Impact of climate change on spider species distribution along the La Plata River basin, southern South America: projecting future range shifts for the genus *Stenoterommata* (Araneae, Mygalomorphae, Nemesiidae)

Nelson E. Ferretti^{1,*}, Miquel Arnedo² & Alda González¹

- 1) Centro de Estudios Parasitológicos y de Vectores CEPAVE (CCT-CONICET-La Plata), Boulevard 120 s/n (e/60-64), AR-1900 La Plata, Argentina (*corresponding author's e-mail: nferretti@conicet.gov.ar)
- ²⁾ Departament de Biología Evolutiva, Ecologia i Ciències Ambientals and Institut de Recerca de la Biodiversitat (IRBio), Universitat de Barcelona, Av. Diagonal 643, ES-08028 Barcelona, Spain

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The La Plata River basin comprises the second largest fluvial system in South America and includes the southernmost remains of the "Atlantic Forest Biodiversity Hotspot". We used species distribution modelling to evaluate potential effects of climate change on six species of *Stenoterommata*. Changes in the size of suitable climatic regions and numbers of known occurrence sites were evaluated within the distribution limits of the studied species. We used MaxEnt (program for modelling species distributions from presence-only species records) to predict current and future suitable areas. Two representative concentration pathways (RCP6.0 and RCP8.5) that represent different greenhouse gas concentration trajectories were modelled for the years 2050 and 2070. The isothermality, temperature seasonality and variation in seasonal precipitation were found to be the top three variables that affect the range of *Stenoterommata* species. Highly suitable habitat was found to increase with time for most species, except for *S. platensis*, whose distribution area may shrink by more than 50% by the year 2070.

Introduction

The Earth's climate is changing at a considerable rate and, according to the climate change scenarios, the changes may be quite pronounced in the subtropical and temperate regions (Christensen *et al.* 2007, Allison *et al.* 2009, Schlaepfer *et al.* 2017). Average global temperature increased by

0.85 °C between 1880 and 2012, and it is likely to increase further by either 0.3–1.7 °C (assuming that global annual greenhouse gas emissions peak between 2010–2020 and declining thereafter), or 2.6–4.8 °C (assuming that emissions continue to rise throughout the 21st century) relative to 1986–2005 by the end of this century (IPCC 2013, Jiang *et al.* 2016). It has been predicted

that this warming would significantly alter the water balance of the South American rainforest (Hirabayashi et al. 2008, Knapp et al. 2008). The La Plata River basin comprises the second largest fluvial system in South America. It also includes the southernmost remains of the "Atlantic Forest Biodiversity Hotspot", one of the most biodiverse and threatened ecosystems in the world (Ribeiro et al. 2011, Arzamendia & Giraudo 2012). Climate change and its effects such as an increase in precipitation have already caused problems in this area since the 1970s, when the average annual river flow increased considerably in some stretches of the rivers. The main effects of the increase in precipitation and river flow were: (i) soil erosion, (ii) increase in water level and flood frequency, (iii) changes in river beds and riparian-environment conditions, and (iv) change in water quality due to re-suspension of sediments during floods (Calhman 2008, Herrera et al. 2014). In recent decades, human activities such as building dams, forestry, farming, fishing, poaching, grazing, urbanization, extraction of wood and tourism increasingly disturbed the La Plata River basin, compromising the conservation status of riparian habitats (Mugetti et al. 2004, Arzamendia & Giraudo 2012).

Currently, in response to changing climate populations shift, contract, expand or become fragmented (Chen et al. 2011, Jiang et al. 2016, Girini et al. 2017). Species' survival in changing climate depends on their ability to adapt to new conditions and/or to disperse to more suitable habitats (Martínez-Meyer et al. 2004, Tingley et al. 2009, Dullinger et al. 2012, Nori et al. 2015). Because of their long life cycles, specific habitat preferences (Ferretti et al. 2012a) and low dispersal capabilities (Coyle and Icenogle 1994, Ferretti et al. 2014), mygalomorph spiders are particularly vulnerable to environmental changes. Therefore, displacement and/or contraction of suitable habitats may unfavourably change their conservation status. In addition, factors such as habitat landscape properties, regular flooding or human disturbance may also represent a threat to the spider species (Hampe 2004, Gallé et al. 2011, Radosavljevic & Anderson 2014). The Neotropical genus Stenoterommata includes medium to small-sized species with restricted geographical distributions. Most species live in burrows constructed under logs or stones as well as in open spaces, usually along rivers or streams, and even in floodplains (Goloboff 1995, Schwerdt & Copperi 2014). The genus includes 15 species, distributed in Argentina, Brazil and Uruguay (Guadanucci & Indicatti 2004; *see* also http://wsc.nmbe.ch), six of which are restricted to the La Plata River basin (Ferretti *et al.* 2012a, 2014).

Exposure to climate change may vary among species and areas, hence understanding this variation is a key to designing accurate conservation policies (Zank et al. 2014, Nori et al. 2015). However, this has not yet been explored in the La Plata River basin or in this group of spiders. Therefore, we aimed to evaluate in what way changing climate conditions would affect the Stenoterommata species habitat and geographic distribution in the La Plata River basin. To achieve this, we used species distribution modelling (SDM) tools to investigate potential effects of climate change predicted for the years 2050 and 2070 under different climate-change scenarios on their diversity in the La Plata River basin. Specifically, we compared present-day modelled Stenoterommata distributions and distributions predicted for the future. We also evaluated the extent of changes in the size of suitable habitats for each species, and how many of the known populations of each species would in future be exposed to unfavourable climatic conditions. The results of this study should provide useful information for future monitoring and conservation efforts across this ecosystem.

Material and methods

Studied species and occurrence data

Based on their distribution limited to the La Plata River basin, the following six *Stenoterommata* species were selected for the study: *S. crassistyla*, *S. iguazu*, *S. palmar*, *S. platensis*, *S. tenuistyla* and *S. uruguai*. The remaining species of the genus are either known from single localities or their distributions extend outside the La Plata River basin (Indicatti *et al.* 2008, 2017).

Presence localities and geographical coordinates were obtained primarily from the literature (Goloboff 1995, Indicatti *et al.* 2008, 2017, Ferretti *et al.* 2010, 2012b, 2014, Ferretti & Pompozzi 2016) and validated by reviewing voucher specimens deposited in the collections of Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" (MACN-Ar) and Museo de La Plata (MLP), Buenos Aires, Argentina. Many additional records were obtained from the Uruguayan arachnid collection at Facultad De Ciencias (FCE-MY), Universidad de la República, Montevideo, Uruguay. When those sources did not provide precise geographic coordinates, we acquired coordinates for the localities from Google Earth (http://earth.google.es/) and Geody (www.geody.com).

Environmental data and climatic variables

In total, 19 bioclimatic variables were obtained from the WorldClim ver. 2.0 database (www. worldclim.org/bioclim), at a resolution of 30 arc sec (Fick and Hijmans 2017). From those, using Pearson's correlation as implemented in ENM-Tools ver. 1.4.4, we selected a subsample (Warren et al. 2008). The choice of a variable from a correlated (r > 0.75) pair (or trio) was done in a preliminary run of the model with all the variables, retaining those with the best percent contribution and permutation importance in MaxEnt. Additionally, the selected variables were considered to be more relevant regarding physiological and ecological requirements of the Stenoterommata species. This procedure was performed separately for each species. The following subset of bioclimatic variables was selected: Bio3 = isothermality, Bio4 = temperature seasonality, Bio10 = mean temperature of warmest quarter, Bio15 = precipitation seasonality, Bio17 = precipitation of driest quarter, Bio18 = precipitation of warmest quarter, and Bio19 = precipitation of coldest quarter. In the case of S. uruguai, due to the small number of presence records, a subset of the four most relevant bioclimatic variables was selected based on percent contribution and permutation importance.

To assess the effects of climate change, projected climate scenarios for the years 2050 and 2070 were inferred using the data from the

Worldclim database. We used the most recent data from CMIP5 (https://cmip.llnl.gov/cmip5/) for the Community Climate System Model (CCSM), which were evaluated as best and tested by many (Radić & Clarke 2011, Farzaneh et al. 2012, Zank et al. 2014). In addition, we used two Representative Concentration Pathways (RCPs) 6.0 and 8.5, which simulate climate system responses to increasing levels of greenhouse gases based on projected human population size, technological advances and socioeconomic trends. RCP8.5 projects considerable changes in climate, while RCP6.0 moderate.

Modelling procedure

The climatic data we used to build the models covered not only the La Plata River basin but also adjacent regions in Paraguay, Uruguay, Brazil, and all Argentina and Chile. We predicted the distribution of Stenoterommata species under different climate scenarios using MaxEnt 3.3.3k (Phillips et al. 2004, 2006), which searches for the maximum entropy density using Robust Bayes Estimation and requires only presence points as input data (Elith et al. 2011). MaxEnt estimates the relation between species presence and environmental variables in a geographic space and draws a model of environmental suitability for the occurrence of a given organism. We estimated the present-day distributions of suitable climatic conditions for Stenoterommata species, predicted future climatic conditions and then compared the present-day and future distributions of suitable climatic conditions. We ran the MaxEnt software using the default settings, which have been validated in studies involving a variety of species and environmental data (Phillips and Dudík 2008, Zank et al. 2014, Jiang et al. 2016). We set the random training data as 100% of the sample given the small number of occurrence records. The output of the MaxEnt model gives continuous habitat suitability, and hence a threshold must be set to define the predictive presence or absence of a species. In this study, we selected the "equal training sensitivity and specificity" option, which minimizes the absolute differences between sensitivity and specificity (Cantor et al. 1999). We set the run to 2000 maximum iterations, allowing the logistic

output format to remove the duplicates from the same grid cell. The present-day and future estimated suitable areas were calculated based on the binary modelling results obtained in MaxEnt. The distribution maps were created by importing MaxEnt models into DIVA-GIS ver. 7.5 (http:// www.diva-gis.org) and then edited with the free software QGIS ver. 2.18 (www.qgis.org). An update (2003) of the map of the ecoregions of the world presented by Olson et al. (2001) was used to clump the obtained models. To evaluate model performance for each species, we calculated the AUC values (Area Under the receiver operating characteristics Curve), which are frequently used to evaluate distribution models based on presence-absence algorithms (Peterson et al. 2011) despite known limitations as a measure of model performance (Franklin 2009). The program automatically calculates statistical significance of the prediction, using a binomial test of omission (Baldwing 2009).

Results

The models of suitable climatic areas yielded high AUC values, ranging from 0.96 to 0.99. Such high values for all models suggest that we accurately captured spider habitat relationships.

The bioclimatic variables that provided the highest contributions to the climatic suitability models were: isothermality (the diurnal temperature range divided by the seasonal temperature range) (Bio3), temperature seasonality (Bio4), and precipitation seasonality (Bio15) (Table 1). Bio3 was among the two most important bioclimatic variables for half of the studied species.

The estimated present-day suitable areas ranged from 138 699 km² for *S. uruguai* to 494 924 km² for *S. palmar* (Fig. 1–6), the average for most of the species being always < 500 000 km² (Table 2).

Predictions for the years 2050 and 2070 indicated the areas with suitable climatic conditions would increase or remain unchanged for most of the studied species (Figs. 2–3, 6). The area of habitats suitable for *S. crassistyla* and *S. platensis* would decrease (Table 2). The area decrease in case of *S. crassistyla* would not be that pronounced, but in case of *S. platensis* a nearly 50% reduction was predicted for the year 2070 (Figs. 1, 4 and Table 2).

The RCP8.5 scenario usually yielded greater increases in suitable areas in 2070. For example, the area of habitats suitable for S. tenuistyla and S. uruguai would double (Figs. 5–6 and Table 2). When examining the response curves of bioclimatic variables we found that the variables related to an increase in temperature seasonality (Bio3 and Bio4) led to an increase in the area of habitats suitable for S. tenuistyla. In case of S. uruguai, the suitable-habitat areas increased with an increasing precipitation (Bio15). Of the studied species, a considerable reduction in the area of suitable-habitat areas was found for S. platensis (Fig. 4): 30% and 50% reduction under the RCP6.0 scenario in the years 2050 and 2070, respectively. Additionally, the Maxent models under the RCP 6.0 and 8.5 scenarios for the year 2070 revealed that the climatic conditions at a number of known present-day locations (e.g., in northeastern Argentina) may no longer be suitable for S. platensis (Fig. 4). For the remaining species, most of the known present-day sites

Table 1. Percentage contributions of the most important climatic variables to the distribution models for each *Stenoterommata* species. Bio3 = isothermality, Bio4 = temperature seasonality, Bio10 = mean temperature of warmest quarter, Bio15 = precipitation seasonality, Bio17 = precipitation of driest quarter, Bio18 = precipitation of warmest quarter, Bio19 = precipitation of coldest quarter.

Species	Bio3	Bio4	Bio10	Bio15	Bio17	Bio18	Bio19
S. crassistyla	51.6	6.1	6.7	35.2	0	0.1	0.5
S. iguazu	13.4	22.8	13.5	23.6	26.7	0	0
S. palmar	62.7	3.5	14	19.8	0	0	0
S. platensis	0	47.9	6.7	35.5	6.5	3.4	0
S. tenuistyla	51.5	34.5	13.9	0.1	0	0	0
S. uruguai	·—	27.5	8.5	49.8	14.2	_	_

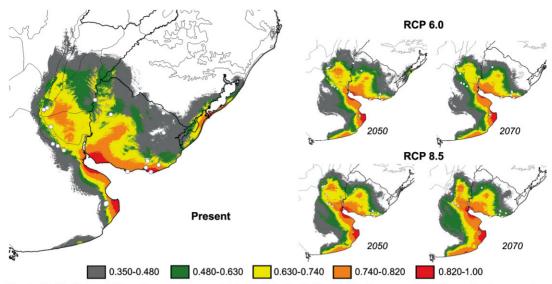


Fig. 1. Distributions of Stenoterommata crassistyla modelled with MaxEnt for the present and two climate scenarios (RCPs 6.0 and 8.5) for the years 2050 and 2070. Colours indicate habitat suitability from low (grey) to high (red).

remained above the presence thresholds in the 2070 projection.

We found that regardless of the scenario and year of projection, the areas suitable for *S. tenuistyla* and *S. uruguai* would considerably increase (Figs. 5–6 and Table 2). Also he areas suitable for *S. iguazu* and *S. palmar* would increase but to a lesser extent (Figs. 2–3 and Table 2).

Discussion

Here we present the first, highly accurate (all AUC scores greater than 0.9) models and poten-

tial distribution maps of mygalomorph spiders in the La Plata River basin for different climatechange scenarios.

As a result of climate change (depending on the scenario), areas of suitable habitats for the studied spiders in the La Plata River basin would change to some extent. Although a considerable decrease in suitable-habitat area was found for only one species, all the others would also face expansions and contractions of their suitable areas as a result of climate change.

The bioclimatic variables that contributed the most to the models, can be used to monitor changes in the environment (Zank *et al.* 2014).

Table 2. Changes in the projected suitable areas for the *Stenoterommata* species expressed as proportions between present and 2050 and 2070 for two climate scenarios (RCP6.0 and RCP8.5). The sign ('+' or '-') indicates either an increase or a decrease in the suitable area, respectively.

Species		Projected area range changes (proportion)					
	Occurrence records	Points used in Maxent*	Suitable area (km²)	RCP6.0		RCP8.5	
				2050	2070	2050	2070
S. crassistyla	17	10016	408030	-0.07	-0.10	-0.05	-0.14
S. iguazu	9	10009	187091	+0.33	-0.21	+0.53	+0.71
S. palmar	18	10014	494924	+0.25	+0.32	+0.61	+0.74
S. platensis	24	10020	281624	-0.30	-0.53	-0.16	-0.21
S. tenuistyla	10	10009	308756	+0.38	+0.45	+0.93	+1.16
S. uruguai	8	10008	138699	+0.11	+0.04	+0.28	+1.44

^{*} background points and presence points used to determine the Maxent distribution.

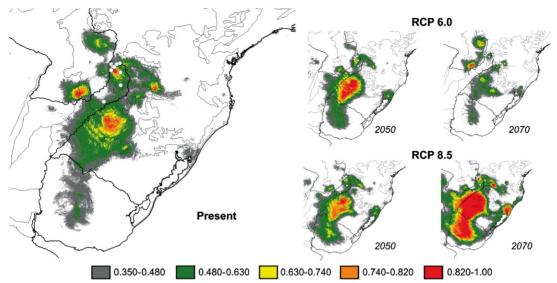


Fig. 2. Distributions of *Stenoterommata iguazu* modelled with MaxEnt for the present and two climate scenarios (RCPs 6.0 and 8.5) for the years 2050 and 2070. Colours indicate habitat suitability from low (grey) to high (red)...

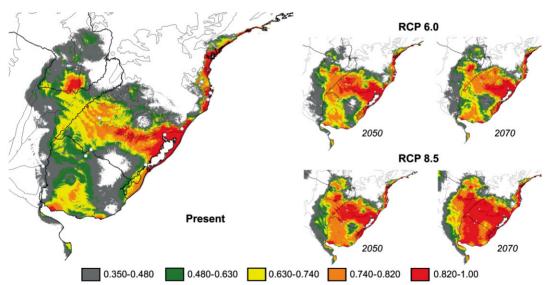


Fig. 3. Distributions of *Stenoterommata palmar* modelled with MaxEnt for the present and two climate scenarios (RCPs 6.0 and 8.5) for the years 2050 and 2070. Colours indicate habitat suitability from low (grey) to high (red).

For instance, isothermality and/or temperature seasonality contributed the most to the models for *S. crassistyla*, *S. palmar*, *S. platensis* and *S. temuistyla*, which suggests that these species are sensitive to temperature oscillations. For these species, the most suitable conditions are between 24.33°S and 38.62°S, the area comprising eastern Argentina, Uruguay and southern Brazil.

A similar distribution pattern was reported for some species of Opiliones, as well as for the spider *Latonigena auricomis*, for which isothermality was the most relevant variable (Jorge *et al.* 2013, Simó *et al.* 2014).

Precipitation of the driest quarter and precipitation seasonality contributed the most to the models for *S. iguazu* and *S. uruguai*, suggest-

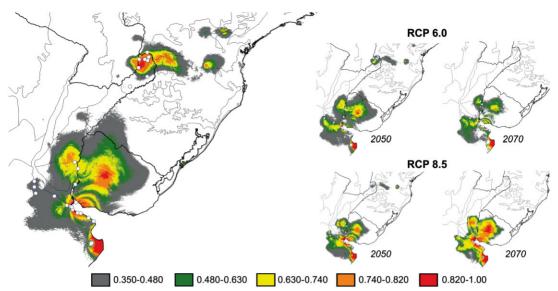


Fig. 4. Distributions of *Stenoterommata platensis* modelled with MaxEnt for the present and two climate scenarios (RCPs 6.0 and 8.5) for the years 2050 and 2070. Colours indicate habitat suitability from low (grey) to high (red).

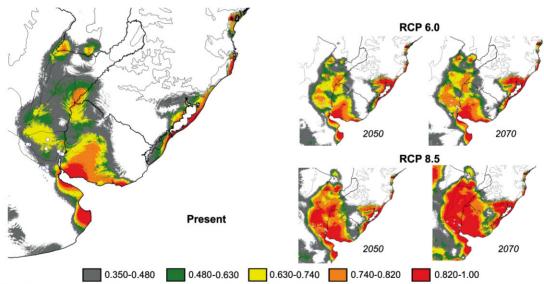


Fig. 5. Distributions of Stenoterommata tenuistyla modelled with MaxEnt for the present and two climate scenarios (RCPs 6.0 and 8.5) for the years 2050 and 2070. Colours indicate habitat suitability from low (grey) to high (red).

ing that for these species precipitation patterns should be monitored. This is consistent with the distributional pattern of these species, which also occur in northern Misiones Province (ecoregions of Atlantic and Parana Forests) along the river banks of the confluences of the Paraná and Iguazú rivers (Goloboff 1995, Ferretti & Pompozzi 2016). Although no considerable reduction in the

suitable areas was found for these species, the expected climate-change driven increase in floods in the Atlantic rainforest, may be a serious threat to the viability of their populations. Also habitats (e.g., river banks) of some other species (such as *Caiman latirostris*) in the Atlantic rainforest have been shown to shrink as a result of increased flooding (Ugarte *et al.* 2013, Herrera *et al.* 2014).

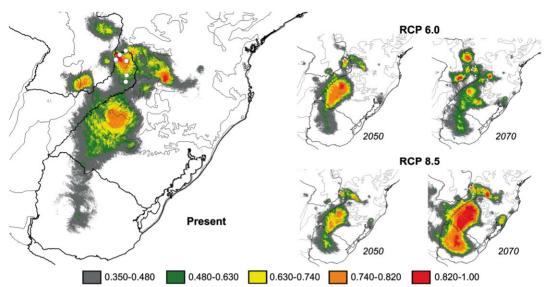


Fig. 6. Distributions of *Stenoterommata uruguai* modelled with MaxEnt for the present and two climate scenarios (RCPs 6.0 and 8.5) for the years 2050 and 2070. Colours indicate habitat suitability from low (grey) to high (red).

Earlier studies concluded that global warming would cause expansions, shifts, or contraction in species' ranges (Yuan et al. 2015, Jiang et al. 2016). Conservation efforts should target those species that are predicted to be more affected by climate change (Zank et al. 2014). Our results reveal that changing climate would affect Stenoterommata species in different ways. The areas suitable for S. iguazu and S. uruguai would expand along the La Plata River towards northern and central Uruguay and south-central and eastern Brazil (ecoregion of Uruguayan Savanna), whereas the areas suitable for S. crassistyla, S. palmar and S. tenuistyla would expand towards southern and central Uruguay (Uruguayan Savanna), southern Brazil (ecoregions of Atlantic Forest, Serra do Mar coastal Forest and Araucaria moist Forest) and the Buenos Aires coast (Humid Pampas). The present-day (and future) expansions towards the northern region of Buenos Aires Province (Argentina), could be related to the uninterrupted increase in rainfall and temperatures during the last decades, as evidenced by southward expansions of species typically present in subtropical areas (Ringuelet 1959, Acosta 2014, Guerrero & Agnolin 2016).

It is worth noting that *S. platensis* was the only species studied whose projected suitable areas were drastically different from the present-day

ones. This species is clearly sensitive to global warming and it is expected that its distribution would drastically decrease by the year 2070. Interestingly, the new suitable areas predicted under different scenarios for 2050 and 2070 suggest an expansion towards southern Buenos Aires Province (Humid Pampas) and south and central Uruguay (Uruguayan Savanna). The average percentage reduction (about 50%) in the number of presence sites along with the reduction in potential ranges, provide an estimate of its vulnerability. In fact, present-day suitable areas, such as those in the Espinal, Humid Chaco and Parana Atlantic Forest, would shrink by 2070, and some (e.g., in ecoregions of Parana Forest and Araucaria moist Forest) may even become unsuitable. Consequently, the remaining suitable areas would be highly fragmented, which may compromise the persistence of the populations inhabiting central Entre Ríos and Misiones provinces in Argentina.

Based on the rate of reduction in the range of suitable conditions, and the percentage of present-day known sites lost by 2070, *S. platensis* should be considered a species of conservation concern due to the effects of global warming. It should, however, be born in mind that there are inherent uncertainties in climate-change analyses (Hampe 2004, Radosavljevic & Anderson 2014), and that factors (such as environmental condi-

tions or human disturbances) other than climate change may also present a threat to spider species (Gallé *et al.* 2011, Kuntner 2014).

The results for the species occurring in fewer than 10 locations, namely *S. iguazu* and *S. uruguai*, should be treated with caution because the predictive power decreases with decreasing sample sizes (Pearson *et al.* 2007). Nevertheless, the low number of known occurrences for several Mygalomorphae species is most likely a consequence of their naturally restricted geographic distributions due to their poor dispersal capabilities, rather than undersampling (Ferretti *et al.* 2014).

The projection of suitable areas under different climate scenarios generated by distributions models provides a tool to improve the assessment of the effects of climate change on biodiversity.

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