 3a. Isolated population at Villa Nueva (VN). White small dots: records of *Discocyrtus testudineus*. Yellow dots in province of Misiones (MIS): records formerly assigned to *D. prospicuus*, now excluded (hereby referred to as *Discocyrtus bucki*). Ecoregions (acronyms underlined) delineated by Olson *et al.* (2001): yungas (*Yu*); dry (sub-xeric) Chaco (*Ch*); humid Chaco (*hCh*); espinal scrubland (*Esp*); humid Pampean steppe (*PS*); Uruguayan savanna (*UrS*); alto Paraná atlantic forests (Paranense forests) (*APF*); light blue: Paraná flooded savanna. Inset: location of depicted area in South America.

TABLE 1. Record set used to build the distribution models of *Discocyrtus prospicuus*, with locality name, geographical coordinates and source of each record. Latitude and longitude are given in degrees. Coordinates of localities denoted with ** are approximate. Extreme geographical points of the range are underlined; localities representing lowest or highest values for bioclimatic (bc) variables are indicated too (variable numbers as in Table 2). New records are indicated as NR, along with collection data.

Province or Departamento	Locality	Longitude (W)	Latitude (S)	bc variables, lowest	bc variables, highest	Source
ARGENTINA						
Corrientes	Yapeyú	-56.8202	-29.4790	—	1, 5, 6, 10, 11, 12	**NR:** 2 ♂, 1 ♀, 1 juv. (CDA-F), 21-v-2010 (J. Vergara, L. Paoloni)
Entre Ríos	Concordia	-57.9949	-31.3733	—	—	Ringuelet 1959
Entre Ríos	Salto Grande	-57.9351	-31.2045	—	—	Ringuelet 1959
Entre Ríos	Yuquerí chico [instead of "Yuquezí " chico]	-58.1077	-31.4251	—	—	Ringuelet 1959
Entre Ríos	El Palmar National Park	-58.2103	-31.8729	—	—	**NR:** 2 ♂, 2 ♀, 1 juv. (MACN), 14–x–1984 (M. Ramírez)
Entre Ríos	Colón, 1-2 km S	-58.1175	-32.2474	—	—	**NR:** 7 ♂, 9 ♀ (CDA-F), 24–xi–2006 (L.E. Acosta, M. García)
Entre Ríos	Banco Pelay, 5 km N Concepción del Uruguay (site 1)	-58.2108	-32.4603	—	8	**NR:** 7 ♀, 1 juv. (LEA 000.367), 25–iii–2006 (L.E. Acosta, M. Garcia)
Entre Ríos	Banco Pelay, 5 km N Concepción del Uruguay (site 2)	-58.2117	-32.4520	—	—	**NR:** 4 ♂, 1 ♀ (CDA-F), 22-xii-2008 (G.D. Rubio)
Entre Ríos	Concepción del Uruguay	-58.2333	-32.4833	—	—	Ringuelet 1959
Entre Ríos	Brazo Largo in the delta	-58.8703	-33.8648	—	—	Ringuelet 1959
Buenos Aires	Baradero	-59.5000	-33.8000	—	—	Ringuelet 1959
Buenos Aires	Otamendi	-58.8985	-34.2193	—	—	**NR:** 11 ♂, 11 ♀ (MACN), 10–x–1982 (A. Roig)
Buenos Aires	Island in Canal Arias **	-58.6667	-34.3167	—	—	Ringuelet 1959
Buenos Aires	Paraná de las Palmas (Canal de la Serna) **	-58.6417	-34.2500	—	—	Ringuelet 1959
Buenos Aires	Arroyo Guayracá, Delta **	-58.6583	-34.3648	—	—	**NR:** 1 ♂, 1 ♀ (MACN), 24–ix–1983 (E. Maury)
Buenos Aires	Paraná Guazú **	-58.8500	-33.9500	—	—	Ringuelet 1959
Buenos Aires	San Antonio River, Delta **	-58.5431	-34.3827	—	—	Ringuelet 1959
Buenos Aires	Río Luján	-58.8909	-34.2792	—	—	Ringuelet 1959
Buenos Aires	Tigre (Las Conchas)	-58.5905	-34.4158	—	—	Holmberg 1876; Ringuelet 1959
Buenos Aires	San Isidro	-58.5005	-34.4625	—	—	**NR:** 3 ♂, 1 ♀ (CDA-F), 15–xi–2007 (E. Flórez)
Buenos Aires	San Isidro Ecological Reserve	-58.4937	-34.4695	—	—	**NR:** 2 ♂ (CDA-F), 15–xi–2007 (E. Flórez)
Buenos Aires	Martin Garcia island	-58.2500	-34.1833	—	—	Ringuelet 1959
Buenos Aires	Buenos Aires, near Palermo**	-58.4166	-34.5667	—	—	Holmberg 1876
Buenos Aires	Santa Catalina Reserve, near Llavallol	-58.4443	-34.7862	—	—	**NR:** 2 ♂, 4 ♀ (CDA-F), 8-iv-2009 (E. Guerrero)

TABLE 1. (continued)

Province or Departamento	Locality	Longitude (W)	Latitude (S)	bc variables, lowest	bc variables, highest	Source
Buenos Aires	Wilde, between Hospital and Los Eucaliptos quarter	-58.3145	-34.6953	—	—	**NR:** 3 ♂, 4 ♀ (CDA-F), 19–x–2007 (E. Guerrero)
Buenos Aires	Ranelagh	-58.1977	-34.7933	—	—	**NR:** 1 ♂ (MLP), 26–viii–1962 (O. de Ferraris)
Buenos Aires	Hudson	-58.1538	-34.7915	—	—	**NR:** 1 ♂ (MACN), 2–ix–1984 (M. Ramírez)
Buenos Aires	Pereira Iraola Park (Berazategui)	-58.1120	-34.8287	—	—	**NR:** 5 ♀, 1 juv. (CDA-F), 20–ix–2007 (E. Guerrero)
Buenos Aires	Punta Lara	-57.9934	-34.8044	—	—	Ringuelet 1959
Buenos Aires	Boca Cerrada (near Punta Lara)	-58.0201	-34.7852	—	—	**NR:** 2 ♂, 4 ♀ (CDA-F), 9–i–2009 (E. Guerrero)
Buenos Aires	Gonnet, under stone in *Eucalyptus* forest	-58.0120	-34.8803	—	—	**NR:** 1 ♂, 1 ♀, 1 juv. (IFSCA), 2–x–2010 (E. L. Guerrero)
Buenos Aires	La Plata	-57.9382	-34.9070	—	—	Roewer 1938; Acosta 1999
Buenos Aires	Berisso: road La Plata - Los Talas	-57.8983	-34.9028	—	—	**NR:** 4 ♂, 4 ♀ (CDA-F), 19–ix–2007 (E. Guerrero)
Buenos Aires	Río Santiago	-57.9142	-34.8440	—	—	Ringuelet 1959
Buenos Aires	Los Talas (Berisso)	-57.8333	-34.8833	—	—	Ringuelet 1959
Buenos Aires	[Balneario] Palo Blanco (near Berisso)	-57.8391	-34.8557	—	—	Ringuelet 1959
Buenos Aires	Atalaya	-57.5183	-35.0266	—	—	**NR:** 3 ♂, 3 ♀ (CDA-F), 14–i–2009 (E. Guerrero)
Buenos Aires	Estancia El Destino, Magdalena, Southern Coastal Park	-57.3878	-35.1325	—	—	**NR:** 3 ♂, 3 ♀ (CDA-F), 9–v–2009 (E. Guerrero)
Buenos Aires	Punta Indio	-57.2269	-35.2765	13	—	**NR:** 1 ♂, 7 ♀ (CDA-F), 15–vii–2009 (E. Guerrero)
Buenos Aires	Costa Chica, in planted willow forest W of Ruta 11	-56.7172	-36.5070	3, 18	9	**NR:** 1 ♂ (IFSCA), 16–i–2010 (E. Guerrero)
Buenos Aires	Las Toninas, 200 m S main entrance (Ruta 11), under trunk near a drain	-56.7121	-36.4934	2	—	**NR:** 1 ♂, 1 ♀, 1 juv. (IFSCA), 17–i–2010 (E. Guerrero)
Buenos Aires	Villa Gesell	-56.9630	-37.2523	16	—	**NR:** 1 ♂, 2 ♀ (LEA 000.325), 14/16–iv–1995 (J.L Farina, C.E. Vorano)
Buenos Aires	Laguna de los Padres	-57.7357	-37.9420	1, 5, 9, 10, 11	—	**NR:** 1 ♂, 1 ♀ (LEA 000.324), 28–x–1988 (J.L. Farina)
Córdoba	Villa Nueva (riverside)	-63.2427	-32.4223	—	—	**NR:** 3 ♂, 6 ♀ (LEA 000.399), 15–xi–1987 (L. Acosta, F. Pereyra)
Córdoba	Villa Nueva, gallery forest near dam	-63.2620	-32.4225	—	—	**NR:** 4 ♂, 4 ♀ (CDA-F),14–ii–2008 (L.E. Acosta, M. García, G. Rubio)

TABLE 1. (continued)

Province or Departamento	Locality	Longitude (W)	Latitude (S)	bc variables, lowest	bc variables, highest	Source
Córdoba	Cabana	-64.3500	-31.2083	—	—	**NR:** 3 ♂ (LEA 000.369), 26–iii–1998 (G. Repossi)
Córdoba	"La Quebrada", road to Mt. Pan de Azúcar	-64.3940	-31.2260	—	—	**NR:** 10 ♂, 11 ♀, 4 juv. (LEA 000.400), 15–iv–1990 (L. Acosta, A. Peretti)
Córdoba	Santa María de Punilla (under woodpile in a house yard)	-64.4703	-31.2808	—	—	**NR:** 8 ♂ (CDA-F), 12–vii–2008 (G. Rubio)
Córdoba	Saldán	-64.3077	-31.3233	—	—	**NR:** 2 ♂ (LEA 000.368), 21–iii–1997 (M.G. Gazzera)
Córdoba	Villa Rivera Indarte	-64.2994	-31.3289	—	—	**NR:** 1 ♂ (LEA 000.401), 4–iii–1994 (M. Burroni)
Córdoba	Villa Warcalde	-64.2985	-31.3358	—	—	**NR:** 2 ♂, 1 ♀ (CDA-F), 12–xi–2006 (L.E. Acosta, M. García)
Córdoba	Argüello (city of Córdoba)	-64.2651	-31.3510	—	—	**NR:** 2 ♂, 1 ♀ (CDA 000.268), i–iv–2001 (C. Mattoni)
Córdoba	Villa Belgrano (city of Córdoba)	-64.2548	-31.3664	—	—	**NR:** 1 ♂ (LEA 000.402), 13–iii–1994 (L. Burroni)
Córdoba	La Bolsa, new bridge to Villa Los Aromos	-64.4305	-31.7245	—	—	**NR:** 3 ♂, 6 ♀ (CDA-F), 31–i–2008 (L.E. Acosta, M. García)
Córdoba	Los Molinos, near bridge	-64.3812	-31.8362	—	—	**NR:** 1 ♂, 4 ♀ (CDA-F), 18–xii–2008 (L.E. Acosta, M. García, G. Rubio, J. Vergara)
Córdoba	Villa Ciudad Parque	-64.5238	-31.9140	—	—	**NR:** 5♂, 5 ♀ (CDA-F), 31–i–2008 (L.E. Acosta, M. García)
Córdoba	Villa General Belgrano	-64.5648	-31.9867	—	—	**NR:** 4 ♂, 5 ♀ (CDA-F), 31–i–2008 (L. Acosta, M. García)
Córdoba	Embalse de Río Tercero	-64.4172	-32.1807	—	—	Ringuelet 1959
Córdoba	Villa de las Rosas	-65.0580	-31.9532	—	4, 7	Acosta 2002
Tucumán	2 km down Villa Nougués (1300 m)	-65.3680	-26.8559	—	13, 16, 18	Acosta 2002
Tucumán	0.8 km down Villa Nougués	-65.3736	-26.8563	—	—	**NR:** 2 ♂, 2 ♀, 1 juv. (CDA-F), 10-i-2010 (L. Acosta)
Tucumán	Road to San Javier, between "comisaría" and "primera confitería"	-65.3390	-26.8055	—	—	**NR:** 3 ♂, 2 ♀ (LEA 000.334), 24–viii–2003 (L.E. Acosta)
Tucumán	4 km from San Pedro de Colalao to Hualinchay (1200 m)	<u>-65.5050</u>	-26.2632	12, 14, 17, 19	—	Acosta 2002

TABLE 1. (continued)

Province or Departamento	Locality	Longitude (W)	Latitude (S)	bc variables, lowest	bc variables, highest	Source
Salta	San Lorenzo (1470 m)	-65.5027	-24.7235	6, 14, 17, 19	2, 15	Acosta 2002
Salta	8 km road to Yacones (*Podocarpus* forest, 1600-1650 m)	-65.4883	-24.6450	6, 14	3	Acosta 2002
Salta	2 km road to Yacones (urbanized, 1420 m)	-65.4741	-24.6958	14, 17, 19	—	Acosta 2002
Jujuy	Yala	-65.4167	-24.1208	4	—	Acosta 2002
URUGUAY						
Artigas	Isla Rica	-57.8840	-30.5311	—	—	Capocasale 1968
Artigas	Isla Zapallo	-57.8737	-30.4989	—	—	Simó, Giuliani and Castellano, unpubl.
Salto	Isla Redonda	-57.9154	-31.1673	—	—	Simó, Giuliani and Castellano, unpubl.
Paysandú	Paysandú	-58.0889	-32.3005	—	—	Simó, Giuliani and Castellano, unpubl.
Río Negro	Fray Bentos, near Botnia	-58.2500	-33.1133	—	—	**NR:** 5 ♂, 1 ♀ (CDA-F), 20–xii–2007 (A. Laborda)
Colonia	Punta Arroyo Limetas	-58.1053	-34.1728	—	—	Capocasale 1968
Colonia	Punta Gorda (near Nueva Palmira)	-58.4175	-33.9117	—	—	Capocasale 1968
Colonia	Nueva Palmira	-58.4136	-33.8662	—	—	Simó, Giuliani and Castellano, unpubl.
Colonia	Colonia	-57.8656	-34.4371	2, 7	—	Simó, Giuliani and Castellano, unpubl.
Colonia	Barrancas de San Pedro	-57.9077	-34.3614	—	—	Simó, Giuliani and Castellano, unpubl.
San José	Arazatí	-56.9992	-34.5577	—	—	Capocasale 1968
Canelones	Villa Argentina, El Águila (1 km W of Atlántida)	-55.7793	-34.7708	15	—	**NR:** 2 ♂, 2 ♀ (CDA-F), 24–x–2006 (L. Acosta, M. Simó)
Lavalleja	Parque Sierra Minas (hotel)	-55.1973	-34.4260	8	14, 17, 19	**NR:** 1 ♂, 5 ♀ (LEA 000.387), xii–2005 (L. Acosta)

Acronyms for repositories. 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 marked as –F); IFSCA (Instituto Fitotécnico de Santa Catalina, Universidad Nacional de La Plata, Llavallol, province of Buenos Aires); LEA (Luis E. Acosta's collection, Córdoba); MACN (Museo Argentino de Ciencias Naturales, Buenos Aires); MLP (Museo de La Plata).

Climate layers. All general GIS operations were made in the software DIVA-GIS, version 5.4 (Hijmans *et al.* 2005b). Models were run using climatic information contained in WorldClim 1.4. (Hijmans *et al.* 2005a), a set of present climate layers averaging the 1950–2000 period. The finest resolution available was used (30 arc second, *i.e.*, about 1 km^2 gridcell). For BIOCLIM models and profile description, all 19 bioclimatic variables contained in WorldClim were considered; they are listed in Table 2, along with the abbreviations that identify each variable ("bc" followed by a number, from 1 to 19). To avoid overparameterizing models in MAXENT we discarded highly correlated variables (Pearson>0.75), conducting pairwise analyses separately for temperature and precipitation variables (Rissler & Apodaca 2007; Kozak *et al.* 2008); correlation was calculated on bc values of 770 points over the entire study region, covering central and northern Argentina, Paraguay, Uruguay and southern Brazil. Given

lack of sound biological information, selection of a variable in a highly correlated pair was based on its relative contribution in preliminary models, run with all variables, to be sure that no relevant predictor was set aside. Eleven uncorrelated bc variables were used in MAXENT, as indicated in Table 2. WorldClim climatic and elevation data were incorporated in DIVA-GIS as .cli files, which are used by the software to derive all 19 bc variables employed to run BIOCLIM. For direct use in MAXENT, raster layers were extracted in DIVA-GIS grid format (.gri and .grd files) using the Climate > Map command.

TABLE 2. Bioclimatic profile of *D. prospicuus* (n=80) showing all 19 bioclimatic variables in the species envelope, as obtained in BIOCLIM: basic statistics and features of the cumulative frequency curves (cum. f.). Curves are characterized as normal (N), sigmoid (S), skewed towards the lower (sk –) or upper end (sk +) and bimodal (B); the number of extreme low (left) and high (right) outliers in the curves are provided. Temperature in Celsius degrees (ºC), precipitation in mm. Abbreviations that precede each bioclimatic variable (bc x) are employed throughout the text and in Table 2. The 11 variables employed in the MAXENT models are asterisked.

Bioclimatic variables	Median	Min–Max	range	SD	cum. f.	outliers
(bc 1) Annual mean temperature	16.74	13.40–20.20	6.80	1.135	N	1–1
(bc 2) *Mean monthly T° range	11.63	8.13–14.79	6.66	1.867	S	0
(bc 3) *Isothermality (2/7 x 100)	46.33	38.67–56.79	18.12	4.195	N	0–4
(bc 4) *T° seasonality (STD x 100)	473.85	380.77–515.50	134.73	26.452	sk +	6–0
(bc 5) *Max T° of warmest month	29.65	26.40–32.90	6.50	1.719	S	0–13
(bc 6) Min T° of coldest month	5.90	0.90–8.90	8.00	1.807	sk +	0
(bc 7) T° annual range (5–6)	24.60	20.20–28.30	8.10	2.059	S	0
(bc 8) *Mean T° wettest quarter	22.12	14.20–24.32	10.12	2.010	sk +	6–0
(bc 9) *Mean T° driest quarter	11.11	8.12–21.17	13.05	2.468	sk –	0 –5
(bc 10) Mean T° warmest quarter	22.65	18.82–25.85	7.03	1.326	N	1–0
(bc 11) *Mean T° coldest quarter	11.03	8.12–14.88	6.77	1.131	N	1–3
(bc 12) Annual precipitation	964	457–1325	868	196.433	N	1–0
(bc 13) Precipitation wettest month	113	93–233	140	24.036	sk –	0–1
(bc 14) Precipitation driest month	52.50	3–83	80	22.925	B	23–0
(bc 15) *Precipitation seasonality (CV)	23.15	7.54–110.88	103.34	27.328	B	0–23
(bc 16) *Precipitation wettest quarter	306	238–595	357	57.580	sk –	0–1
(bc 17) Precipitation driest quarter	174	11–277	266	75.920	B	23–1
(bc 18) *Precipitation warmest quarter	281.50	200–595	395	57.950	sk –	0–4
(bc 19) *Precipitation coldest quarter	174.50	11–316	305	79.386	B	23–1

Modeling. Distribution models were built with two methods: BIOCLIM (inbuilt in DIVA-GIS) and MAXENT. Results obtained with BIOCLIM were considered exploratory, and, aside the obtention of a suitability map, let us perform some initial operations, like extracting bioclimatic values and inspecting cumulative frequencies. BIOCLIM is a frequency-based algorithm, which defines an orthogonal multi-dimensional hyper-space (envelope) that bounds values of all bioclimatic variables for the species (*i.e.*, its bioclimatic profile). This way, the climatic tolerance limits of the species are determined; projecting these results onto a map, grid cells with values matching the envelope are scored as "suitable", often displaying their "suitability degree" as a percentile ranking. More details on BIOCLIM can be found in Finch *et al.* (2006) and Acosta (2008). MAXENT was performed using version 3.3.1. of the software (Phillips *et al.* 2009). This algorithm, described by Phillips *et al.* (2006) and Phillips and Dudik (2008), is a general method for making inferences from incomplete information and involves elaborated computational analyses. It follows the principle that an estimated distribution must agree with all available information, and is thus aimed to find the probability distribution closest to uniform (of maximum entropy) subject to constraints imposed by presences and environmental data across the study area (Pearson *et al.* 2007). MAXENT also produces predictive maps by classing grid cells' suitability, but in this case continuous probabilities from 0 to 1 are expressed. Suitable and not suitable cells need to be differentiated by the adoption of a threshold rule: following

Liu *et al*. (2005), and to minimize the tendence of overprediction yielded by this method, in this study "equal training sensitivity plus specificity" threshold was applied. Different settings were experimented to calibrate the best results. Most settings were maintained in their default (recommended) values, except for maximal number of background points (set to 20000), and maximum iterations (to 3500). Logistic output was chosen. Features selection was made automatically by the software ("auto" option), following default rules dependent on the number of records (product, hinge, threshold, quadratic and linear feature types were used). Additional runs were performed varying the regularization multiplier from 1 (default) to 0.5. Variables do not contribute equally to the final output, so that a jackknife analysis (available in the software) was used to estimate the relative importance of each one. ASCII files of resulting predictive maps were imported into DIVA-GIS grid format for visualization and grid operations. Cumulative frequency plots were graphed using Systat 7.0 ©.

Evaluation, input variants, importance of variables. Evaluation was made through the AUC assessment, incorporated in MAXENT as a part of the analysis; AUC values over 0.8 are considered a "good" model performance; above 0.9 the accuracy is considered "high" (Luoto *et al*. 2005). To assess how dependent to the actual dataset the model is, 10 replicate runs were made using the subsample option and setting the random test percentage in 25 (random seed selected) (Phillips *et al*. 2009). This yielded 10 output maps, each produced with 60 training points (randomly selected for each replicate), using the remaining 20 as test points, to calculate AUC for each run. Moreover, models were built using BIOCLIM and MAXENT with localities of specified areas eliminated from the dataset (yungas excluded: 73 points left, or yungas + central sierras excluded, 59 points left), to test the models' ability to predict those areas. To determine the relevance of each variable in the final model we made use of different measures, available in MAXENT (Table 3). The percent contribution is a heuristic estimate obtained by adding or subtracting (in each iteration of the training algorithm) the increase or decrease in regularized gain to the contribution of the corresponding variable (Phillips *et al*. 2009). Another way to assess the relative importance is the jackknife test, in which models are built either setting aside one variable at a time, or using a variable in isolation (Table 3 and Fig. 8). As stated above, percent contribution and jackknife results of preliminary runs with all variables was also used as criteria to retain relevant variables when discarding correlated variables.

TABLE 3. Relative importance of bc variables in the distribution model of *D. prospicuus,* according to different measures yielded by MAXENT: percent contribution of each variable to the whole model; jackknife training gain with each variable set aside at a time, and jackknife training gain with each variable run in isolation. Variables are ordered following the first column (% contribution); highest scores in the second and third columns are highlighted in bold.

	Variable % contribution	Training gain without	Training gain with only
bc3 – isothermality	25.5632	2.9864	**1.4687**
bc4 – temp seasonality	19.4775	**2.8772**	**1.3338**
bc11 – mean T° coldest quarter	18.7901	**2.9373**	**1.4569**
bc16 – precip wettest quarter	9.8638	2.9711	0.9732
bc19 – precip coldest quarter	9.1634	**2.9254**	0.9674
bc18 – precip warmest quarter	7.7258	2.9756	0.9762
bc8 – mean T° wettest quarter	5.2301	2.9479	0.9117
bc15 – precip seasonality	2.9581	**2.8994**	0.7355
bc9 – mean T° driest quarter	0.7440	2.9830	**1.2043**
bc5 – max T° warmest month	0.2520	2.9795	0.6144
bc2 – mean monthly T° range	0.2320	2.9825	0.5219

Results

Localities included and excluded. The complete verified records set, with geographical coordinates and indicating new records, is listed in Table I. The type locality "Las Conchas" (Holmberg 1876) and the present locality of Tigre (Ringuelet 1959) are the same (Acosta 1999). There are several previous references for "Capital Federal" or Buenos Aires —the same city indeed (Roewer 1929; Ringuelet 1959; Acosta 1999)— but were disregarded

because of being imprecise and impossible to be geo-referenced. The only exception is Holmberg´s (1876) indication to "near Palermo", an old record further confirmed by additional material. "Isla Catalina", in the Paraná delta (Ringuelet 1959) was not located. "Bahía Blanca", type locality of *Discocyrtus spinosus* Roewer, 1916 —currently junior synonym of *D. prospicuus* (Acosta 1999)— was discarded due to being highly unlikely (Ringuelet 1959; Acosta 2002). It should be noted that the reference for "Punta Rasa", type locality of *Discocyrtus exceptionalis* Mello-Leitão, 1933 —another synonym of *D. prospicuus* (Acosta 1999)—, was demonstrated to be a misspelling for the actual label statement, "Punta Lara" (Galiano & Maury 1979). Based on the examination of MACN 4028, 4605, 2410 (studied by Ringuelet 1959) and unpublished materials from province of Misiones, *D. prospicuus* is considered not to occur there; localities cited by Ringuelet (1959) from that province (San Javier, Santa María, Iguazú and Puerto Londero; see Fig. 1) are therefore excluded, and referred to as *Discocyrtus bucki* Mello-Leitão, 1935 (first citation of this species for Argentina); we were unable to check materials MLP 24172 and 24175, which are presumably lost.
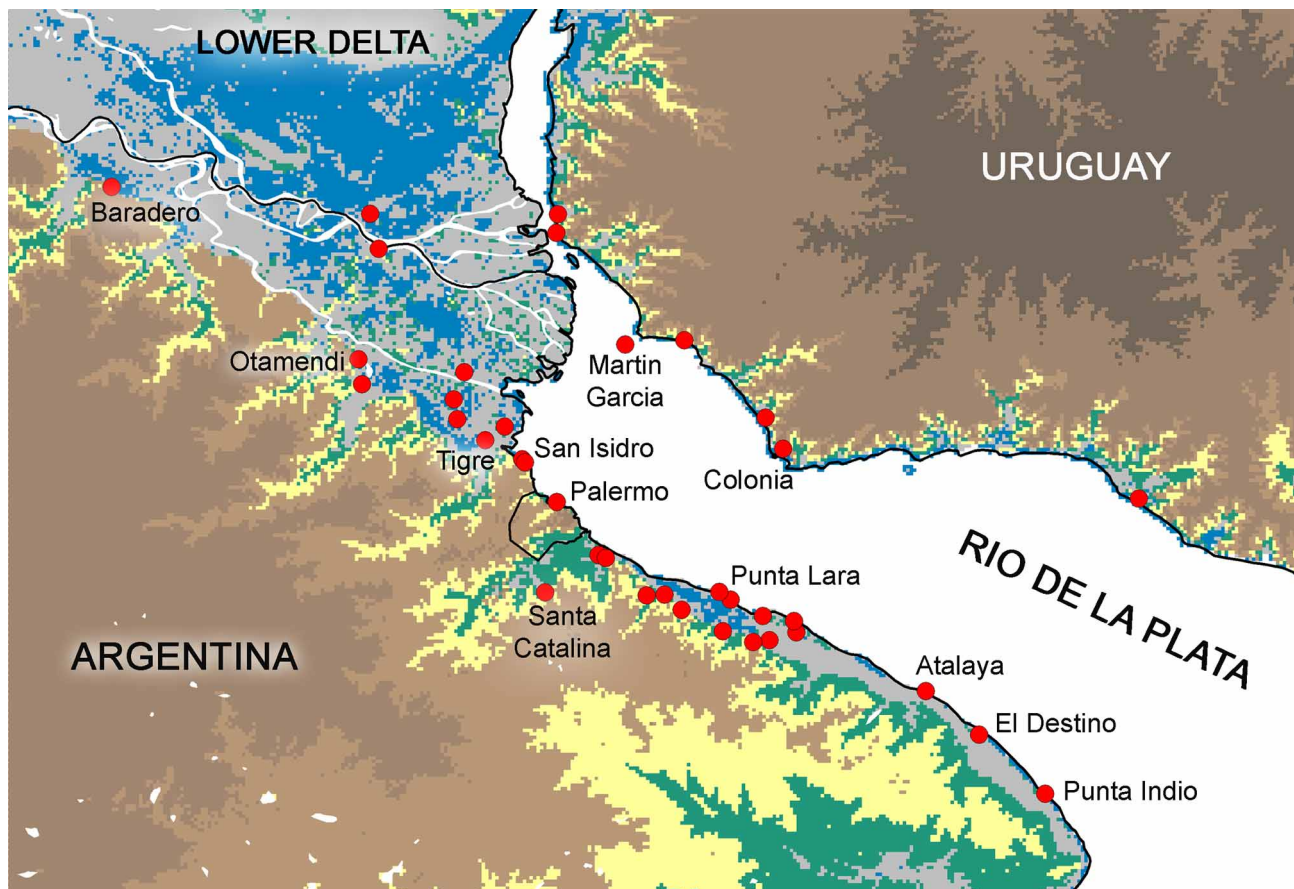
FIGURE 2. Detail of records of *D. prospicuus* on the lower Paraná delta and inner Río de la Plata. Colors indicate elevation above present sea level, as follows: 0–2 m (blue), 2–6 m (grey, together with the former represents surfaces under sea level at the maximal transgression 6,000 yr BP), 6–12 m (green), 12–20 (yellow), 20–30 m, 30–100 m, above 100 m (different brown levels).

Habitat features and areas of occurrence of *Discocyrtus prospicuus*

Río de la Plata-Atlantic coast. In northern province of Buenos Aires, records of *D. prospicuus* align in a narrow, continuous strip 280 km long, from Baradero, on the borders of the Paraná delta, up to Punta Indio, on the southern RLP coast (Figs. 1–2). This portion is influenced by the fluvial dynamics of the RLP and was shaped by Quaternary changes in sea level (Cavalotto 2002). The limit of the maximal marine transgressions (6.5 m a.s.l. at ~6000 yr BP; Cavalotto 2002) is indicated through a cliff or step ("barranca"), which can be 20 m high on the Paraná River, gradually decreasing to scarcely 1 m or lower on the southern RLP (Haene 2006; Vilanova *et al.* 2006). Southwards, the species range follows the Atlantic coast, with records confirmed from Las Toninas up to the vicinity of

Mar del Plata (Figs. 1, 5). Though no intermediate record exists (*i.e.*, from the semicircular inflection of Samborombón Bay), if occurrences were proven to be continuous, the overall strip length would be of 650 km along the borders of Paraná River, RLP and the seacoast. The most striking feature of this part of the range is its narrowness, in almost no case surpassing the width of 10 km from the coast.

Habitats occupied by *D. prospicuus* show significant variations along such an extended range. In the northern sector, barrancas on the Paraná River are typically covered by a vegetation type known as "talar", *i.e.*, forests dominated by the tortuous tree *Celtis ehrenbergiana* (Klotzsch) Liebm. (Celtidaceae) (referred to as *Celtis tala* Gillies ex Planch. in most of the literature) (Parodi 1940; Burkart 1957; Cabrera 1976; Haene 2006; Torres Robles & Tur 2006). "Talares" represent a slender southwards projection of the "espinal" ecoregion, where this tree is elsewhere quite widespread (Cabrera 1976). Above the barranca, Pampean grasslands develop forming the so called upper terrace; below it, the lower terrace consists of low, gently-sloping flooding plains of halophilic steppes and swamps (Violante & Parker 2004; Torres Robles & Tur 2006). An alluvial thickening of the terrain, the "albardón", normally develops on the borders of the lower terrace and frequently sustains patchy gallery forests. Our observations in Otamendi (northern Buenos Aires; see Fig. 2) revealed *D. prospicuus* in the barranca, in which talares are nowadays reduced by human pressure and mixed with dense forests of exotic arboreal species (Chichizola 1993; Guerrero 2011). In this area the species seems not to exist in the albardón gallery forest, replaced there by its congener, *D. testudineus*. According to records further south, *D. prospicuus* is present in marginal forests in the lower delta and beyond (Tigre, San Isidro, Punta Lara). Except for a presumably small overlapping area, presence of *D. prospicuus* in gallery forests seems to start where the range of *D. testudineus* meets its southern end. On the lower delta, subtropical-like gallery forests are well developed and dense, forming the so called marginal "selvas", its southernmost representative being the "selva" at Punta Lara, near La Plata (Cabrera & Dawson 1944; Fig. 2). From this point onwards, the southern RLP coast has vey flattened and irregular relief, with coastal albardones and Quaternary marine beach ridges bearing scattered or aggregated trees up to Punta Indio. Despite from La Plata onwards true barrancas vanish, talares persist as patchy, edaphic formations, irregularly following shelly or sandy longitudinal ridges on the coastal plains (Parodi 1940; Cabrera 1976; Haene 2006; Vilanova *et al.* 2006). On the southern RLP coastal plains *D. prospicuus* can be quite common both in marginal tree patches and in talares, also in sites with human disturbance or invaded by exotic vegetation. Humidity and variety of retreats seem to constrain the presence of this species, which, for example, was not found in talares distant from the coast or too young (*i.e.*, offering few or small fallen trunks), nor in coastal shrubs, swamps or grasslands. In the Atlantic portion, talares grow on littoral dunes and other elevated sites, reaching –37.942°S at Sierra de los Padres, near Mar del Plata (Haene 2006). Though not strictly associated, *D. prospicuus* and talares have an interesting similarity in this strip-like extension of their ranges parallel to the coast, both reaching approximately the same southernmost point. Records on the Atlantic portion come from dense forests of planted trees, like willows or eucalypts. In summary, localities of *D. prospicuus* in the Paraná-RLP stretch arrange around the maximal transgression limit or below, in a N–S sequence as follows: (a) barrancas on the Paraná River; (b) gallery forest in the lower delta up to Buenos Aires; and (c) coastal plains from there up to Punta Indio (Fig. 2). It is remarkable that records in (b) and (c) suggest that the species is associated with (and probably limited to) relatively young areas, formed in the Holocene. In fact, coastal plains started to emerge after 6000 yr BP., their full present extension reached only after 3000–2000 yr BP; the lower delta is even younger (Cavalotto 2002).

Uruguay River and northern RLP banks. Records of *D. prospicuus* follow a linear pattern along a part of Uruguay River from –29.479°S (Yapeyú, province of Corrientes) up to its mouth into the RLP (Fig. 1). These records are very likely continuous with the species range along the Uruguayan side of the RLP (again, a narrow strip). Although complete records filling the gap are lacking, they might also be considered continuous with the RLP part of the range. Habitat observations available in this sector are few; in Colón, Banco Pelay and Fray Bentos (Fig. 5), presence in shady marginal forests seems to be the rule. Except for the first 60 km, gallery forests do not continue on the northern side of RLP (Hueck & Seibert 1972; Nores *et al.* 2005), but records of *D. prospicuus* still concentrate close to the riverbanks. In the case of Villa Argentina (Fig. 5) captures were made less than 30 m from the sandy shore, on a cliff covered by tall grass and with heavy human disturbance. Only the easternmost record comes from an inland site (Parque Sierra Minas, Fig. 5); specimens dwelled in a very shady and humid ravine, forested with exotic trees, in a location with tourist activity.

Northwestern Argentina. Distribution of *D. prospicuus* in NW Argentina agrees with its association with humid and shady forests (as described above), a condition met in montane forests and rainforests (yungas ecoregion) (Acosta 2002). Although records roughly align in a N–S strip, samplings in the NW revealed that *D. prospic-*

uus does not occupy the area continuously, but rather, populations appear quite isolated from each other (Fig. 1). Elevations range from 650 to 1600 m a.s.l. Records from Sierra de San Javier (road to San Javier, Villa Nougués), from province of Salta (San Lorenzo, road to Yacones) and Jujuy (Yala) are consistent in their east-facing orientation, intense precipitation rates in summer, presence of primary dense yungas vegetation, and from slight to severe human alteration. General conditions in the yungas and in the species core area are not closely similar, as shown by divergences in the variables cumulative curves and the overall bioclimatic profile. The most important difference concerns the precipitation seasonality, the yungas suffering a more drastic decrease in winter. Nevertheless, in "dry" months these east-facing slopes often receive an important amount of "horizontal precipitation" (mist), which is not reflected in the precipitation rates, but likely counterbalances the precipitation decrease in winter (Hunzinger 1995). One locality in the well surveyed province of Tucumán (near San Pedro de Colalao; Fig. 5) is remarkable because of its apparent isolation, within a yungas area but much less humid than all mentioned regions. The species was only detected near an irrigation ditch in a shady spot; the ditch was made on a slope terrace, and water infiltrated to the surrounding terrain, generating a distinct humid site. A microclimatic condition, rather than a general climatic one, seems to guarantee the habitat suitability for the species in that site.

Sierras of Córdoba. Findings in the sierras of central Argentina (Fig. 1) do not strictly comply with the habitat descriptions above. In that area the range is not strip-like, encompassing several localities on the eastern base and low elevation slopes of the mountains, especially in the Sierras Chicas and Calamuchita areas (Fig. 5), from 400 to 900 m a.s.l. One single record exists also on the western side of the sierras. These presences are difficult to interpret as a whole. The sierras of Córdoba were originally covered by montane forests, a special type of chacoan forest indeed (Torrella & Adámoli 2006). These montane forests were naturally dense only in favored areas, but long ago they were almost completely devastated by human activity (Luti *et al.* 1979). The region does not have large rivers, but moderate to small streams with marked seasonal regimes instead. In general the area is sub-xeric, with marked precipitation decrease in the dry period (winter). A basal belt, however, is deemed to correspond to a semi-humid regime, with no water deficit (Capitanelli 1979). Interestingly, all *D. prospicuus* records in the sierras fall within or very near of this belt. Furthermore, mountains offer plenty of sheltered sites in which local conditions of exposure, vegetation and/or vicinity to streams generate shady and protected spots in middle of semi-dry surroundings. It should be noted that for most records of *D. prospicuus* in the sierras, shadow and humidity are normally ensured by exotic trees. Dense and humid riparian forests with mixed native–feral trees were found to hold abundant *D. prospicuus* populations in Los Molinos (Fig. 3) and on the Suquía riverbanks near Saldán, but most captures (*e.g.*, Villa Ciudad Parque, Cabana, Villa General Belgrano, La Bolsa) were clearly associated with dense artificial forests, with intense human activity nearby (specimens were often caught under humid bricks and masonry rubbish). Proximity to water also seems to be the case for most records. Some degree of tolerance to eventual summer floods is presumed for *D. prospicuus* (one day after heavy rains and once the flood level decreased, a lot of specimens were found sheltered amongst still moist entangled sticks, brought by the flood and kept trapped at the base of trees and bushes).

Villa Nueva. In addition to the described areas, *D. prospicuus* was found in a single locality (Villa Nueva) in middle of the plains in province of Córdoba, on the borders of Ctalamochita River (Fig. 1: 3a). This isolated part of the range is in many aspects the most intriguing. Ctalamochita River originates in the sierras, 130 km W of Villa Nueva, close to several localities of the species; it flows 350 km further eastwards into the Paraná River. Like other rivers in Córdoba plains, Ctalamochita River sustained some degree of natural gallery forests in its middle course (Hueck & Seibert 1972). Repeated searching along the riverbanks (upstream and downstream of Villa Nueva) and in many localities in Córdoba plains yielded no *D. prospicuus,* but frequently other *Discocyrtus* instead, mainly *D. dilatatus* (Acosta 1995). The only records for the species in this whole region are two sites in Villa Nueva, on the southern banks of Ctalamochita river. The collecting sites, humid and shady, were a human-disturbed one (captures under trunks and bricks, even near an abandoned construction) and a natural gallery forest with signs of frequent floods. There is a remarkable fact in Villa Nueva (both sites): it is the only locality where *D. prospicuus* and *D. testudineus* were found together (*i.e.*, collected under the same trunk). Coexistence of *D. prospicuus* + *D. dilatatus* or *D. testudineus* + *D. dilatatus* is quite common (L.E.A. unpubl. data).

Bioclimatic profile. A summary of the conditions that represent the bioclimatic tolerance range of *D. prospicuus* is displayed in Table 2. With a permissive envelope cutoff (0.005 percentile), 65 out of 80 observations (81.2%) are kept within all possible bi-dimensional envelopes, the rest being outsiders in at least one envelope. Applying a stricter percentile (0.025, generally used as a standard), localities still within the 19-variables envelope fall to 55 (68.8% overall).

FIGURE 3. Habitat of *Discocyrtus prospicuus*. Mixed native – feral forests on the river banks near Los Molinos (province of Córdoba). Photo: G. Rubio.

Values reflect conditions typical for temperate to temperate-cold climate (mean annual temperature ranged between 13.40°C and 20.20°C). Closer inspection into the cumulative frequecies reveals some interesting features. Most variables are distributed in either a normal, slightly sigmoid or skewed fashion, with small to moderate number of outliers (Table 2). In particular, this description applies for all temperature variables, with four variables skewed to higher values (bc4 —see Fig. 4—, bc6, bc8) and one to the lower end (bc9). In other words, most localities concentrate at (relatively) high temperature seasonality; the minimum temperature of the coldest month and the mean temperature of the wettest quarter are only seldom low; and the mean temperature of the driest quarter tends toward cool conditions. It is in precipitation variables where localities differ the most, with the interrupted cumulative curve indicating strong bimodality and outlierness in bc14, bc15, bc17 and bc19 (see also Fig. 4). In this analysis, all 23 localities placed west of –63° are outliers for the four mentioned bc variables. Differences split the record set in two separate groups: those of the core area (RLP-Uruguay River) on one side; and all the rest (province of Córdoba and the NW), the latter characterized by heavy seasonality due to substantial decrease in precipitation in the drier/cooler periods (in large parts of the region involved, winter is the dry season). This climatic gap is likely in accordance with a large geographic separation (discussed below).

Localities in the NW are collectively the northernmost, westernmost and with higher elevation records, and bear many extreme bc values as well (Table 1). In general, these localities are the driest during dry/cold periods, and the wettest during wet/warm periods; hence high precipitation seasonality appear to be the most relevant limiting factor in the region. In the NW temperatures are generally low, albeit with little seasonality (bc4).

The southernmost localities (those on or near the Atlantic coast) are characterized by having the lowest precipitation in wettest (fall) or warmest (summer) periods, though they are far from being dry sites; indeed, precipitation seasonality there is among the lowest (the lowest record held however by Villa Argentina, on the Uruguayan side of the RLP estuary). As expected, in those southern localities temperatures are among the lowest. On the opposite Yapeyú (Fig. 5), geographically the closest site to subtropical conditions, is accordingly the warmest locality (higher values for bc1, bc5, bc6, bc10 and bc11) and with higher annual precipitation (bc12).
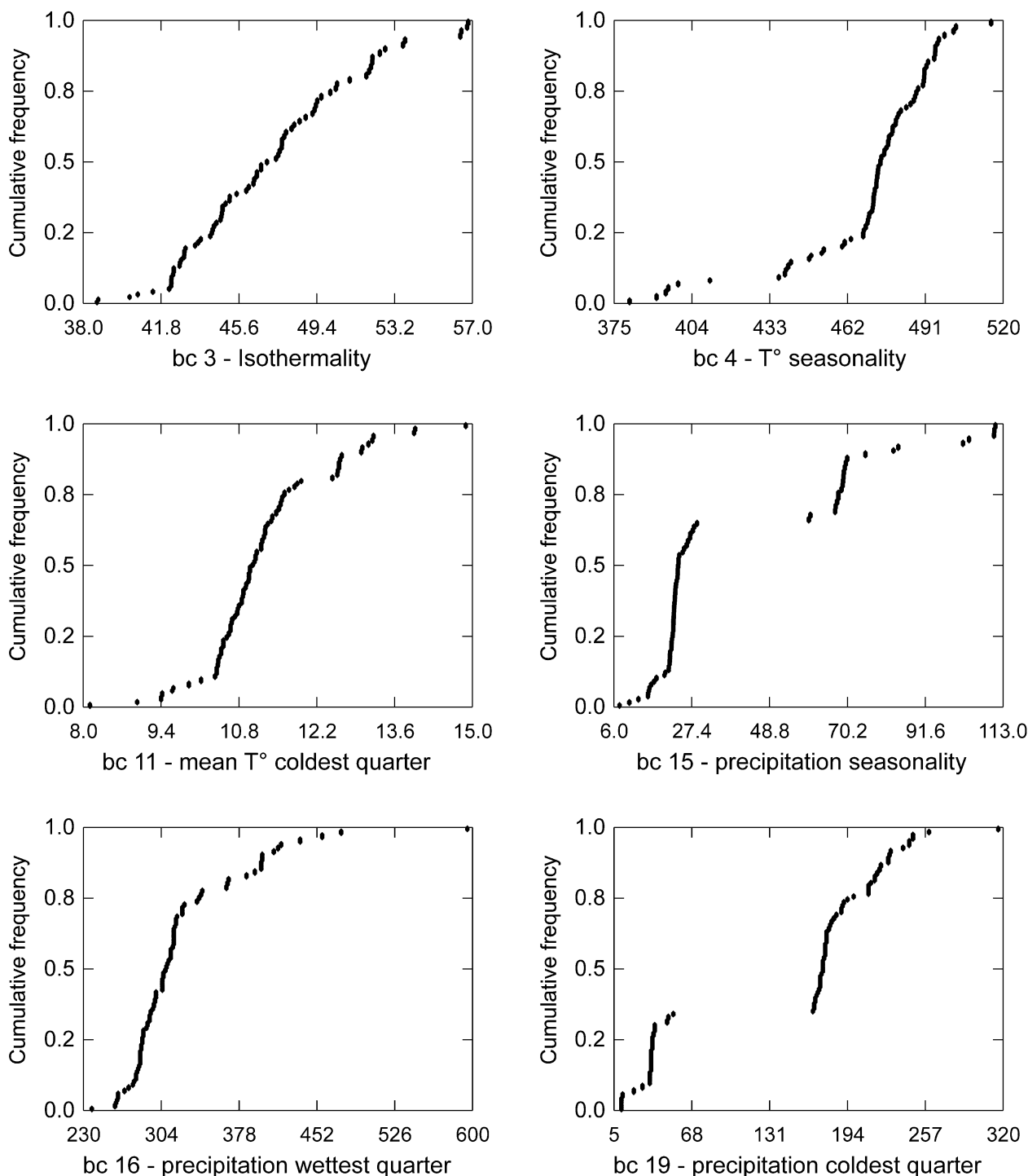
FIGURE 4. Records set of *D. prospicuus* plotted for cumulative relative frequency for the six most relevant bc variables, as determined by their contribution to the MAXENT models and the jackknife analysis.

Potential range. Predicted distribution obtained with BIOCLIM and MAXENT have many areas in common but significant discordance in one large region (Fig. 5). The range modeled with BIOCLIM (shown in Fig. 5 in its true/ false output, the entire envelope displayed) is clearly larger. It embraces not only the RLP-Uruguay River region, but wide portions in both sides, covering the eastern one third of Uruguay, most of province of Entre Ríos and a thick strip on northeastern province of Buenos Aires. From the latter, a southwards projection reaches the southern localities on the Atlantic. Between approximately 33.5°S – 31°S this core area is broadly continued westwards, to reach and entirely cover the Sierras of Córdoba, where only the higher environments are excluded. After a gap, the range reappears in the NW in two main sectors associated to the yungas ecoregion, in Tucumán and Salta-Jujuy

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provinces (Fig. 5). Despite variations depending on the settings adopted, most of these regions are also reflected in MAXENT models, though substantially more restricted around actual records. In fact, the preferred model (beta multiplier = 1) shown in Fig. 5 (binary prediction) and Fig. 6 (probabilities displayed) covers more tightly the RLP and Uruguay River area. This model recognizes isolated strips on the Atlantic coast, but leaves out the southernmost and easternmost records (Laguna de los Padres and Parque Sierra Minas). The MAXENT model shows a westerly projection as well that covers the delta region, but it does not further join the central sierras. A separate predicted area is then recognized around all records in province of Córdoba, *i.e.*, covering both sierra regions (higher environments included) and a part of the plains, up to Villa Nueva. As with BIOCLIM, the NWA portion of the range is displayed with MAXENT as a clear disjunction too, in a patchy though more connected manner. Overall, MAXENT concentrates the highest probability in four sectors (Fig. 6): around the RLP and lower Paraná delta; a coastal strip on the Atlantic, between Punta Rasa and Villa Gesell; a reduced central sector in the sierras of Córdoba; and a large stretch on Tucumán mountains.
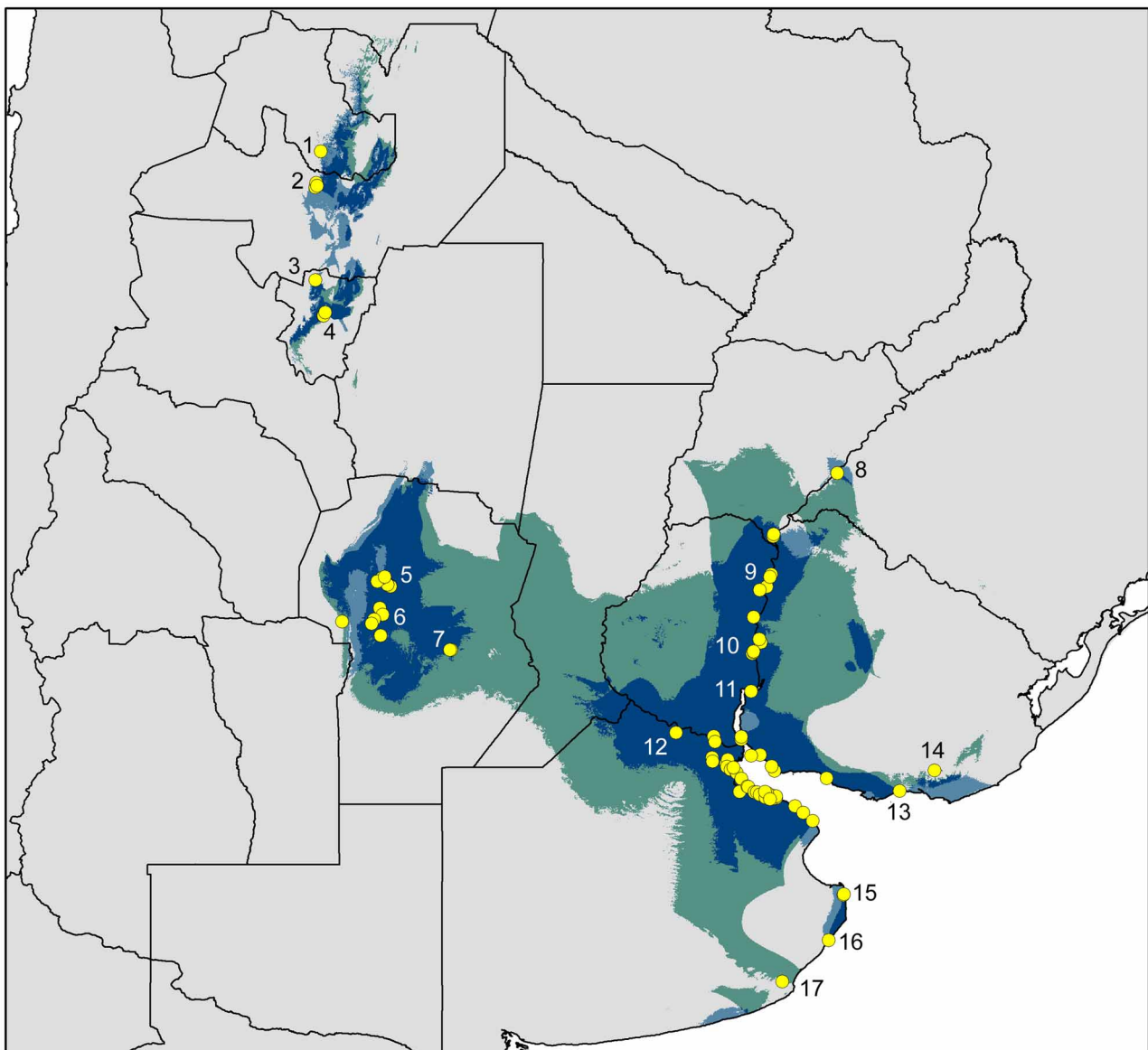
FIGURE 5. Predicted distribution of *Discocyrtus prospicuus*: overlay of models obtained with BIOCLIM (green; true-false, full extension) and MAXENT (light blue; binary), showing the overlapping areas (dark blue). Records: yellow dots. Selected localities (or groups of localities) are referenced as follows: 1. Yala, 2. San Lorenzo and road to Yacones, 3. San Pedro de Colalao, 4. Sierra de San Javier (road to San Javier and Villa Nougués), 5. Sierras Chicas area, 6. Calamuchita area, 7. Villa Nueva, 8. Yapeyú, 9. Concordia, 10. Colón and Banco Pelay, 11. Fray Bentos, 12. Baradero, 13. Villa Argentina, 14 Parque Sierra Minas, 15. Las Toninas and Costa Chica, 16. Villa Gesell, 17. Sierra de los Padres. References for localities in the RLP area: see Fig. 2.
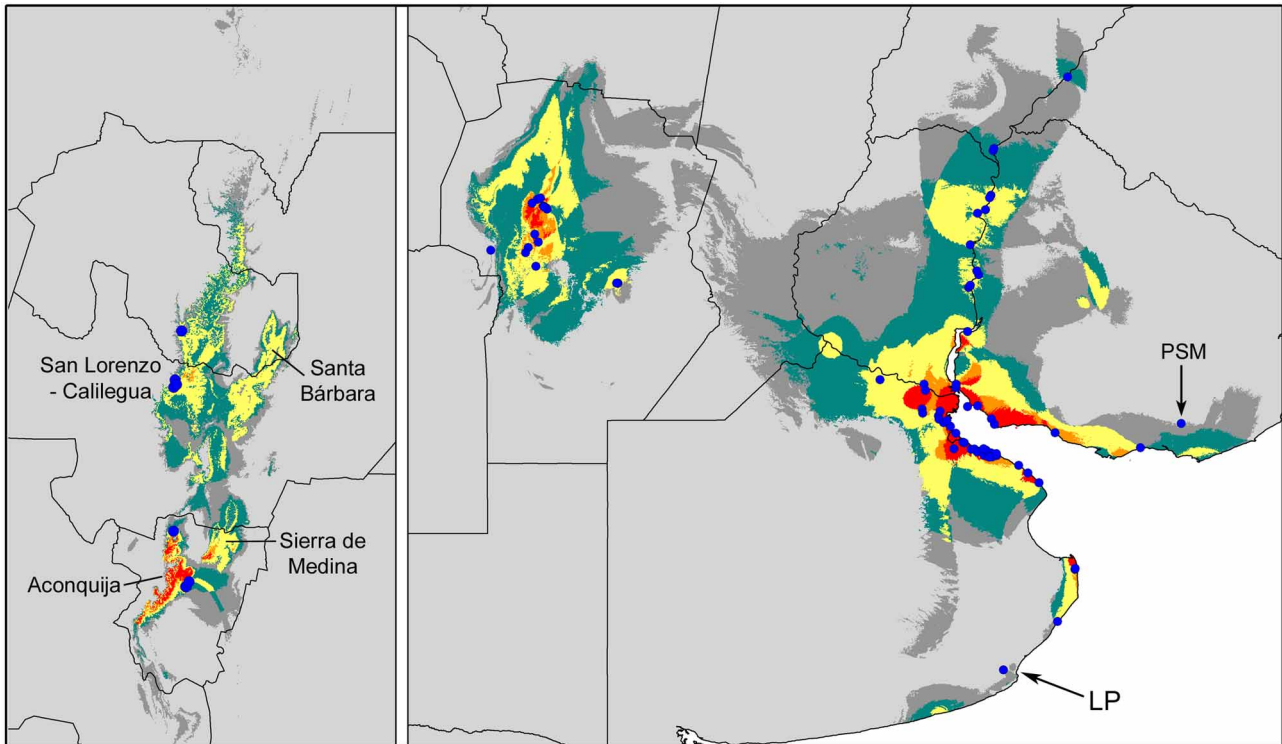
FIGURE 6. MAXENT distribution model of *Discocyrtus prospicuus*, displaying presence probabilities (green: 0.279–0.48, yellow: 0.48–0.75, orange: 0.75–0.82, red: above 0.82). Grey: all areas below the selected threshold (equal training sensitivity plus specificity); darker grey: probabilities above 0.130 (minimum training presence). Blue dots: records. Left map: main sectors recognized by the models in the NW. Right map: actual records left out of the threshold (LP: Laguna de los Padres, PSM: Parque Sierra Minas).

Accuracy assessments. All training runs (using all 80 points) made with MAXENT had a high AUC value, indicating its high computational accuracy, as widely proven for this method (Elith *et al.* 2006; Sangermano & Eastman 2007). The 10 replicates analysis (subsample procedure) required some additional calibration. An initial run was made using exactly the same settings as the above "preferred model", but results were unsatisfactory, because of a tendency to over-predict and, above all, the consistent appearance of some undesirable new sectors. The most important of these was a strip along the Valles Calchaquíes (western side of the Aconquija), in province of Tucumán (Fig. 7). It is biologically unlikely that such a xeric valley, placed on the orographic shadow and corresponding to the "monte" ecoregion (Brown & Pacheco 2006), can be a part of the potential distribution of a humidity-dependent harvestman like *D. prospicuus* (no harvestman species is known from that area: Ringuelet 1959; Acosta 2002). It seems that models, based indeed on relatively few records, were affected by the random elimination of some specific points, suggesting a marked sensitivity to the actual record set. Since each replicate was performed with less than 80 points, the subsample treatment also differed from the normal run in that threshold and product features were not selected by the software. To overcome this relaxed prediction we reduced the regularization multiplier (or beta multiplier) from 1 to 0.5, obtaining a lower incidence of the undesirable prediction in the Valles Calchaquíes (much smaller and present in only 3 out of 10 replicates). The overlay of all 10 prediction maps (Fig. 7) is in general consistent with the single model made with all 80 records. AUC of all 10 runs, both for training and test points, scored as excellent: average training AUC, 0.9912 (range 0.9891–0.9934), average test AUC 0.9840 (range 0.9740–0.9897). It is to be noted that models obtained by the 10 replicates procedure consistently left as negative the higher belts of the sierras in Córdoba (Fig. 7), as the BIOCLIM prediction did (Fig. 1); such a result looks much more realistic than the single model run with all points, which scores this unlikely area with low to medium probabilities (Fig. 6). No model was exact in detecting the presumable true absence of *D. prospicuus* in the plains between the RLP area and the central sierras, nor the isolated condition of Villa Nueva, though results from BIOCLIM, which display a broad continuous bridge, look worse. However, AUC values obtained for BIOCLIM models were always high (0.920–0.955 in a five-replicates run, 25% of records randomly set aside).
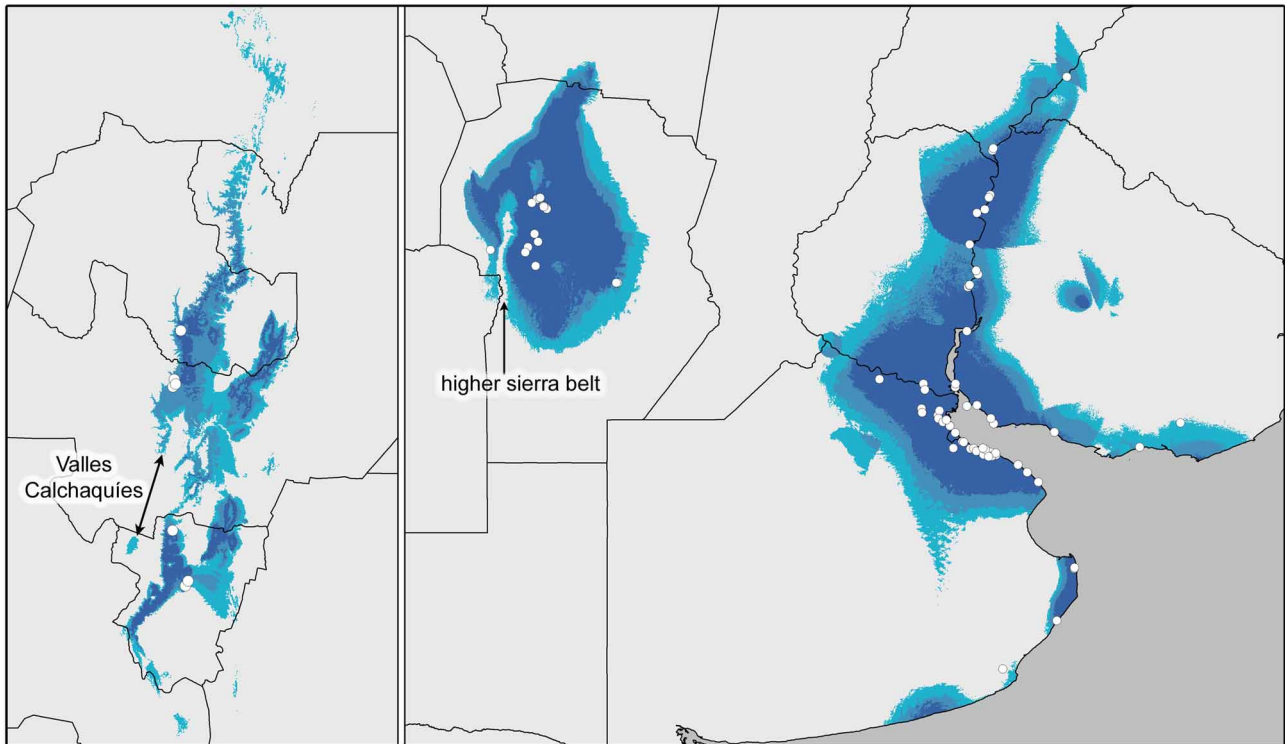
FIGURE 7. Overlay of 10 replicates of the MAXENT model, using the subsample procedure, with 25% of the data set used for test (random seed activated; beta multiplier = 0.5). Dark blue: predicted in all 10 runs; medium blue: predicted in 6–9 runs; light blue: predicted in 1–5 runs. White dots: presence records.

Importance of variables. Percent contribution calculated by MAXENT (Table 3) showed variables bc3 and bc4 ranking highest, *i.e.,* two temperature predictors closely related to annual climatic stability. As for precipitation variables, the most relevant were bc16 and bc19. Results obtained with the jackknife test (Table 3 and Fig. 8) agreed only partially with the preceding ones. The variable that decreased the gain the most when omitted was bc4 (temperature seasonality), which therefore appears to have the most information that is not present in the other variables; bc4 also ranked among variables with highest gain when used in isolation, *i.e.,* those having the most useful information by themselves. In overview, bc3, bc4, bc11, bc15, bc16 and bc19 were the most influential (their cumulative curves are shown in Fig. 4). By contrast, bc2 and bc5 appeared among the least relevant.

Disjunctions. Models obtained with both MAXENT and BIOCLIM consistently agreed in the recognition of the *a priori* most relevant disjunction, that of the NW sector, corresponding to the yungas of Tucumán, Salta and Jujuy (Figs. 5, 6, 7). All models display more or less continuous areas on the Aconquija-Cumbres Calchaquíes range, on the adjacent Sierra de Medina in Tucumán, on a strip crossing from San Lorenzo in Salta to Calilegua National Park in Jujuy, and on the isolated Santa Bárbara mountains east of the latter (see references on Fig. 6). Detailed limits and connections between these four sectors vary a lot among models, but only the two former have actual records. As stated before, climatic conditions of localities in the NW differ strongly from the core area in some relevant variables, especially those concerning precipitation seasonality. In spite of those differences, if models are built with all seven NW records removed, a small portion in province of Tucumán is still recovered, both with BIOCLIM (Fig. 9A) and MAXENT (Fig. 9B), although not matching the known records. In this treatment, predictions with MAXENT show the highest probabilities on the southern Aconquija flanks (Fig. 9B); the area predicted with BIOCLIM is smaller and placed at lower elevation (Fig. 9A).

Other parts of the potential range show less congruence among methods, the most relevant being the portion in the province of Córdoba, recovered either in isolation (MAXENT) or continuous (BIOCLIM) with the RLP region (Fig. 5). In light of our samplings with negative results, predictions obtained with MAXENT appear more realistic: Córdoba and RLP sectors were always kept disconnected (even with the 10-replicates run, beta=1, overpredicting). However (and interestingly), if probabilities scores below the selected threshold are displayed, for example that of minimum training presence, a connection similar to that of BIOCLIM tends to appear (Fig. 6). With BIOCLIM, the

presumed negative region is crossed by a broad connection between RLP and Córdoba, at medium to high percentile levels. This is a clear indication that for the 19 variables employed, this whole region falls within the rough species envelope. Why the species seems not to occur there is a meaningful question stemming from these results, and one that we will try to address later.
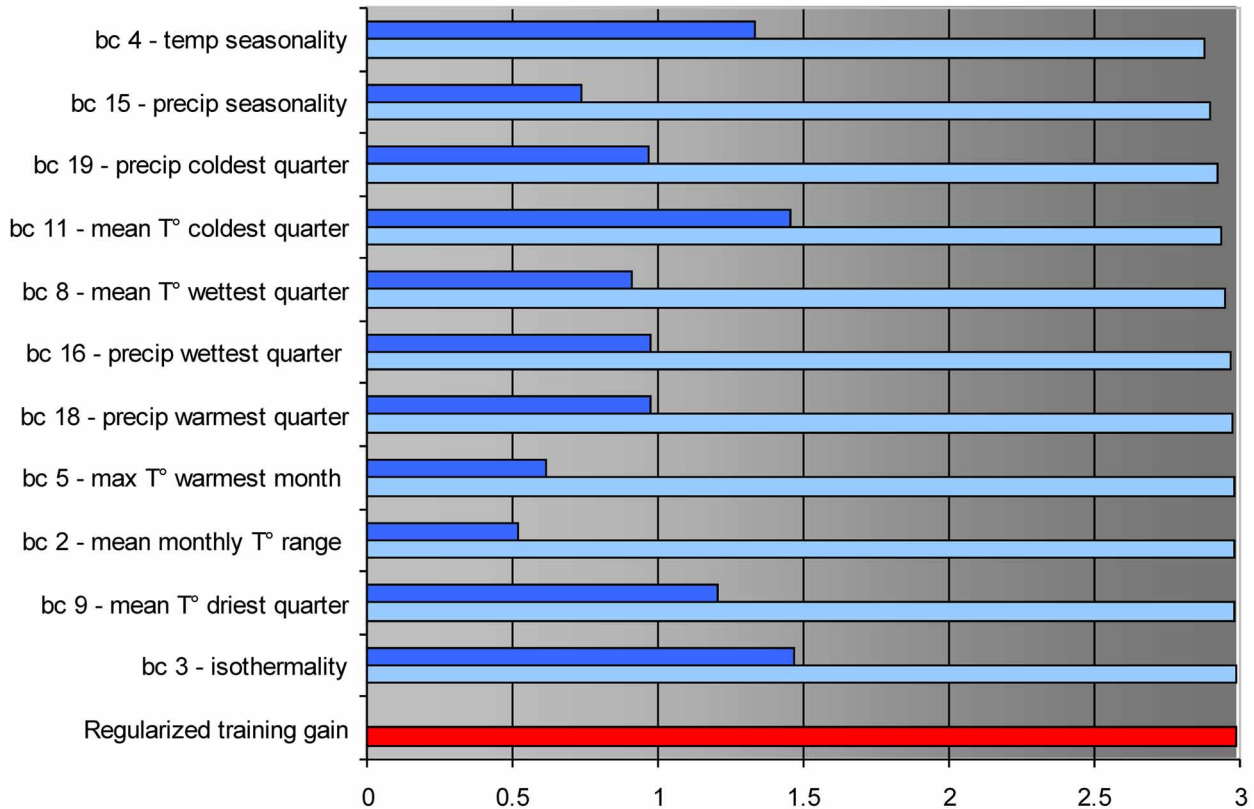
Jackknife of regularized training gain

FIGURE 8. Results of the jackknife test performed to determine the relative importance of the 11 bc variables employed in MAXENT. Red bar: regularized training gain with all variables (2.9892). Light blue bars: training gain with variable excluded (less gain, probable higher importance; variables are ordered following this value); dark blue bars: training gain with variable alone.

One further input variant was performed, in this case excluding together all 7 records from the NW and all 14 from the central sierras (only records from Villa Nueva were maintained, assuming them as a different habitat situation, plains instead of mountains). In this case, MAXENT was completely unable to recover presence in the province of Córdoba (Villa Nueva dropped out of the threshold), but surprisingly, a small prediction area was still recovered in Tucumán, between 1500 and 2000 m a.s.l. (Fig. 9C). With this treatment the BIOCLIM model, as expected, recovered just a few isolated low-percentile grid cells around Villa Nueva, with the core area not surpassing the province of Santa Fe; and again, a few scattered presence grid cells appeared in Tucumán. It seems that climatic information contained in localities of the core area alone are not enough to account for the complete tolerance range of *D. prospicuus*. In overview, Córdoba appears to be the least predictable portion.

Predicted presence in other peripheral locations are also highly dependent on the actual records. The area along Uruguay River depends in its northern portion on Yapeyú not being removed (as is the case in some of the subsample replicates). Indeed, this whole region is hardly predicted, tending to reflect low probabilities or patchy areas even with records not removed (Fig. 6). There is also variability in the way predicted areas on the Atlantic coast are depicted, either represented by small separate patches (MAXENT) or continuous to the RLP region through a diagonal crossing the province southwards (BIOCLIM). The 10-replicate procedure supported a similar but incomplete connection, but only when records on the Atlantic are present.
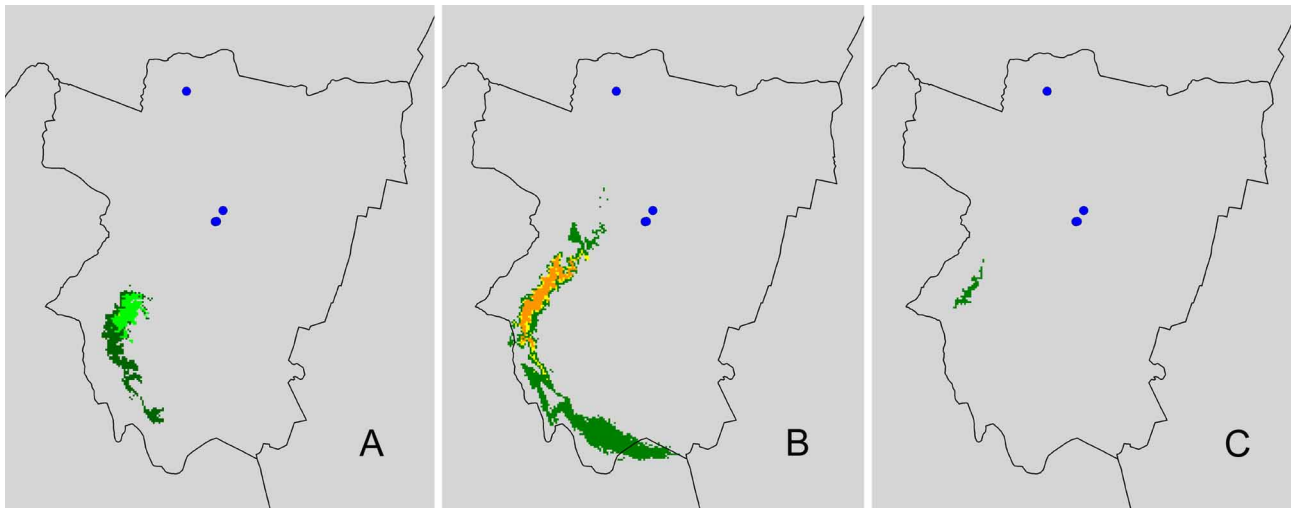
FIGURE 9. Distribution models built with selected records removed, detail of predictions in province of Tucumán. A–B: without all 7 points from NW Argentina (A using BIOCLIM, B using MAXENT); C: without 7 points of NW and 14 points from sierras of Córdoba (MAXENT). Blue dots: actual records of the species.

Discussion

The results described above confirm our initial assumption for *D. prospicuus*: aside from its apparent preference for humidity and shadow, habitat conditions are diverse and distributional constraints are not easily assessed. Although hitherto assigned to the Mesopotamian opiliofauna (Acosta 2002), its range crosses several ecoregions, quite marginally and none widely occupied (Fig. 1). The species was found from close to the seashore to near 1600 m a.s.l. The first conclusion is that *D. prospicuus* seems to be tightly restricted to narrow environmental conditions, more limited than the area predicted by bioclimatic analyses: the potential range largely overestimates the actual range.

In any case, the bioclimatic analysis proved its usefulness in gaining relevant information on the species profile, which was previously completely unknown. We can now state, for example, that the various areas occupied by *D. prospicuus* share a temperate to cool climate (annual mean temperature between 13.40 and 20.20ºC). Elevations of localities in NWA and Córdoba sierras contrast with that of the core area, where the species can be found at sea level; this likely reflects the requirement that temperature not surpass the aforementioned thermic range (*e.g.*, in the yungas, altitude would compensate the latitudinal temperature increase). This might be also reflected by the record in Yapeyú, holding extreme values for several variables correlated with high temperatures (Table 2), and its "behavior" in the suitability maps: all predictions encompass that locality with difficulty. Precipitation predictors show more variation (*e.g.*, annual precipitation ranges from 457 to 1325 mm), though microclimatic humidity might overcome the problem of water deficit in some cases. In the MAXENT models obtained, variables related to even climate during the year, like bc3 (isothermality), bc4 (temperature seasonality) and to a lesser extent bc15 (precipitation seasonality) were among those contributing the most to the final results. Standard measures of model accuracy ranked as high, and different computational treatments in general showed agreement in the main conclusions as well. As already emphasized, predictions of main parts of the range (RLP-Atlantic-Uruguay core area; sierras of Córdoba; yungas) fairly agree in both modeling methods. BIOCLIM and MAXENT also consistently supported the alleged yungas-Mesopotamian disjunction, one of the initial aims of this study.

There were, however, some major disagreements that deserve attention (Fig. 5). The most evident refers to the sector between the RLP area and the central sierras, MAXENT depicting these areas as separate, while BIOCLIM predicted a broad connection. Cumulative curves demonstrate that some precipitation variables are bimodal (*e.g.*, bc15, bc19), leaving a gap of missing values actually corresponding to the blank region. If no percentile cut-off is applied, the orthogonal envelope used by BIOCLIM simply embraces the whole distribution between end values, being thus unable to detect such a negative zone. The distribution gap is well reflected by MAXENT since its methodology computes the point records as constraints, thus tending to concentrate positive prediction around actual

records (at least in areas with good points density). Nonetheless, if MAXENT results are displayed with a more relaxed threshold (like minimum training presence, Fig. 6), a broad connection between sierras and RLP starts to appear, recalling that obtained with BIOCLIM. This strongly suggests that the area does contain climatic features matching in some way the conditions met in the real distribution. This observation leads to a crucial question: if the intermediate region has potentially suitable climate for *D. prospicuus*, why does the species not exist there (except for the isolate at Villa Nueva)? Indeed, the mismatch between actual and predicted ranges opens a more general inquiry: why do all models overpredict the species range? In fact, no distribution model, not even MAXENT with regularization multiplier 0.5, was able to properly take into account the astonishing narrowness in the RLP-Atlantic area, as an example. Similarly, the actual distribution of *D. prospicuus* in the yungas or in Córdoba sierras seems to be more restricted than any model prediction can display. There appears not to be a simple answer to those disagreements, and it can be suspected that one or more additional limiting factors exist, which are not represented in the bc variables used to build models. Considering the evidence at hand, presence of a (supposedly) competing species and availability of constant air humidity are examined as possible explanatory factors.
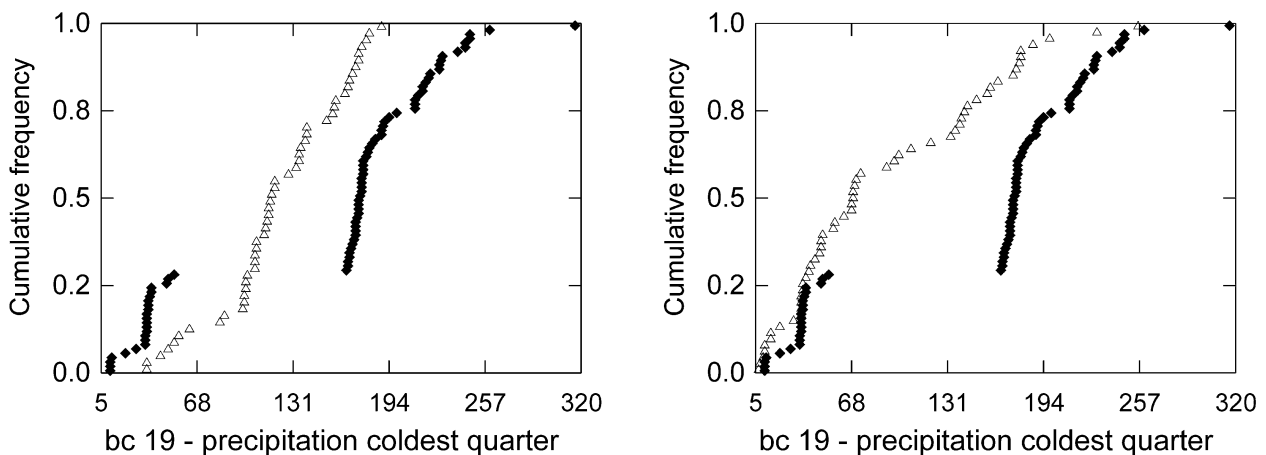

FIGURE 10. Cumulative frequency plot of variable bc19, comparing the curves of (left) *D. prospicuus* (black) vs. *D. testudineus* (n=54, white), and (right) *D. prospicuus* vs. *D. dilatatus* (n=60, white).

Biotic factors: Assuming *D. prospicuus* to be primarily a shady forest dweller, one can wonder why it does not extend northwards in the gallery forests of Paraná River (regardless of the fact that Paraná gallery forest in this area are not continuous; Nores *et al.* 2005). We have already mentioned a presumed exclusion with its congener, *D. testudineus*. The latter species is widespread in the Mesopotamian area (Ringuelet 1959, Acosta 2002; see also Fig. 1), Otamendi (northern province of Buenos Aires) being its southernmost record. At this locality, overlap with *D. prospicuus* was detected just in a narrow strip of sympatry in the barrancas, but gallery forests are only occupied by *D. testudineus*. At a larger scale, the distribution map displays a similar exclusion in the delta area: *D. prospicuus* was recorded in the distal portion of the delta (the "lower deltaic plain" of Colombo *et al.* 2000) and its southern barrancas, while the collecting records of *D. testudineus* are distributed over the rest of the delta and its cliffs (Fig. 1). As in Otamendi, some overlapping of the ranges can be expected (*cf.* the northernmost record of *D. prospicuus* at Baradero, not confirmed in this study). In any case, where *D. testudineus* no longer exists, *D. prospicuus* enters the marginal selvas, as already explained. The upper and medium Paraná delta is thus an overestimate incurred both by BIOCLIM and MAXENT (Figs. 5, 6, 7), suggesting therefore climatic uniformity along the whole geomorphological unit. Interestingly, other independent patterns match the *Discocyrtus* exclusion. While the delta was formed by alluvial contribution of the Paraná River, vegetation of its distal end (lower delta) shows more floristic similarities with gallery forests of the Uruguay River; the rest of the delta (that occupied by *D. testudineus*) has a clear "Paraná-like" vegetation character (Burkart 1957). The approximate limit between these two distinguishable botanical components was placed around the –59.1° longitude (Burkart 1957), surprisingly paralleled by the range separation in *Discocyrtus* (the last presence of *D. testudineus* placed less than 20 km from that longitude). Further south, gallery forests on the RLP contain mixed floristic elements, but with accentuated prevalence of Uruguayan species (Cabrera & Dawson 1944; Burkart 1957). This strongly suggests *D. prospicuus* as a harvestman primarily

associated to riparian vegetation of the Uruguay River. The alleged species exclusion might persist in the province of Córdoba: in no site were *D. testudineus* and *D. prospicuus* found together; the former has a very limited advance in the sierras, and the latter is not present in the plains. The only exception is so far the remarkable coexistence in Villa Nueva.

The distributional gap left by *D. prospicuus* between RLP and Córdoba sierras is filled by the predicted ranges of *D. testudineus* and *D. dilatatus* (Acosta 2007; L. Acosta & J. Vergara, in prep.). But while the latter species, as stated, should not conflict with *D. prospicuus*, the bioclimatic profile of *D. testudineus* might reveal further interesting clues. Cumulative frequencies of most variables (bc1, bc5–bc13, bc16, bc18) show roughly similar curves in *D. testudineus* and *D. prospicuus*, either normal, sigmoid or skewed, although in the former they are displaced towards warmer and more humid climate; bc4 curves match almost completely. In contrast, all curves that are bimodal in *D. prospicuus* (bc14, bc15, bc17, bc19) share a remarkable behavior: they are not interrupted in *D. testudineus*, and frequencies mostly concentrate in the gap left by *D. prospicuus* (Fig. 10, left, exemplified on bc19). Frequencies of *D. dilatatus* do not show such a disruptive appearance but smoothly embrace the whole range instead (Fig. 10, right), leaving *D. testudineus* as the main suspect for the geographical exclusion.

Further abiotic factors: Localities in RLP, Atlantic coast and Uruguay River suggest that the species is tightly limited to sites close to water, probably depending upon specific requirements of air humidity. This factor is not directly reflected in the bioclimatic variables used in the models. Large water masses have a direct influence on humidity in coastal localities. This factor might help moderate seasonal variation (a preferred climatic condition for *D. prospicuus,* as bioclimatic analyses suggest), even though its effective influence may be limited to a few kilometers from the coastline. In some RLP sites, *D. prospicuus* has demonstrated remarkable surface activity during the "dry" months (winter). In that cold period, in spite of moderate precipitation decrease, fog frequency is high in this area. Presence of fog was argued to be a significant microclimatic factor in the Uruguay riverbanks, allowing subtropical plant species to progress southwards in narrow gallery forests, amongst more mesic regions (Nores *et al.* 2005). Also for some yungas areas (like Sierra de San Javier, where *D. prospicuus* occurs) fog was deemed to compensate for the precipitation decrease in winter, ensuring humidity during the year (Hunzinger 1995). Winter surface activity was observed for the species in the yungas too, reinforcing the hypothesis of a probable critical requirement for the species: to have humidity available along the entire year. On the other hand, extreme proximity to water might represent a risk of eventual floods. Besides our observations in Córdoba sierras and in Villa Nueva (see above), the main parts of the core range (RLP and Uruguay River) are subject to regular flooding during the rainy season; flooding may also result from other meteorological phenomena, such as the storms known as "sudestada". In either case, water levels may be often raised by several meters (Nores *et al.* 2005). In all regions we found evidence that *D. prospicuus* is facultatively able to climb (*e.g.*, we found it sheltered under bark 1 m high, and climbing on the wall of an abandoned construction, around 2 m high). Collectively, these observations help reinforce the picture of a marginal range.

The preceding discussion was based on the assumption that all described patterns reflect natural conditions. However, as frequently mentioned previously, in its area of occurrence *D. prospicuus* not only proved to tolerate human activity well, but in some cases potentially accrue indirect benefit from it, and possibly with respect to range expansion (*e.g.*, humid exotic forests, surrounded by sub-xeric native vegetation, as frequent in Córdoba sierras). This raises an additional question on the species' distribution: can some parts of the range be explained by human introduction? Presence in Córdoba sierras, not predictable at all when points are removed, looks at least suspect at the light of our modeling results. As most of the natural vegetation was destroyed there, it is still possible that secondary forests served as a kind of "last refuge" for the (supposedly) original populations; but with equal likelihood, they might also represent the factors that enabled a synanthropic colonization. In the case of another disjunct species (*Geraeocormobius sylvarum*, see Acosta 2008), introduction in the yungas was also considered possible. However, the latter species provided very few actual records in the yungas, and in a very small area, resulting in a weak prediction even with all points in use (Acosta 2008). This is contrary to the case of *D. prospicuus* (even with all records removed, a small prediction in the yungas is still recovered). At present knowledge, it cannot be ruled out that the patterns observed are actually the combined results of an intricate original range, obscured by the species' plasticity and human expansion. Further hypothesis testing should be pursued using complementary approaches, including molecular methods (*e.g.*, phylogeography), but these investigations are beyond the scope of the present study.

Acknowledgments

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