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New records and distribution modeling of *Gryne orensis* (Sørensen) (Opiliones: Cosmetidae) support the Mesopotamian–Yungas disjunction in subtropical Argentina

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Abstract

The presence of *Gryne orensis* (Sørensen) (Opiliones: Cosmetidae) in a Yungas locality (northwestern Argentina) is reported for the first time, providing new evidence for the Mesopotamian-Yungas disjunct pattern. Combining a total of 19 new Mesopotamian records with previous, reliable citations from the literature, a dataset of 45 points was used to model the potential distribution of the species, using the presence-only methods BIOCLIM and MAXENT. Models supported the existence of a distributional gap across the Semiarid Chaco. The imprecise literature record from "El Impenetrable", province of Chaco, is assigned to three tentative locations to evaluate if models are affected by their inclusion; in all cases, the disjunction was maintained. It was thereby estimated that the actual record might have originated in a site closer to the Humid Chaco and/or associated to streams. This paper also provides a statement of the bioclimatic profile and identification of major environmental constraints that define the range of *G. orensis*.

Key words: Neotropical Region, disjunction, bioclimatic profile, potential distribution modeling, MAXENT, BIOCLIM

Introduction

As defined by Acosta (2002), the Argentinean opiliogeographical area called "Mesopotamia (*sensu stricto*)" covers an extensive humid and sub-humid plain, mainly arranged along the surroundings of middle and lower courses of Paraná and Paraguay rivers. It comprises provinces of Corrientes and Entre Ríos, extending westward in a strip along the eastern borders of the provinces of Formosa, Chaco and Santa Fe (*i.e.*, over the Humid Chaco ecoregion; Olson *et al.* 2001), up to a narrow projection reaching northern Buenos Aires (Acosta 2002). Along the Paraguay River, many Mesopotamian species also extend into eastern Paraguay while some probably even distribute further north. While most typical Mesopotamian species follow the described pattern closely, a number of entities—like *Discocyrtus dilatatus* Sørensen, 1884, *D. prospicuus* (Holmberg, 1876), *D. testudineus* (Holmberg, 1876) (Gonyleptidae: Pachylinae) and *Pectenobunus paraguayensis* (Canestrini, 1888) (Sclerosomatidae: Gagrellinae), among others—spread further into the inland province of Córdoba, reaching the base of the central Sierras (Acosta 1995, 2002). A few species revealed a disjunct pattern, with populations isolated in montane rainforests of Northwestern Argentina (NWA from now on), *i.e.*, the Yungas ecoregion (Brown *et al.* 2006). Thus far, species that exhibit this disjunct pattern are three gonyleptids: *Discocyrtus dilatatus* and *D. prospicuus* (Mesopotamian *sensu stricto*) and the Misiones species *Geraeocormobius sylvarum* (Holmberg, 1887), the latter actually representing a disjunction between Yungas and Paranense (Alto Paraná) forests (Acosta 1995, 2002, 2008; Acosta & Guerrero 2011).

This pattern has been given a central role in biogeographical hypotheses invoking climate change scenarios. In fact, between the Mesopotamian and Yungas conditions there is a separation, about 400–500 km wide, consisting of thorny Semiarid Chaco, where no harvestmen population from either of the adjacent regions are deemed to subsist (Acosta 1995, 2002). The presence of species on both sides of the sub-xeric Chaco has been attributed to

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past (Pleistocene?) expansions of the humid conditions, in which Mesopotamian harvestmen might have expanded their ranges up to NWA, then followed by a retraction phase, leaving isolated populations in the Yungas, as we see them today (Acosta 1995, 2002, based on Nores 1992). Of course, if such an environmental scenario took place it must have affected several species; so that the more *taxa* that are involved, the better the evidence for such a scenario. In this context, the finding of the Mesopotamian cosmetid *Gryne orensis* (Sørensen, 1879) in a Yungas locality in the province of Jujuy, hereby first reported, provides evidence for another species that supports the generality of the disjunction.

So far, *Gryne orensis* has been recorded (somewhat patchily) over a huge area stretching 1800 km, from the Brazilian State of Mato Grosso do Sul in the North, to the province of Buenos Aires in the South. As with many Neotropical harvestmen, there are many gaps in our distributional knowledge of this and other Mesopotamian species, partly because of the scarcity of records, but also due to some doubtful old citations. In this paper, we provide 19 new localities for *G. orensis*, in some cases filling in gaps of the previous citations. Almost all known records fit well in the Humid Chaco ecoregion, as defined by Olson *et al.* (2001) (Eastern Chaco of Ragonese & Castiglioni 1970; Humid Chaco + Iberá Marshes, *sensu* Brown *et al.* 2006), together with its southward projection, the "Paraná flooded savanna" (Fig. 1). In a recent contribution, Guerrero (2012) gave some new records for the species, among them the hitherto southernmost locality (Vuelta de Obligado, province of Buenos Aires), as well as the report of this cosmetid in the Semiarid Chaco, where Mesopotamian harvestmen are presumably not able to subsist (namely, in the "El Impenetrable" region). Although not precise enough, the latter record is at the same time meaningful, since it might open the disjunction case again: Is the range of *G. orensis* really disjunct? Or is the record at El Impenetrable evidence for continuous connection of both sides through intermediate populations? In this paper we use a distributional modeling approach, based on two broadly accepted methods (BIOCLIM and MAXENT), to characterize the bioclimatic constraints that shape the range of *G. orensis*, and to learn what the available records are able to tell us about these patterns.

Methods

Data acquisition. All published records for *G. orensis* were taken into account and analyzed. Any locality that remained unrecognizable, imprecise, or zoogeographically suspect (*i.e.*, suggesting an unlikely location for the species) was set aside for modeling purposes (but see an exception for the record from El Impenetrable below). Species recognition relied mainly on Ringuelet (1959). The record set was completed with the new localities, obtained in this survey through manual search and collecting, under bark or fallen tree trunks and piles of bricks (Acosta *et al.* 2007). The full dataset (El Impenetrable not included) comprised 45 unique points (Table 1, also displayed on Fig. 1). Localities from the literature were identified and geo-referenced using printed road maps, gazetteers and Google Earth ©, crosschecked for accuracy; those coordinates are not expected to exactly match the actual collecting points, but the broad spatial scale used in this paper makes such an imprecision negligible (Acosta 2008). Our captures were geo-referenced *in situ* using a Garmin ® GPS.

Acronyms. CDA (Cátedra de Diversidad Animal I, Facultad de Ciencias Exactas, Físicas y Naturales, Universidad Nacional de Córdoba; conventional collection is indicated with a 000.xxx accession number; freezer collection denoted as –F).

Climate layers. Preparation of digital layers and other GIS operations were made using the free software DIVA-GIS, version 5.4 (Hijmans *et al.* 2005b). Present climatic information was obtained from the WorldClim 1.4. dataset (Hijmans *et al.* 2005a), which contains values for 19 bioclimatic (bc) variables—listed in Table 2—averaging the 1950–2000 period, at a resolution of 30 arc second (about 1 km^2 grid cell). 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 to run BIOCLIM. For use in MAXENT, raster layers were extracted in DIVA-GIS grid format (.gri and .grd files) using the "Climate > Map" command. In MAXENT, the inclusion of highly correlated variables was prevented by keeping only one of a correlated pair (Pearson>0.75). Correlation was determined with pairwise analyses, made separately for temperature and precipitation variables (Rissler & Apodaca 2007; Kozak *et al.* 2008; Acosta & Guerrero 2011); it was calculated on values of 770 points over the study region, *i.e.*, central and northern Argentina, Paraguay, Uruguay and southern Brazil. Considering that thorough biological information on the importance of variables is lacking, choice in a highly correlated pair was defined by its overall scoring (computing together all four estimators of the variables importance; see below and Table 3) in preliminary models, run with all

19 variables. This procedure was aimed to avoid discarding a presumably relevant predictor. In sum, 11 bc variables were used in MAXENT, as indicated in Tables 2 and 3.

Modeling. Two presence-only modeling methods were employed, BIOCLIM and MAXENT. BIOCLIM was run as an inbuilt functionality of DIVA-GIS, both to get predictive maps, to extract bioclimatic values that characterize the species profile, and to inspect the curves of cumulative frequencies. As explained in Acosta (2008, and references therein), BIOCLIM—a frequency-based algorithm—defines an orthogonal multi-dimensional hyper-space (envelope) that bounds the climatic preferences of the modeled species; projected on a map, it classes as "suitable" those grid cells matching the envelope values. MAXENT, computationally more sophisticated, is deemed to outperform most other modeling algorithms (Elith *et al.* 2006; Hernández *et al.* 2006). A description of the method can be found in Phillips *et al.* (2006), Phillips and Dudík (2008) and Elith *et al.* (2011). We ran MAXENT using version 3.3.3k (Phillips *et al.* 2011). Most settings were kept in their default values, except for "maximal number of background points" (set to 20000), and "maximum iterations" (to 2500). Feature selection was made automatically by the software ("auto" selected); logistic option was selected for map output. Because predictive maps yielded by MAXENT classify suitability as continuous values from 0 to 1, a threshold rule is needed to differentiate "suitable" and "not suitable" grid cells; following Liu *et al.* (2005) and Acosta and Guerrero (2011), "equal training sensitivity plus specificity" threshold was applied in this paper, unless otherwise indicated. Default MAXENT models are based on a single run. These results were contrasted with 20 replicate runs, using the "subsample" option of replicate type, and random test percentage set to 20 ("random seed" selected). By this procedure, 20 output maps were produced, each using 36 training points and 9 test points. Because each run uses a randomly different dataset for training, the model shown in Fig. 2 summarizes all 20 replicates through the median values, using the average threshold. Overlay of results for comparative purposes was made on binary maps, in the case of BIOCLIM showing the entire suitability range ("True/False", 0–100 percentiles); in MAXENT, the binary map obtained by applying the threshold rule referred to above. Suitability levels are only displayed on Fig. 2.

Accuracy of models; importance of variables. Results were evaluated through the AUC (Area Under Curve) assessment, incorporated in MAXENT; AUC values over 0.8 are considered a "good" model performance; above 0.9 the accuracy is considered "high" (Luoto *et al.* 2005). In the case of the 20 replicate runs, AUC was calculated for each run. The relative importance of each variable was estimated through four different measures, available in MAXENT (Phillips *et al.* 2011): (a) percent contribution, *i.e.*, the increase in regularized gain being added to the contribution of the corresponding variable, in each iteration of the training algorithm; (b) permutation importance, resulting from the values of each environmental variable on training presence and background data being randomly permuted, the model then reevaluated on the permuted data; resulting drop in training AUC is normalized to percentages; (c) the jackknife analysis, considering the training gain either with one variable omitted at a time (the bc decreasing gain the most when omitted is deemed to have the most information not present in other variables); or (d) run with a given variable in isolation (that with highest gain has the most useful information by itself). Rating of variables did not result the same for all these four estimators, so the ranking shown in Table 3 reflects an overall scoring (a+b-c+d).

Input variants. To test if presence at El Impenetrable affects the prediction of the disjunct pattern (by increasing the environmental range), three extra datasets were used (n=46), each including alternative "variants" for representing that vague region (see Fig. 3 and Table 1): a) a milder option, set at Villa Rio Bermejito, b) an intermediate point (Las Hacheras), and c) the most rigorous site (Fuerte Esperanza). The default dataset contains no record for El Impenetrable. Further, additional models were built for each of the four datasets, with the single record at the Yungas deleted, to test if climatic information contained in Mesopotamian records is enough to predict presence in NWA.

Results

Localities included and excluded. The complete georeferenced record set of *G. orensis* is presented in Table 1, including 19 new records and 26 previous citations deemed to be correct (Sørensen 1879, 1895; Roewer 1912, 1925, 1938; Ringuelet 1959; Valentinis de Martinez 1974; Soares & Soares 1985; Guerrero 2012). The type locality ("Riacho de Oro": Sørensen 1879) was located at the mouth of the mentioned stream into Paraguay River, following Sørensen (1884) (at that time, transportation in the area was fluvial). This was the only known record for the species until Roewer started to study specimens held in European collections; but some of those old references

TABLE 1. Record set of *Gryne orensis*, with locality names, geographical coordinates and source of each record. Latitude and longitude are in decimal degrees. Coordinates of asterisked localities (**) are approximate; extreme geographical points of the range are underlined. Localities representing lowest or highest values for bioclimatic (bc) variables are indicated with numbers as in Table 2 (sites of El Impenetrable not considered); for sites in El Impenetrable, whenever applicable, extreme values are bracketed. New records are indicated as NR, along with collection data.

Province, State or Departamento	Locality	Longitude (W)	Latitude (S)	bc lowest	bc median	bc highest	Source
BRAZIL							
Mato Grosso do Sul	Corumbá: Carandazinho [1]	-57.5401	-<u>18.6626</u>	4, 7	—	1, 3, 6, 9, 11	Roewer 1925
PARAGUAY							
Concepción	Colonia Sargento José E López	-56.9150	-22.3797	—	—	—	Soares & Soares 1985
Concepción	Rio Apa [2]	-57.9600	-22.0817	—	—	18	Roewer 1938
Concepción	Colonia Risso, río Apa (today Puerto Risso, by Paraguay river)	-57.8150	-22.3743	—	—	—	Sørensen 1895
Concepción	Estancia Postillón, near Puerto Max (Estancia not found, coordinates are of Puerto Max) **	-57.7725	-22.6282	—	12	—	Roewer 1912
Alto Paraguay	Puerto Casado (today Puerto La Victoria)	-57.9373	-22.2828	—	—	8, 10	Ringuelet 1959
San Pedro	San Pedro [de Ycuamandiyú]	-57.0800	-24.0913	—	—	—	Sørensen 1895
San Pedro	San Estanislao	-56.4532	-24.6637	2	—	—	Ringuelet 1959
Caaguazú	San Joaquín	-56.0450	-25.0283	5	—	12, 13, 16	Roewer 1912
Guaira	Villarrica	-56.4500	-25.7833	—	8	—	Sørensen 1895
Central	Colonia Thompson, 20 km S of Asunción	-57.5115	-25.4610	—	—	—	Soares & Soares 1985
Central	Asunción	-57.6333	-25.2833	—	—	—	Sørensen 1895
ARGENTINA							
Formosa	Colonia Dalmacia	-57.9070	-25.8502	—	2	—	**NR:** 5 ind. (CDA-F), 3-xii-2011 (J. Vergara, R. González-Ittig. L. Vaschetto)
Formosa	Monte Lindo Grande	-58.2260	-25.7080	—	7, 16	—	**NR:** 6 ind. (CDA-F), 3-xii-2011 (J. Vergara, R. González-Ittig. L. Vaschetto)

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TABLE 1. (Continued)

Province, State or Departamento	Locality	Longitude (W)	Latitude (S)	bc lowest	bc median	bc highest	Source
Formosa	Formosa	-58.1667	-26.1900	—	—	—	Ringuelet 1959
Formosa	Herradura, Camping La Florencia	-58.3038	-26.4825	—	—	—	**NR:** 6 ind. (CDA-F), 3-xii-2011 (J. Vergara, R. González-Ittig. L. Vaschetto)
Formosa	San Francisco de Laishi	-58.6255	-26.2384	—	—	2	**NR:** 1 ind. (CDA-F), 3-xii-2011 (J. Vergara, R. González-Ittig. L. Vaschetto)
Formosa	Pirané	-59.1000	-25.7333	—	—	5	Ringuelet 1959
Formosa	El Colorado	-59.3582	-26.3356	—	1, 9, 11	—	**NR:** 4 ind. (CDA-F), 4-xii-2011 (J. Vergara, R. González-Ittig. L. Vaschetto)
Chaco	Riacho de Oro (mouth) ** LOCUS TYPICUS	-58.5678	-27.0390	—	15, 18	—	Sørensen 1879
Chaco	Río de Oro, by National High road 11 bridge	-58.7796	-26.8835	—	7	—	**NR:** 7 ind. (CDA-F), 2-xii-2011 (J. Vergara, R. González-Ittig. L. Vaschetto)
Chaco	Picada Guaycurú **	-58.9753	-27.0254	—	3, 4, 8	—	Ringuelet 1959
Chaco	El Impenetrable**						Guerrero 2012
	at Villa Rio Bermejito	-60.2671	-25.6442	—	—	—	
	at Las Hacheras	-60.9902	-25.3902	—	—	—	
	at Fuerte Esperanza	-61.8377	-25.1688	[12, 13]	—	[2, 5, 7]	
Chaco	Colonia Benítez	-58.9500	-27.3333	—	10, 14	—	Ringuelet 1959
Chaco	Bridge at Colonia Benítez	-58.9661	-27.3352	—	14	—	**NR:** 6 ind. (CDA-F), 2-xii-2011 (J. Vergara, R. González-Ittig. L. Vaschetto)
Chaco	Resistencia	-58.9917	-27.4517	—	—	—	Sørensen 1895
Chaco	Río Tragadero, 1 km to Puerto Antequera (in decaying tree stump)	-58.8692	-27.4332	—	5, 17, 19	—	**NR:** 44 ind. (CDA 000.846), 24-ii-2005 (L. Acosta, G. Rubio, P. Olivero, M. García)
Misiones	Posadas (University Campus)	-55.8883	-27.4338	15	—	14, 17, 19	**NR:** 3 ind. (CDA-F), 24-x-2010 (P. Iglesias)
Corrientes	Colonia Carlos Pellegrini	-57.1667	-28.5333	—	—	—	Guerrero 2012
Corrientes	Laguna Soto (camping place, under half-buried brick debris) [3]	-58.7350	-27.4600	—	12	—	**NR:** 69 ind. (CDA 000.843), 23-ii-2005 (L. Acosta, G. Rubio, P. Olivero, M. García)

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TABLE 1. (Continued)

Province, State or Departamento	Locality	Longitude (W)	Latitude (S)	bc lowest	bc median	bc highest	Source
Corrientes	Rio Empedrado, by National High road 12 bridge	-58.7638	-27.8634	—	—	—	**NR:** 11 ind. (CDA-F), 2-iv-2012 (J. Vergara, L. Vaschetto, C. Argañaraz)
Corrientes	Manantiales	-58.1017	-27.9217	—	6, 9, 11, 13	—	Guerrero 2012
Corrientes	Mburucuyá	-58.2233	-28.0467	—	—	—	Ringuelet 1959
Corrientes	Saladas	-58.6474	-28.2625	—	—	—	**NR:** 3 ind. (CDA-F), 1-iv-2012 (J. Vergara, L. Vaschetto, C. Argañaraz)
Corrientes	Santa Lucía [4]	-59.0947	-28.9857	—	5	—	**NR:** 21 ind. (CDA 000.844), 25-ii-2005 (L. Acosta, P. Olivero, M. García)
Corrientes	Esquina	-59.5330	-30.0088	—	—	—	**NR:** 10 ind. (CDA 000.845), 26-ii-2005 (L. Acosta, P. Olivero, M. García)
Entre Ríos	Paraná	-60.5333	-31.7188	3	—	—	Guerrero 2012
Santa Fe	La Invernada, Reconquista Dept. **	-59.4527	-29.0338	—	—	—	Ringuelet 1959
Santa Fe	Madrejón “Don Felipe”, La Capital Dept.	-60.6008	-31.6500	—	—	—	Valentinis de Martinez 1974
Santa Fe	Santa Fe: General Belgrano city park [5]	-60.7133	-31.6633	—	—	—	**NR:** 1 ind. (CDA 000.744), 16-vi-1988 (L. Acosta)
Santa Fe	Santa Fe: esplanade avenue in front of Technological University [5]	-60.6747	-31.6177	—	—	—	**NR:** 12 ind. (CDA 000.842), 17-vi-1988 (L. Acosta)
Santa Fe	Villa Constitución, Isla del Sol	-60.3257	-33.2165	—	—	4, 7	**NR:** 14 ind. (CDA 000.847), 2-iii-2007 (L. Acosta, M. García)
Santa Fe	Villa del Medio, left bank of Arroyo del Medio	-60.2683	-33.2840	6, 8	—	7	**NR:** 2 ind. (CDA 000.848), 2-iii-2007 (L. Acosta, M. García)
Buenos Aires	San Nicolás	-60.2333	-33.3333	9, 11, 13, 16, 18	—	7	Guerrero 2012
Buenos Aires	Vuelta de Obligado Reserve, Salamanca cave	-59.8184	-<u>33.5919</u>	1, 10	—	—	Guerrero 2012
Jujuy	3 km from Caimancito	-<u>64.5597</u>	-23.7175	12, 14, 17, 19	—	15	**NR:** 9 ind. (CDA-F), 6-xii-2011 (J. Vergara, R. González-Ittig. L. Vaschetto)

[1] Coordinates of Carandazinho according to Straube (2010). It was cited as “Corumba, Distrikt Matto Grosso (Carandasiko)” by Roewer (1925, 1927).

[2] Because of the imprecision of Roewer´s (1938) citation, coordinates were based on the additional sample: “Rio Apa, 4 km from confluence into Río Paraguay, 14-i-1987 (F. Pereyra), 5 ind. (CDA 000.364)”.

[3] Found in a multi-species aggregation with *Discocyrtus dilatatus* and *Holmbergiana weyenberghii* (Holmberg, 1876) (Sclerosomatidae, Gagrellinae).

[4] Under an unearthed stump, together with *D. testudineus, Parapachyloides uncinatus* (Sørensen, 1879), *Hernandaria scabricula* Sørensen, 1884 and *Metalibitia* sp.

[5] The reference of Mello-Leitão (1931) for “Santa Fe” is hereby replaced by these two more precisely georeferenced localities.

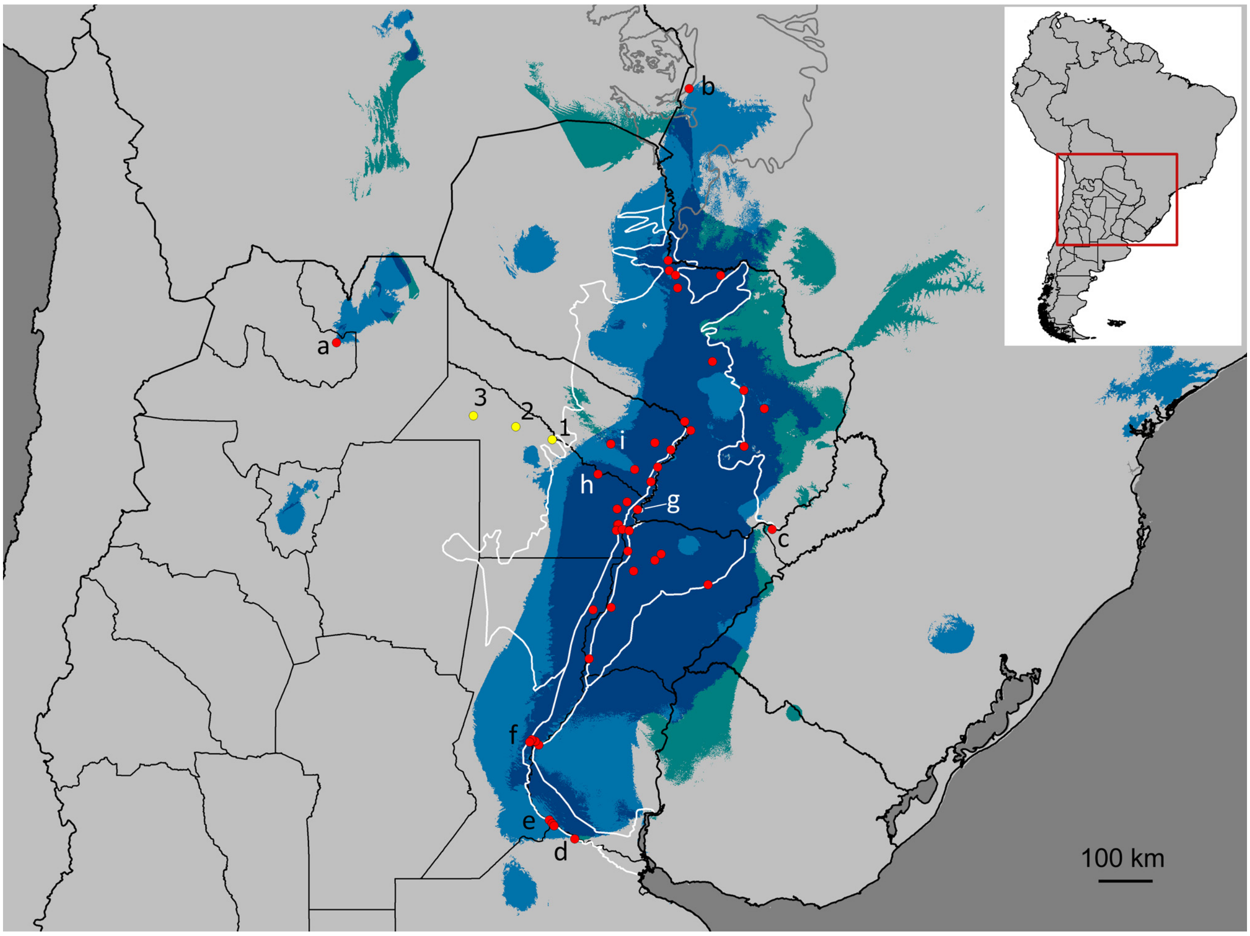

FIGURE 1. Locality records (red dots) and predicted distribution of *Gryne orensis* built with the default dataset (n=45). Map displays the overlay of models obtained with BIOCLIM (green; true-false, full extension) and MAXENT (light blue; single run, binary), overlapping areas in dark blue. White outline: Humid Chaco and Paraná flooded savanna; grey outline: Pantanal (ecoregions according to Olson *et al.* 2001). Selected localities: a. Caimancito, b. Carandazinho, c. Posadas, d. Vuelta de Obligado, e. Villa Constitución-Villa del Medio-San Nicolás, f. Santa Fe (2 points)-Madrejón Don Felipe, g. Riacho de Oro (type locality), h. El Colorado, i. Pirané. Yellow dots in province of Chaco indicate the three tentative localities for El Impenetrable: Villa Río Bermejito (1), Las Hacheras (2) and Fuerte Esperanza (3).

are problematic, unless the species range is accepted to be unusually large. For example, Roewer (1923) reports material from "Brasilien (Bahia?)", while Roewer (1927) provides several distant localities: Caballo Cocho (in the Peruvian Amazonia!, 3º54.403'S 70º30.912'W), "Rio Tocantin" (assigned by Kury, 2003 to Cametá: 2º15.246'S 49º30.770'W) and the imprecise statement "Paraguay". Until vouchers of those records are examined, we prefer not to consider them in the final set for modeling. The reference for "Bahia Blanca" (Roewer 1912) should be disregarded too, because of being highly unlikely, with many suspect citations (Ringuelet 1959; Acosta 2002). In regard to "Corumbá: Carandazinho" (Roewer 1925, 1927), it is one of three collecting sites of Alfredo Borelli in the Mato Grosso (Giglio-Tos 1900, Salvadori 1900). Its location was long disputed, so we adopted here the assessment of coordinates given by Straube (2010). The indication of "[Enrico] Festa" as collector (Roewer 1925) seems an obvious mistake: we found no evidence that Festa ever visited the region (see *e.g.*, Peracca 1904), but, suggestively, harvestmen from Turin´s Museum reported by Roewer (1925) were collected by either one of the mentioned Italian naturalists. For that material, an old printed catalogue merely states: "Gryne arensi (sic) Soer. (Op. 44) (s. 1) Corumbà (Matto Grosso). Det. Roewer 1925". Carandazinho is the only record that extends the species range far into the Pantanal ecoregion (Fig. 1), an area showing diffuse Chacoan influence, but especially a marked ecotonal character (Pott *et al.* 2011). Among the newest references, that for El Impenetrable (Guerrero 2012) deserved a special treatment, as stated above. "El Impenetrable" is the name of a not well delimited, 40,000 km^2 large region in the Semiarid Chaco (Basterra 2004, Greenpeace 2012), and such an imprecise statement would normally be enough to discard it for modeling (our default model was actually built without any point referable to

El Impenetrable). However, considering its probable meaning in support or against the disjunction hypothesis, an attempt was made to take this reference into account. In the 1970s (the material cited was collected in 1973), roads and paths in El Impenetrable were relatively scarce with far fewer than those available today. Hence the above proposed three putative locations were selected considering accessibility in 1973, and representing a kind of gradient, from the mild Humid Chaco into the inhospitable Semiarid Chaco (Fig. 3): Villa Río Bermejito (close to the boundaries of the mentioned Chacoan ecoregions: Brown *et al.* 2006), Las Hacheras in between, and near Fuerte Esperanza (a locality founded in 1978, indeed).

Bioclimatic profile. Values that describe the range of climatic conditions suitable to *G. orensis*, as extracted from the record set, are summarized in Table 2. Overall, climatic values in the species profile reflect conditions typical for subtropical to temperate humid climate (mean annual temperature ranged between 17.1°C and 25.9°C; annual precipitation between 790 and 1768 mm). Curves of cumulative frequencies are either normal or slightly sigmoid for most variables (13 out of 19 – those describing pure mean or extreme climatic values), suggesting little dispersion in spite of the geographical extension (except for the outliers, when present). This is especially remarkable for six precipitation variables with normal curves (Table 2). Skewed curves affect variables related to climatic stability, suggesting most localities concentrated at high (bc4, temperature seasonality) or low values (bc3, isothermality; bc15, precipitation seasonality). The only variable clearly bimodal is bc18, but no evident correlation for this behavior was found. Number of outliers is generally low, but for some variable types, presence of outliers often affects similar groups of neighboring localities. For example, the southernmost points (Vuelta de Obligado, San Nicolás, Villa del Medio, Villa Constitución; Fig. 1) are consistently the coldest – they are outliers for bc1, bc5, bc6, bc8 to bc11. In some of the same variables (bc1, bc8, bc9), northern localities (Corumbá, some Paraguayan sites) are grouped as the warmest outliers.

TABLE 2. Bioclimatic profile of *Gryne orensis* (n=45, points for El Impenetrable not included) (BIOCLIM): basic statistics of the 19 bioclimatic variables, along with 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 (T°) in Celsius degrees (ºC), precipitation in mm. Abbreviations of bioclimatic variables (bc x) as in text and Table 3. 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	21.67	17.09–25.87	8.78	2.134	S	8–5
(bc 2) Mean monthly T° range *	11.64	10.44–13.42	2.98	0.681	N	1–3
(bc 3) Isothermality (2/7 x 100) *	50.39	47.10–66.27	19.17	3.791	sk–	0–2
(bc 4) T° seasonality (STD x 100) *	420.09	223.91–485.40	261.49	58.607	sk+	1–0
(bc 5) Max T° of warmest month *	33.30	31.00–34.60	3.60	1.014	sk+ [a]	6–0
(bc 6) Min T° of coldest month	10.50	5.30–16.90	11.60	2.722	N	4–1
(bc 7) T° annual range (5–6)	22.90	16.70–26.00	9.30	2.226	S	1–0
(bc 8) Mean T° wettest quarter *	24.35	20.33–28.22	7.88	1.865	S	3–5
(bc 9) Mean T° driest quarter *	16.55	11.33–23.00	11.67	2.854	S	4 –5
(bc 10) Mean T° warmest quarter *	26.72	22.98–28.62	5.63	1.430	sk+	8–0
(bc 11) Mean T° coldest quarter	16.55	11.33–22.73	11.40	2.694	S	8–1
(bc 12) Annual precipitation	1246	790–1768	978	201.603	N	1–3
(bc 13) Precipitation wettest month *	160	118–226	108	20.114	N	0–1
(bc 14) Precipitation driest month *	41	4–95	91	14.641	N	1–3
(bc 15) Precipitation seasonality (CV) *	39.82	16.83–91.82	74.99	10.821	sk–	1–2
(bc 16) Precipitation wettest quarter	442	301–591	290	58.621	N	4–1
(bc 17) Precipitation driest quarter	139	18–329	311	51.564	N	1–4
(bc 18) Precipitation warmest quarter	403	265–479	214	59.262	B	4–0
(bc 19) Precipitation coldest quarter *	139	18–329	311	51.511	N	1–4

[a] Cumulative curve of bc5 looks almost like a 45º diagonal, most value ranges showing relatively high frequecy; it increases only gradually towards the upper end.

Climatic divergence at Caimancito, the westernmost and sole point in the Yungas, does not affect temperature variables, even standing close to median for bc1 (annual mean temperature), bc3 (isothermality) and bc4 (temperature seasonality); on the contrary, precipitation is the lowest, both annually (bc12), in the driest month (bc14) or quarter (bc17), and in the coldest quarter (bc19) (Table 1). It is to be noted that precipitation variables appear more restrictive than temperature ones only in NWA. As for the northernmost point (Carandazinho, Mato Grosso do Sul), it appears extreme (as end value or as outlier) in many temperature variables (bc1, bc3, bc4, bc6 to bc9, bc11), but it is an outlier in just one precipitation bc denoting seasonality (bc15). On the other side, several sites near the type locality (Colonia Dalmacia, Monte Lindo Grande, Picada Guaycurú, Colonia Benítez, Río Tragadero, Riacho de Oro, El Colorado) very often represent median values of bc curves (Table 1); this indicates the sector as fairly average for the overall climatic conditions, as reflected by the high suitability degree displayed in predictive maps (Fig. 2). With a standard envelope cutoff (0.025 percentile), 26 points out of 45 (57.8% overall) remain inside all possible bidimensional envelopes, the rest falling outside in at least one envelope. Some extreme geographic points, like Caimancito (Yungas), Carandazinho and Vuelta de Obligado keep being outsider even with relaxed cutoffs (0.005 to 0.0005), emphasizing their divergence with the bulk of the records.

It was expected that, if included in the profile analysis, El Impenetrable would show in some way a strong bioclimatic divergence. However, this proved true just for Fuerte Esperanza (the most rigorous locality), and for a few variables alone, which reflect temperature differences along the year, or a reduced precipitation rate: bc2 (mean monthly temperature range—otherwise represented by San Francisco de Laishi), bc5 (maximal temperature of warmest month—Pirané), bc7 (temperature annual range—Villa Constitución, Villa del Medio and San Nicolás), bc12 (annual precipitation—Caimancito) and bc13 (precipitation of the wettest month—San Nicolás). In addition, Fuerte Esperanza was outlier for bc14–bc16 and bc19. Las Hacheras and Villa Río Bermejito, only ranking as outliers for bc2 and bc15, did not evidence any substantial difference with the main range.

Potential range. Predictive maps yielded by BIOCLIM and MAXENT do not match exactly, although they have a broad overlap (Fig. 1). Results with BIOCLIM fit in general more tightly to the actual records, especially in the southern part of the range and in NWA. As a remarkable difference, BIOCLIM predicts some divergent projections in the North, like the broad one on the Paraguayan-Bolivian boundary, towards (but not reaching) the Yungas in southern Bolivia. It is also worth noting the ample prediction in the latter area, whilst suitability on the Argentinean Yungas is much weaker. Potential range obtained with MAXENT (Figs. 1, 2) appears in general more permissive: it reaches generously the southernmost (and beyond) and northernmost points, and the strip embracing the Humid Chaco is wider. Prediction in NWA consists of two main patches, together with a third spot farther in Bolivia (Figs. 1, 2): they are spread in the province of Tucumán in the South, the province of Salta (Caimancito area) in the middle, and the Bolivian Yungas in the North. The middle patch near Caimancito is well defined in the default run (Fig. 1), but weaker in the 20-replicates median (Fig. 2). A closer inspection of the 20 replicates shows some dependence of the middle sector on the actual training records. Five runs resulted with this patch not recovered; of those, three lacked the Caimancito record, as expected, but two contained it, indicating it can fall outside of the suitable area even if present in the dataset. All remaining runs had the point included, but even so, seven resulted in suitable areas not strictly embracing the record (three with the suitable area represented by just scattered grid cells). Only eight out of 17 runs that contained Caimancito in the dataset had the point within a well-defined middle patch. All 20 runs consistently recovered the Tucumán spot; the Bolivian sector was absent in three runs, and was weakly recovered in four runs. In other words, prediction was more stable in Tucumán and Bolivia than around Caimancito. In no case did maps obtained with MAXENT show such a transverse strip between Paraguay and Bolivia, but instead, an intermediate predicted area in the middle of the Paraguayan Chaco was fairly constant (besides some isolates in Brazilian territory). Models insinuated an interesting digitation towards central Chaco (Figs. 1, 2), considering that points at El Impenetrable were not present in this dataset. Highest suitability with MAXENT concentrates along the Paraguay-Paraná axis (Fig. 2), from Río Apa southwards, especially in provinces of Chaco and Formosa, *i.e.*, around the records holding median values in the overall distribution. The use of a more relaxed threshold, like "Maximum training sensitivity plus specificity" meant a limited enlargement of the predicted area (larger in the South). Interestingly, with "Minimum training presence" (even more permissive), the small Chaco digitation gets larger and nearly encompasses two localities of El Impenetrable (Fig. 2). Models obtained with MAXENT performed consistently well, all training runs built with the complete dataset having high AUC. The overlay of the 20 replicate models (not shown), as the median model shown in Fig. 2, agreed well with the single-run model made with all 45 records. AUC of all 20 runs scored as excellent: average training AUC, 0.9762 (range 0.9717–0.9800).

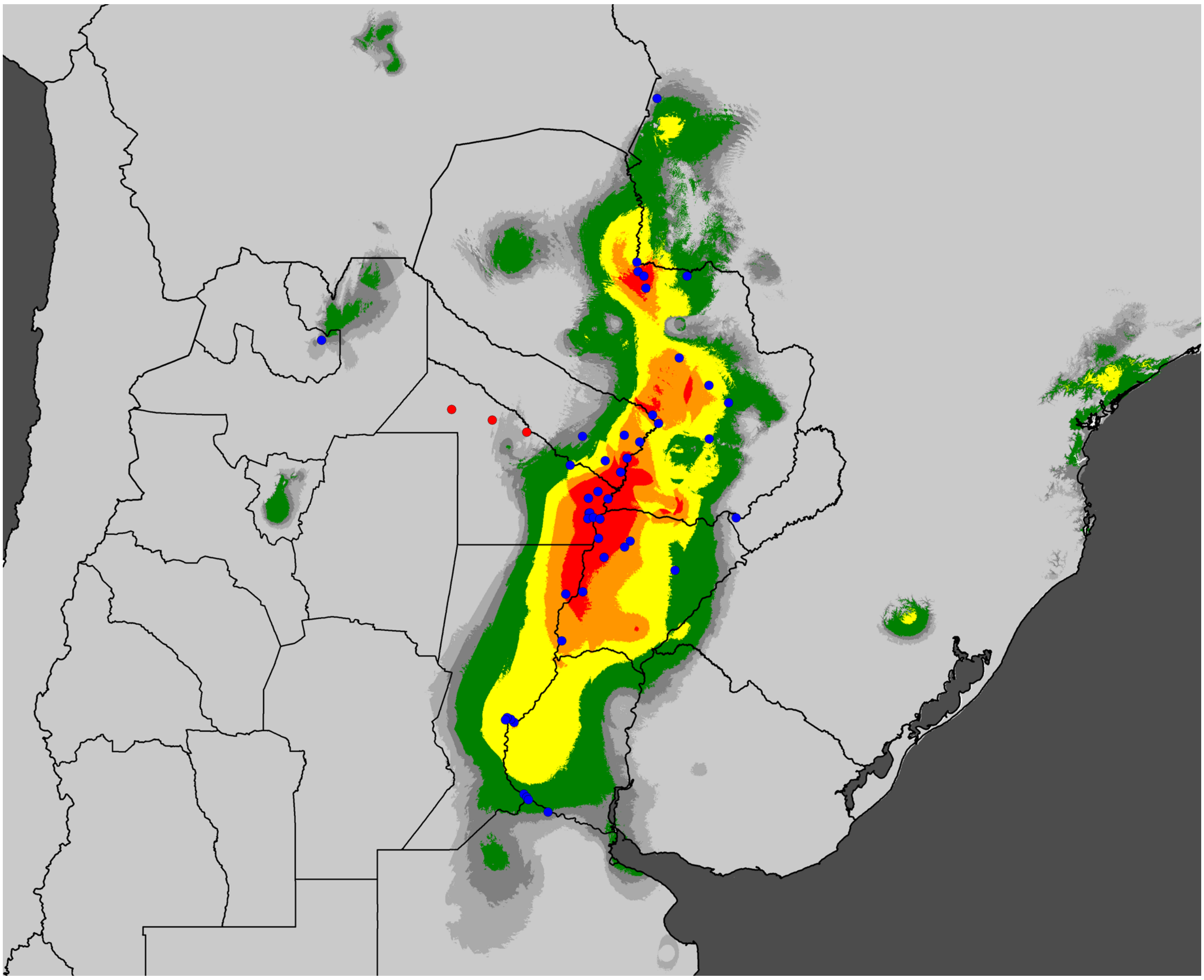

FIGURE 2. Potential distribution model of *Gryne orensis*: median values of the 20-replicates run with MAXENT (default dataset, random test percentage 20%); thresholds displayed are the average of the 20 replicates (average training AUC 0.9762). In the random selection of training points, Caimancito was used in 17/20 runs, Carandazinho in 14/20 runs. Suitability levels: green: 0.15–0.36; yellow: 0.36–0.58; orange: 0.58–0.72; red: above 0.72. Grey: areas below the default threshold (equal training sensitivity plus specificity); darker grey: suitability above 0.112 (maximum training sensitivity plus specificity); medium grey: above 0.0801 (minimum training presence). Blue dots: training records; red dots in province of Chaco: tentative records at El Impenetrable (not used in this model).

Importance of variables. As shown on Table 3, only two variables rank among the most relevant in all four estimators: bc4 (temperature seasonality) and bc14 (precipitation of the driest month). In a second level, bc2 (mean monthly temperature range), bc19 (precipitation of the coldest quarter), and bc15 (precipitation seasonality) also prove a meaningful influence overall, though not necessarily for each and every estimator analyzed. In other words, the most important predictors include three variables describing climatic regularity along the year (bc4 on top, to some extent also bc2 and bc15), and two bc suggesting that low precipitations in driest/coldest periods may be also critical (bc14, bc19). Some relevance is suggested by two variables presumably accounting for the influence of highest extreme temperatures (bc10, and especially bc5). On the contrary, precipitation in wet periods (bc13) or temperatures in dry ones (bc9) show little or no significance in these models. Pure annual average (temperature) or cumulative (precipitation) values were already dismissed as predictors at the correlation analysis stage, due to their overall poor scoring in the preliminary run. Temperature and precipitation agreed in their limiting character when moving from the Mesopotamia into the sub-xeric Chaco. As stated above, Fuerte Esperanza, our most rigorous choice to represent El Impenetrable, is at or near end values in six precipitation predictors (describing both absolute values and seasonality), as well as two temperature variables (bc5 among these) which best account for the extreme high temperatures. Local relevance of bc5 is supported by a quick inspection with the analysis “Bioclim—Most limiting factor" (not shown in this paper), in which this variable appears as a narrow fringe bordering the whole Chaco gap (*i.e.*, indicating it as the most limiting there). In the Yungas around Caimancito, reduction of precipitation both annually and in cold/dry periods seems the most influential locally.

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

Variable	Percent bc contribution	Permutation importance	Training gain without	Training gain with only	Score
bc4—temperature seasonality	23.016	**32.751**	2.366	0.843	54.244
bc14—precipitation driest month	**39.634**	13.345	2.345	**1.170**	51.804
bc2—mean monthly T° range	3.236	24.244	**2.337**	0.552	25.695
bc10—mean T° warmest quarter	21.247	0.062	2.376	0.533	19.467
bc19—precipitation coldest quarter	2.036	11.427	2.340	0.814	11.938
bc5—max T° warmest month	0.189	12.334	2.375	0.549	10.697
bc15—precipitation seasonality	8.801	0	2.380	1.080	7.500
bc8—mean T° wettest quarter	0.964	4.376	2.355	0.341	3.325
bc13—precipitation wettest month	0.493	1.079	2.371	0.984	0.185
bc3—isothermality	0.382	0.381	2.378	0.572	-1.042
bc9—mean T° driest quarter	0	0	2.384	0.535	-1.849

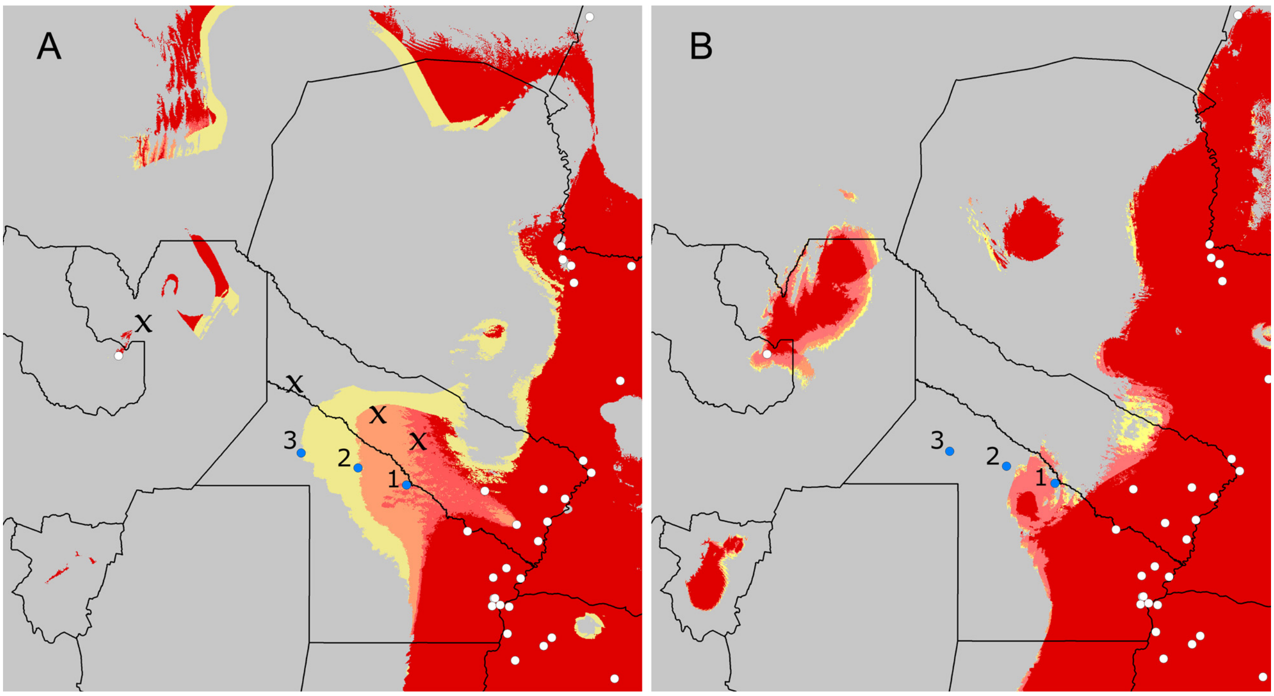

FIGURE 3. Binary distribution models built with BIOCLIM (A) and MAXENT (B), showing the region around the Semiarid Chaco. Maps are overlaid to display changes of the default model (intense red) when points at El Impenetrable are added in the dataset (one at a time): light red, area added with Villa Río Bermejito (1); orange, area added with Las Hacheras (2); yellow, area added with Fuerte Esperanza (3). White dots: localities of the default dataset; blue dots: tentative records at El Impenetrable (numbers as referred to above). Crosses in 3A: localities sampled in the dry Chaco that yielded negative results for Mesopotamian harvestmen.

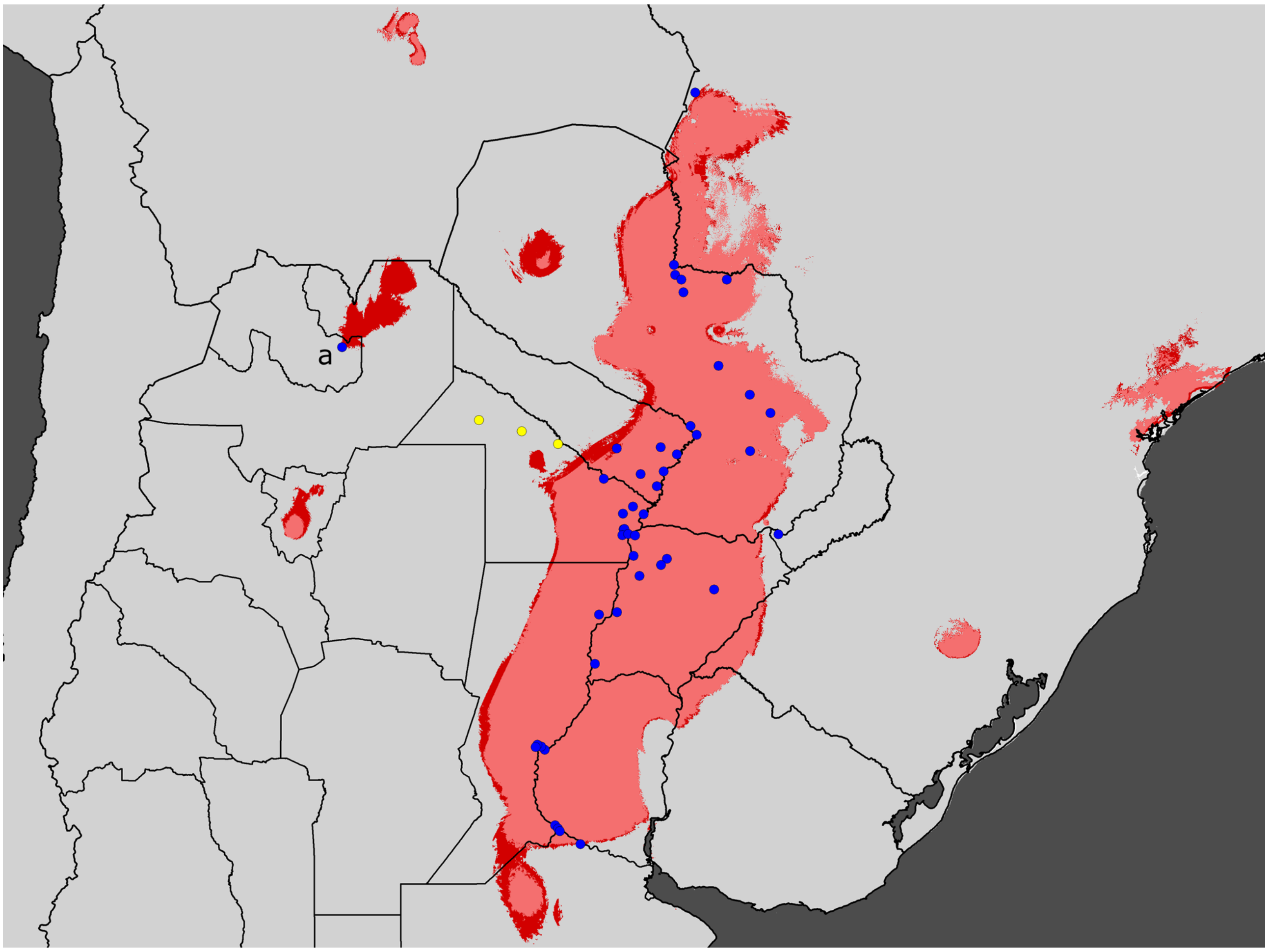

FIGURE 4. Overlay of two binary MAXENT models, one built with the default dataset (45 points, AUC: 0.975), the second with record at Caimancito (a) deleted (44 points, AUC: 0.977); shared areas by the two models (overlap) are displayed in light red; areas lost with the smallest dataset are shown in dark red. Blue dots: training records, yellow dots in province of Chaco: tentative records at El Impenetrable (not used in this model).

The trans-Chaco disjunction. Analyses using the default database support the separation between the main Mesopotamian range and the Yungas, both with BIOCLIM and MAXENT (independent on how relaxed the selected threshold is). Both methods agree in insinuating a small westward digitation in Chaco or Formosa provinces, in some way associated with the lowest course of the Bermejo River or neighboring streams (Figs. 1, 2). This is especially remarkable if using a highly relaxed threshold in MAXENT (Minimum training presence), in which case the modest projection turns larger to cover two of the three putative sites at El Impenetrable, though never joining the Yungas (Fig. 2). The next step was then to investigate the effects of the inclusion of one tentative point in the aforementioned region on the disjunct pattern. Again, there were differences between methods. BIOCLIM showed a direct correlation with each locality added (Fig. 3 A). Either with the inclusion of Villa Bermejito or Las Hacheras, the former projection thickened as to embrace (marginally) the involved locality. The inclusion of Fuerte Esperanza had stronger effects because it not only enhanced a bit more the projection (up to that point), but also caused a marginal expansion of predicted ranges all around the Chaco. In any case, even using this extreme assumption for El Impenetrable, the disjunction was maintained (Fig. 3 A). With MAXENT, the behavior of the predictions was not as straightforward. The enlargement of the middle Chaco projection is very similar in all cases, regardless of which point was selected for El Impenetrable: it covers Villa Río Bermejito and approaches Las Hacheras, but always leaves Fuerte Esperanza far away (Fig. 3 B). For all three points, "Maximum training sensitivity plus specificity" as an alternative threshold gave more restrictive results. Only if the highly permissive "Minimum training presence" threshold was set, and strictly for Fuerte Esperanza, broad connections across the Paraguayan Chaco and along Pilcomayo and Bermejo Rivers appeared, together with many other unrealistic widenings of ranges throughout (in provinces of Córdoba and most of Buenos Aires, for example). "Minimum training presence" produced similar predictions for Villa Río Bermejito and Las Hacheras, resembling that obtained with BIOCLIM at the latter site; *i.e.*, the disjunction was kept. Potential areas predicted in NWA demonstrated to be highly dependent on the deletion of the record at Caimancito (single run, n=44), as expected in the light of results of the random 20-replicates above. With MAXENT, when that point is omitted the entire Mesopotamian range suffers generalized clipping, as in most sectors in the Yungas (Fig. 4). Nonetheless, MAXENT still predicts one small sector in the province of Tucumán using Mesopotamian records alone (the southern patch, constant in the 20-replicates). In contrast, models built in BIOCLIM without Caimancito are completely unable to recover any suitability in the Yungas (with the exception of very few scattered grid cells of lowest suitability in Tucumán, and only when the dataset comprised Fuerte Esperanza).

Discussion

Harvestmen stand for well-appreciated models in biogeography, principally because of the remarkable endemism shown by many species, like those of the Brazilian Atlantic forests, the Argentinean Yungas or the Peruvian Andes, sometimes with strikingly narrow areas (Acosta 2002, 2006; Pinto-da-Rocha *et al.* 2005). Mesopotamian harvestmen, in contrast, have been long recognized to possess extensive ranges, often spread over thousands of square kilometers (Acosta 2002, 2008). There is a physical background for this kind of range: living on such an endless plain, Mesopotamian harvestmen meet no effective geographical barrier to their spread, so environmental gradients start to play a more apparent role as range constraints. This renders them well-suited for potential distribution modeling. As with other Mesopotamian species (Acosta 2002, 2007), the worsening of suitable current conditions towards the Semiarid Chaco proved once again to be one major bioclimatic boundary for *G. orensis*. The finding of a separate population in NWA emerges as a relevant fact that strengthens the evidence for the disjunct pattern, already known for a few Mesopotamian harvestmen (Acosta 1995, 2002, 2008). Notwithstanding the presumed generality of the disjunction, some differences in the four harvestmen involved suggest that more than one historical event is probably needed to explain the pattern.

Both modeling methods consistently supported the plausibility of the disjunction for *G. orensis*. At the same time, results reveal some kind of "marginality" in the Yungas, as indicated by the difficulty of being predicted with Mesopotamian points alone. As seen, results with MAXENT were slightly better, although the prediction did not match the exact Yungas portion where the actual point belongs. BIOCLIM achieved a very weak prediction there, only with the help of the speculative record at Fuerte Esperanza. Predictability in the Yungas was already verified in other disjunct species, like *Discocyrtus prospicuus* and *D. dilatatus* (Acosta 2007, 2008, Acosta & Guerrero 2011, Vergara & Acosta, in prep.); additionally some "pure" Mesopotamian harvestmen show suitable areas projected in the Yungas as well (including, *e.g.*, *D. testudineus* and the gagrelline *Pectenobunus paraguayensis*; Acosta 2007). As for the core area itself, the potential range of *G. orensis* resembles closely the general pattern observed in most Mesopotamian species (insofar as enough records are available), *i.e.*, tightly arranged along the Paraguay-Paraná Rivers "hub", and from there expanding more or less to both sides. These results provide, for the first time, a comprehensive summary of climatic conditions that characterize the profile of *G. orensis*, a fact so far completely ignored in its details for most Neotropical harvestmen (Acosta 2008). Now there are values (as provisional as record points are) describing how much humidity and temperature this species needs, and how much seasonality or extreme climate it tolerates, as informed by the records themselves. For the moment, these results can be compared with only two species, *D. prospicuus* and *D. dilatatus* (Acosta & Guerrero 2011; Vergara & Acosta, in prep.). Despite many differences, one variable (bc4) ranks high for relative importance in all three species. Whether this represents a general trend among Mesopotamian harvestmen needs to be further tested.

The inclusion of tentative records for El Impenetrable led us to interesting remarks. Our results suggest that the original record (whose precise location is unknown) most likely comes from a site closer to the Humid Chaco (Las Hacheras and Villa Bermejito with similar chances); a capture in middle of the sub-xeric Semiarid Chaco was much less supported. Even with El Impenetrable considered (*i.e.*, implying an artifactual enhancement of the tolerance limits in the dataset), models were, at reliable threshold settings, unable to falsify the disjunction hypothesis. These results seem endorsed by the severity of climatic conditions of the Semiarid Chaco, with extremely high temperatures and evapotranspiration rates (the latter not included in our study) (Ragonese &

Castiglioni 1970). Most of this ecoregion, encircled by the 47º isotherm of maximal temperatures (with absolute record—48.9ºC—in eastern province of Salta), was called the "South American pole of heat" (Prado 1993). Besides our reasoning for selecting localities that were accessible in 1973, it seems clear that, the farther we move into the Semiarid Chaco, the more that suitable habitats will be confined to riversides for *G. orensis*. Our own captures of *G. orensis* in some Mesopotamian localities (Villa Constitución; Santa Lucía; Colonia Dalmacia; El Colorado), as well as references in the literature (Valentinis de Martínez 1974), indicate this long-legged cosmetid as a frequent dweller of floodplains, on the margins of permanent or intermittent streams. An intricate network of tortuous rivers and "riachos" in the Humid Chaco, full of swamps and abandoned meanders, bordered by gallery forests, offers optimal ecological conditions for *G. orensis* in the eastern side of provinces of Formosa and Chaco (and adjacent areas in Paraguay); these favored conditions rapidly diminish towards the west (Ragonese & Castiglioni 1970, Ramella & Spichiger 1989, Nores 1992). Such micro-environmental details cannot be properly accounted for by methods used in the present study, so the continuity of the species across the Chaco (*e.g.*, along riparian vegetation) remains here untested.

Observations at hand, however, do not support the continuity. Surveys across the Semiarid Chaco are scarce, trapped in a "sampling vicious-circle" (the meager success, due to aridity, will not attract much interest of harvestmen collectors there). The only semi-systematic collecting in the region was carried out by us, consisting of an E–W transect along National Highway 81 in the province of Formosa (the same followed by Nores 1992), with some detours to Bermejo River. These samples retrieved a picture that might be considered consistent to the alleged Chaco gap: in our fieldwork Mesopotamian harvestment abruptly "vanished" from El Colorado onwards, maintaining the negative recording in all surveyed Chaco localities along almost 500 km. Negative localities included: Villa Rio Bermejito; meander near Estanislao del Campo; near Las Lomitas; Highway 39, bridge over Teuquito river; 50 km S Ingeriero Juárez—only samples of the Chaco cosmetid *Gnidia holmbergii* (Sørensen, 1884) in the latter—; and Pichanal (the first one indicated as 1 in Fig. 3 A, the rest depicted as crosses). Caimancito was our first site where either a Mesopotamian or Yungas harvestman reappeared. In any case, the disjunction of *G. orensis* is a provisional statement that needs consolidation in more parts of the range. As Silva (1994) warned for avian distribution, the gap in the Argentinean Chaco does not mean that Mesopotamian and Yungas ranges cannot be connected elsewhere, for example, through central Brazil or southern Bolivia, where harvestmen distribution is still poorly documented. The transverse "bridge" insinuated by the BIOCLIM model (Fig. 1, but not recovered by MAXENT) should at least draw our attention as a potential area of future research.

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