

# Niche modelling of the Chilean recluse spider *Loxosceles laeta* and araneophagic spitting spider *Scytodes globula* and risk for loxoscelism in Chile

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**Abstract.** In Chile, all necrotic arachnidism is attributed to the Chilean recluse spider *Loxosceles laeta* (Nicolet) (Araneae: Sicariidae). It is predated by the spitting spider *Scytodes globula* (Nicolet) (Araneae: Scytodidae). The biology of each of these species is not well known and it is important to clarify their distributions. The aims of this study are to elucidate the variables involved in the niches of both species based on environmental and human footprint variables, and to construct geographic maps that will be useful in estimating potential distributions and in defining a map of estimated risk for loxoscelism in Chile. *Loxosceles laeta* was found to be associated with high temperatures and low rates of precipitation, whereas although *S. globula* was also associated with high temperatures, its distribution was associated with a higher level of precipitation. The main variable associated with the distribution of *L. laeta* was the human footprint (48.6%), which suggests that this is a highly invasive species. Similarly to other species, the distribution of *L. laeta* reaches its southern limit at the Los Lagos region in Chile, which coincides with high levels of precipitation and low temperatures. The potential distribution of *L. laeta* in Chile corresponds to the distribution of cases of loxoscelism.

**Key words.** Loxoscelism, niche.

## Introduction

Loxoscelism is the necrotic arachnidism caused by the bites of spiders of the genus *Loxosceles* (Vetter, 2008). In Chile, all necrotic arachnidism is attributed to the Chilean recluse spider *Loxosceles laeta* (Canals & Solís, 2014; Canals *et al.*, 2015a), a solitary spider that is found within houses, usually in dark corners, cracks, closets and clothing, but may sometimes be found outdoors. *Loxosceles laeta* inhabits South America. It is common in Chile, as well as in Peru, Ecuador, Argentina,

Uruguay and the south of Brazil. It has been introduced into North America and has been reported in Central America, Canada (in Vancouver, BC), in the U.S.A. (Cambridge, MA and in Florida), Finland and Australia (Gonçalves-de-Andrade & Tambourgi, 2003). In Chile, reports of this species range from Arica to the Bio-Bio region (Schenone, 2004), but there are reports of loxoscelism in more southern regions such as the Los Lagos region (Ríos *et al.*, 2007).

The biology of this species and its predators is not well known (Fernandez *et al.*, 2002; Alfaro *et al.*, 2013; Canals & Solís, 2014). In Chile, *L. laeta* has been reported to feed on flies,

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moths and other small arthropods (Canals *et al.*, 2015a). Its activity is preferentially nocturnal (Schenone, 2004). The epidemiology of incidents of loxoscelism coincides with nocturnal activity and also suggests larger spider populations and greater activity during the summer (Schenone, 2004; Taucare-Ríos *et al.*, 2013). Bites of *L. laeta* are more frequent at night and in the warm season, reflecting the nocturnal activity of this species and the fact that its populations are more active and abundant in spring and summer (Schenone, 2004; Canals & Solís, 2014).

*Scytodes globula* is a member of a group of spiders known as spitting spiders, which are recognized as having araneophagic habits (Gilbert & Rayor, 1985), and is a predator of *L. laeta* (Canals *et al.*, 2015a). These spiders are active during twilight and at night and their thermal preferences and desiccation tolerances are similar to those of *L. laeta* (Alfaro *et al.*, 2013; Canals *et al.*, 2013). *Scytodes globula* is distributed in South America in Chile, Bolivia, Argentina, Brazil and Uruguay. Like *L. laeta*, this species is common in human dwellings and in the gardens of houses in central Chile (Fernandez *et al.*, 2002).

These two species have similar thermal preferences (Alfaro *et al.*, 2013; Canals *et al.*, 2013), are nocturnal and have low energy requirements (Canals *et al.*, 2015a, 2015b, 2015c). Although their energy requirements overlap substantially, they differ in trophic niche because *L. laeta* is mainly entomophagic and *S. globula* is mainly araneophagic (Gonçalves-de-Andrade & Tambourgi, 2003).

There are no systematic studies on the distributions and the potential niches of these species in Chile; any reports are scarce.

The associations between the ecological characteristics and epidemiologies of these species highlight the need to elucidate their potential distributions, niches and interactions with predators in order to understand their biology and to construct risk maps for loxoscelism and devise possible methods of biological control. This is the aim of spatial epidemiology, which is understood as the study of the spatial variation of the exposition probability (risk) to a disease or the incidence of a disease (Ostfeld *et al.*, 2005). There are many recent studies of spatial epidemiology in infectious diseases (Ostfeld *et al.*, 2005), but only one of the risk for spider bites (Saupe *et al.*, 2011). Conceptually, risk maps may be classified in three categories: (a) ecological maps of the potential distribution of vectors; (b) eco-epidemiological maps that integrate parameters of the interplay between vectors and the pathogen, and (c) disease incidence maps (Ostfeld *et al.*, 2005). In the case of loxoscelism, ecological maps are the most appropriate.

The thermal axis has been reported as a variable that allows estimations of the potential distribution of *L. laeta*, but not of its predator (Canals *et al.*, 2015d). The aims of this study are to understand the variables involved in the niche–biotope duality in both species based on environmental and human footprint variables, and to construct geographic maps that will be useful both in estimating the potential distributions and overlap of these species and in estimating the risk for loxoscelism in Chile.

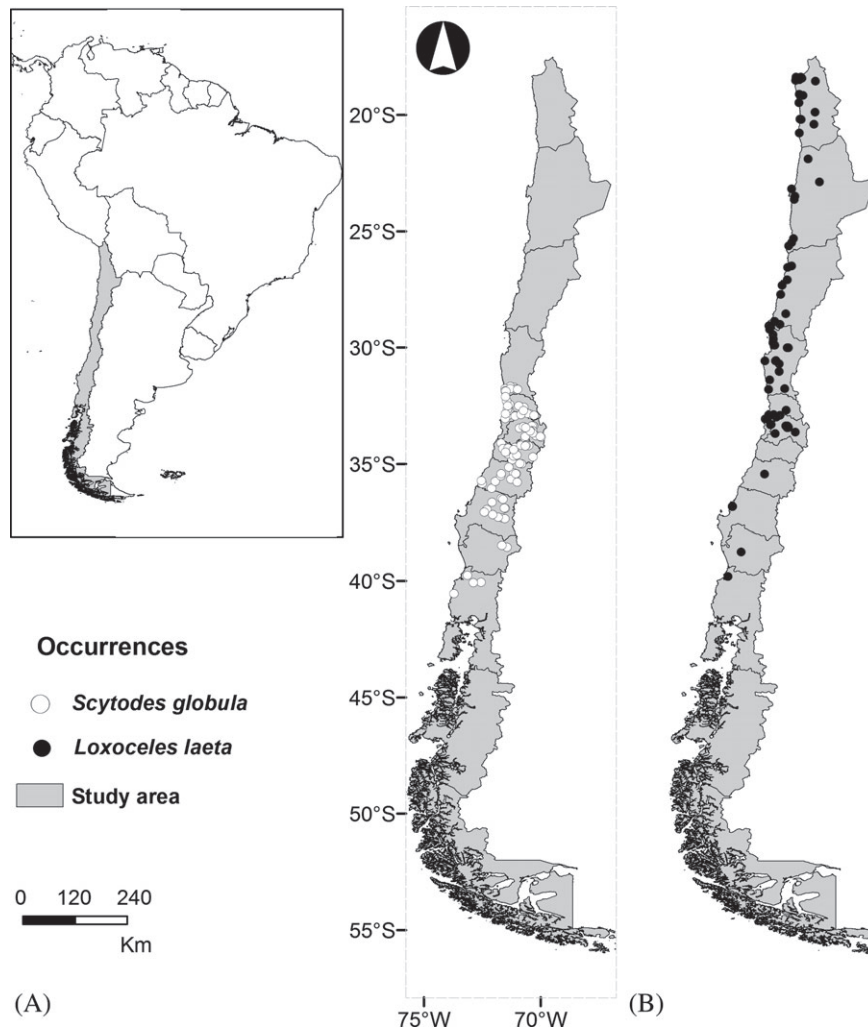
## Materials and methods

### Occurrence data

Data on the occurrences of *L. laeta* and *S. globula* in continental Chile were obtained from the National Museum of Natural History, the Zoology Museum of the University of Concepción, the Museum of the University of La Serena in Chile and the Museum of the Butantan Institute in Brazil. These records cover long time periods from at least 1950 onwards. Duplicate records and records presenting obvious errors in georeferencing or identification (e.g. records in the ocean) were excluded. Records in oversampled locations were also excluded based on subsampling among very close pairs of points in order to reduce sampling bias (Peterson *et al.*, 2011). Each point of occurrence was separated by at least 1 km from any other point. The data were filtered according to the following criteria: (a) the information must include an accurate georeference; (b) the data must be derived from the examination of specimens, and (c) the data must include the name of the zoologist who determined the species in order to avoid taxonomic problems. After filtering, a total of 124 points of occurrence of *L. laeta* and 88 of *S. globula* were obtained (Fig. 1).

### Climatic niche and environmental data

The dataset of environmental variables was composed of proxy bioclimatic variables. Bioclimatic variables were obtained from the Worldclim database, an online public repository (<http://www.worldclim.org/>), with a spatial resolution of 30 arc-seconds ( $\approx 1 \text{ km}^2$ ). This dataset included a total of 19 bioclimatic variables selected according to their possible association with the biology of spiders, which summarize information on temperature and precipitation. First, niche modelling was explored with these variables, the altitude and a human footprint index. Later, because variable collinearity may lead to over-fitting (Beaumont *et al.*, 2005), a principal components analysis (PCA) with the original climate variables across the entire study region (i.e. the area accessible by the species) was performed using NicheA software (Qiao *et al.*, 2014) to transform the often-correlated original environmental variables (Peterson *et al.*, 2011) into new, uncorrelated variables; this procedure also allowed the abstract environmental space to be displayed efficiently in NicheA, summarizing most of the environmental information in a three-dimensional scenario (Qiao *et al.*, 2014). Eleven variables were related to temperature: B1 = mean annual temperature; B2 = mean diurnal range [mean of monthly (maximum temperature–minimum temperature)]; B3 = isothermality (B2/B7) (\*100); B4 = temperature seasonality (standard deviation\*100); B5 = maximum temperature in the warmest month; B6 = minimum temperature in the coldest month; B7 = annual range of temperature (B5–B6); B8 = mean temperature during the wettest quarter; B9 = mean temperature during the driest quarter; B10 = mean temperature during the warmest quarter, and B11 = mean temperature during the coldest quarter. Eight variables were related to precipitation: B12 = annual precipitation; B13 = precipitation during the wettest month;



**Fig. 1.** Distribution of occurrences of (A) *Scytodes globula* and (B) *Loxosceles laeta*.

B14 = precipitation during the driest month; B15 = precipitation seasonality (coefficient of variation); B16 = precipitation during the wettest quarter; B17 = precipitation during the driest quarter; B18 = precipitation during the warmest quarter, and B19 = precipitation during the coldest quarter. The final variable was altitude (ALT).

In addition, a global measure of the human footprint, the human influence index (HII), at the same scale ( $\approx 1 \text{ km}^2$ ) was included. This is an index produced by the Wildlife Conservation Society (WCS) and the Center for International Earth Science Information Network of Columbia University (<http://sedac.ciesin.columbia.edu/data/set/wildareas-v2-human-footprint-geographic/data-download>). This index was constructed from the Last of the Wild Project Version 2, 2005 (LWP-2) and corresponds to a standardized index of human influence. The HII is a set of global data estimated from nine layers that include details on population density, land use and infrastructure (construction areas, nocturnal lighting, land cover) and human access (coastlines, roads, railway lines, navigable creeks) (Sanderson *et al.*, 2002; Gallardo *et al.*, 2015).

First, descriptive statistics were calculated and Student's *t*-tests were performed for each variable to compare findings between species. Next, a PCA was performed for each species. Using this information and based on occurrences, NicheA calculates and displays the convex polyhedron in the environmental space automatically. In this way, the niche overlap (of convex polyhedrons) between the two species was quantified. The niche breadth (standardized Levin index B) for each species was estimated. The index value varies from 0 to 1; values of  $> 0.6$  indicate a generalist selection of the niche axis. Niche similarity measurements in NicheA were based on Jaccard's index (Qiao *et al.*, 2014). Jaccard's index is used to compare the similarity of finite sample sets and is defined (in the present case) as the volume of the overlap between species divided by the volume of the union of the polyhedrons of the same species. This index ranges from 0 (no overlap) to 1 (complete overlap). The variation coefficient of the main components of *L. laeta* in areas with and without the predator *S. globula* were compared using the Bartlett test (Bt).

A discriminant analysis was performed to find the variables (or combinations of variables) that explained the niche differences between the species. For this analysis, a PCA was performed with only temperature-related variables (PCTi) and was followed by another with only precipitation-related variables (PCPi), selecting the relevant orthogonal components with the Kaiser criterion (eigenvalue: > 1) to obtain a set of independent variables: PCTi, PCPi, ALT and HII. These new variables were used in the discriminant analysis.

#### Potential distribution models

Using the first PCAs, which represented >95% of total variance, and occurrence data, species distribution models (SDMs) were constructed for both species, using Maxent, a machine-learning method that assesses the distribution probability of a species by estimating the distribution probability of maximum entropy (Phillips *et al.*, 2006). This software generally performs better than other software commonly used for SDMs using presence-only datasets (Ortega-Huerta & Peterson, 2008). Specific options were a bootstrap subsampling with 50 replicates, random seeding and the mean of replicates as output. To achieve SDM regularization, the models were smoothed to avoid over-parameterization (Phillips *et al.*, 2006). Regularization refers to the smoothing of a model to make it more regular and is conducted in order to avoid fitting too complex a model. Smoothing was achieved by modifying a b-parameter (i.e. the value that smooths the model, making it more regular); b = 1 was the best choice as it led to the most conservative model (Peterson *et al.*, 2011), penalizing over-parameterization.

Maxent output was converted to binary maps using an error rate of E = 10% among occurrence points, and thus using the highest threshold that included 90% of training presence points, a modification of the least training presence threshold idea (Peterson *et al.*, 2007). The error rate (E) is the proportion of occurrence data that is expected to place the species erroneously under inappropriate conditions as a consequence of incorrect species identification, errors in georeferencing, errors in the spatial positioning of occurrences and errors in environmental data, among other factors, and is estimated via the exploration and error-checking of occurrence data (Peterson *et al.*, 2007). To study the goodness-of-fit of the models, the area under the curve (AUC) in the receiver operating characteristic (ROC) analysis, and the Boyce index of the average model and the Akaike information criterion (AIC) and Bayesian information criterion (BIC) of the best model were used.

## Results

#### Niche space analysis

All variables characterizing the niches of *L. laeta* and *S. globula* were different. For example, the mean  $\pm$  standard deviation (SD) annual temperature (B1) was  $15.2 \pm 2.1$  °C for *L. laeta* and  $12.9 \pm 3.0$  °C for *S. globula* ( $t = 6.64$ ,  $P < 0.05$ ); mean  $\pm$  SD temperature seasonality (B4) was  $3.05 \pm 0.75$  °C for *L. laeta* and  $4.07 \pm 0.65$  °C for *S. globula* ( $t = -10.36$ ,  $P < 0.05$ );

**Table 1.** Factor loadings of the principal components based on occurrences of both species *Loxosceles laeta* and *Scytodes globula*. PC1, PC2 and PC3 are the values of the three main principal components.

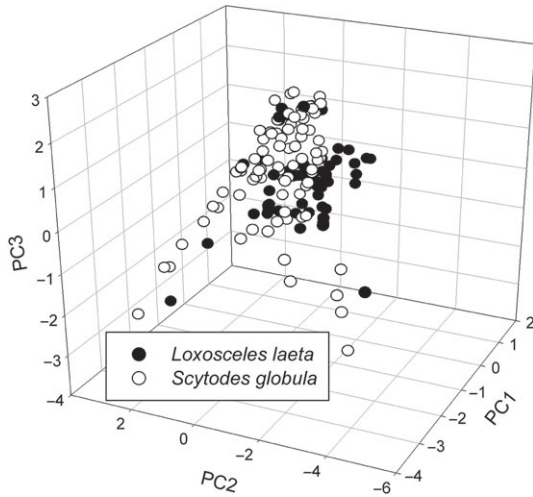
Variable	PC1	PC2	PC3
ALT	-0.44	0.75*	-0.21
B1	0.90*	-0.29	0.24
B2	-0.62	0.50	0.50
B3	-0.01	0.48	-0.45
B4	-0.61	0.23	0.73*
B5	0.17	-0.08	0.95*
B6	0.86*	-0.47	-0.10
B7	-0.64	0.36	0.65
B8	0.87*	-0.24	-0.10
B9	0.67	-0.33	0.60
B10	0.73*	-0.25	0.59
B11	0.92*	-0.33	-0.03
B12	-0.85*	-0.50	0.03
B13	-0.85*	-0.42	0.12
B14	-0.71*	-0.59	-0.18
B15	0.54	-0.04	-0.10
B16	-0.85*	-0.45	0.10
B17	-0.73*	-0.59	-0.17
B18	-0.73*	-0.52	-0.22
B19	-0.85*	-0.45	0.10
HII	0.33	-0.38	0.07

\*Significant loadings of > 0.7.

mean  $\pm$  SD annual precipitation (B12) was  $274.3 \pm 371.6$  mm for *L. laeta* and  $754.8 \pm 488.2$  mm for *S. globula* ( $t = -8.13$ ,  $P < 0.05$ ); mean  $\pm$  SD precipitation seasonality (B15; variation coefficient) was  $1.39 \pm 0.78$  for *L. laeta* and  $1.04 \pm 0.13$  for *S. globula* ( $t = 4.62$ ,  $P < 0.05$ ), and the mean  $\pm$  SD human blood index (HII) was  $60.9 \pm 26.3$  for *L. laeta* and  $39.4 \pm 16.0$  for *S. globula* ( $t = 6.81$ ,  $P < 0.05$ ).

Using the Kaiser criterion, the three main components for *L. laeta* were selected, explaining 83.5% of total variance. These three components (PCL1, PCL2 and PCL3) explained 45.4, 21.8 and 16.3% of the variance, respectively. The first component was associated positively with four temperature variables, mainly with annual mean temperature (B1) and the mean temperature of the coldest quarter (B11), and negatively associated with all precipitation-related variables. The second component was associated with altitude (ALT), and the third component with the maximum temperature of the warmest month (B5) and temperature seasonality (B4). The three main components for *S. globula* referred to 94.7% of total variance: PCS1, PCS2 and PCS3 explained 49.7, 25.0 and 20.0% of variance, respectively. Similarly to *L. laeta*, the first component was positively associated with six temperature-related variables, especially B1 and B11, and negatively associated with precipitation-related variables. Again, similarly to *L. laeta*, the second component was related to ALT, and the third component to B5 and B4. When both species were considered together, the three main components explained 85.0% of total variance: PC1, PC2 and PC3 explained 50.2, 18.7 and 16.0% of variance, respectively, and were equivalent to those for *L. laeta* alone (Table 1).

A comparison of the coefficients of variation for each of the three components (PC1, PC2 and PC3) for *L. laeta* in zones with and without the presence of *S. globula* found no significant



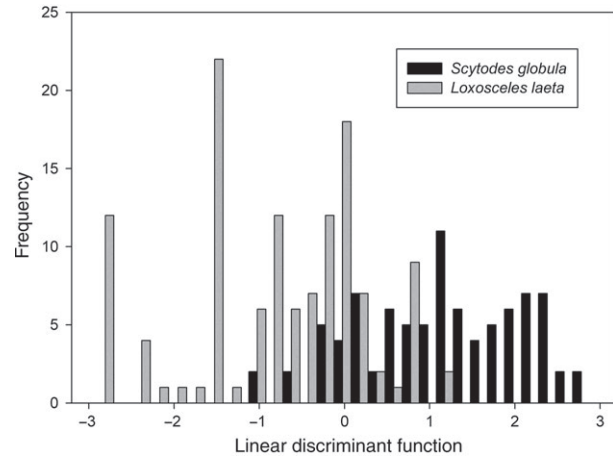
**Fig. 2.** Niche reconstruction of *Loxosceles laeta* and *Scytodes globula* based on the first three principal components (PC1, PC2, PC3).

differences in PC1 or PC2 (Bt = 2.63,  $P = 0.104$  and Bt = 0.92,  $P = 0.33$ , respectively). The coefficient of variation for PC3 for *L. laeta* in zones without *S. globula* (CV = 0.854) was lower than that in zones with *S. globula* (CV = 6.27; Bt = 37.01,  $P < 0.001$ ). The standardized niche breadths were  $B = 0.34$  for *L. laeta* and  $B = 0.46$  for *S. globula*. The niche overlap was  $J = 0.2581$  (Fig. 2).

The PCA of temperature-related variables (to perform discriminant analysis) selected two axes, PCT1 and PCT2, explaining 88.8% of total variance, whereas the PCA of precipitation-related variables selected only one axis, PCP1, explaining 82.1% of total variance. All variables associated with PCT1 other than B2 referred to mean temperatures; B2 corresponds to mean diurnal range and was interpreted as an axis of mean load of temperatures. The variables associated with PCT2 referred to seasonality (B4) and maximum temperature and were interpreted as an axis of thermal ranges. All precipitation-related variables except seasonality were associated with PCP1, which thus may be interpreted as an axis of precipitation load. With these variables, ALT and the human footprint (HII), the linear discriminant function was:  $0.20ALT + 0.58PCT1 + 0.32PCT2 - 0.53PCP1 - 0.48HII$  ( $\Lambda - Wilks = 0.5$ ,  $F_{2,206} = 38.95$ ,  $P < 0.001$ ) with 81.0% correct classification (Fig. 3). All variables except ALT contributed to explaining the niche separation of the species (ALT,  $P = 0.14$ ; HII,  $P < 0.001$ ; PCT1,  $P = 0.006$ ; PCT2,  $P < 0.001$ ; PCP1,  $P = 0.003$ ). The temperature axes PCT1 and PCT2 showed positive scores for *L. laeta* and negative scores for *S. globula*; the opposite occurred with the precipitation PCP1 scores. The scores of HII were positive for both species, but higher in *L. laeta* than *S. globula*.

*Geographic space analysis*

When all variables were used separately to model the distribution of each species, a good level of adjustment emerged: the mean  $\pm$  SD AUC was  $0.975 \pm 0.004$  for *L. laeta* and



**Fig. 3.** Frequency histogram of the scores of the linear discriminant function for *Loxosceles laeta* and *Scytodes globula* based on the principal components of the variables in the occurrence sites.

**Table 2.** Variables that contribute to explaining the geographical distribution of *Loxosceles laeta* and *Scytodes globula* in Chile, given as estimates of the relative contributions of environmental variables to the Maxent model.

<i>L. laeta</i>		<i>S. globula</i>	
Variable	Contribution	Variable	Contribution
HII	48.6%	B5	25.9%
B18	18.5%	HII	20.6%
ALT	6.1%	B19	13.2%
		B15	13.2%
Total	73.2%		72.9%

The model is re-evaluated on the permuted data, and the resulting drop in area under the curve is shown in the table, normalized to percentages. ALT, altitude; B5, maximum temperature in the warmest month; B15, precipitation seasonality (coefficient of variation); B18, precipitation during the warmest quarter; B19 = precipitation during the coldest quarter; HII, human influence index.

$0.977 \pm 0.002$  for *S. globula*, but the variables explaining their distribution differed between the species (Table 2). For *L. laeta* the main variables were the human footprint (HII), precipitation in the warmest quarter (B18) and ALT, whereas for *S. globula* the main variables were maximum temperature in the warmest month (B5), human footprint (HII), precipitation in the coldest month (B19) and precipitation seasonality (B15).

The PCA of the bioclimatic variables (to generate the layers) showed four main components that explained 92.4% of the climatic variability of Chile. The first component was related mainly to precipitation (B12, B14, B17 and B18) and daily temperature range (B2); the second component was related to temperature (B1, B5, B6, B9, B10 and B11) and ALT; the third component was related to temperature range (B7) and variables related to maximum precipitation (B13, B16 and B19), and the fourth component referred to the variability in temperature and precipitation (B3, B4, B15, B18) and ALT. As in the analyses in which the variables were used separately, the main contributions

**Table 3.** Goodness-of-fit of the models for *Loxosceles laeta* and *Scytodes globula* with and without the human footprint.

	AUC	BI	AIC	AICc	BIC
Without HII					
<i>L. laeta</i>	0.930 ± 0.01	0.958	1455.8	1468.7	1489.0
<i>S. globula</i>	0.940 ± 0.01	0.916	1665.8	1670.5	1690.2
With HII					
<i>L. laeta</i>	0.936 ± 0.01	0.968	1439.1	1456.2	1476.4
<i>S. globula</i>	0.945 ± 0.01	0.967	1629.5	1633.4	1651.7

AUC, area under the curve in the receiver operating characteristic (ROC) curve; BI, Boyce index; AIC, Akaike information criterion uncorrected; AICc, Akaike information criterion corrected; BIC, Bayesian information criterion; HII, human influence index.

for *L. laeta* come mostly from PC2 (temperature) and PC1 (precipitation). For *S. globula*, the main contribution comes from PC3 (maximum precipitation) and in similar proportions from PC1 and PC2. The adjusted models for *L. laeta* and *S. globula* with and without the inclusion of HII are shown in Table 3. The overlap of the potential distribution of the species varied from 25.5 to 32.6% using all variables, with and without HII, respectively (Fig. 4).

## Discussion

Niche analyses and analyses of the potential distributions of species both allow for the detection of variables relevant to the survival and reproduction of the species in question, and facilitate the identification of suitable habitats and prediction of potential distributions. This is relevant in the case of invader species and particularly in species of medical importance, such as species of the genus *Loxosceles* (Wiens *et al.*, 2010; Saupe *et al.*, 2011). Adaptive evolution in the distribution range that is invaded may alter the fundamental niche, particularly when the niche is wide (Colwell & Rangel, 2009). For example, although synanthropy is not the main factor in the distribution of *Loxosceles reclusa* in the U.S.A., the species is able to extend its naturally restricted distribution with the help of human infrastructure (Saupe *et al.*, 2011).

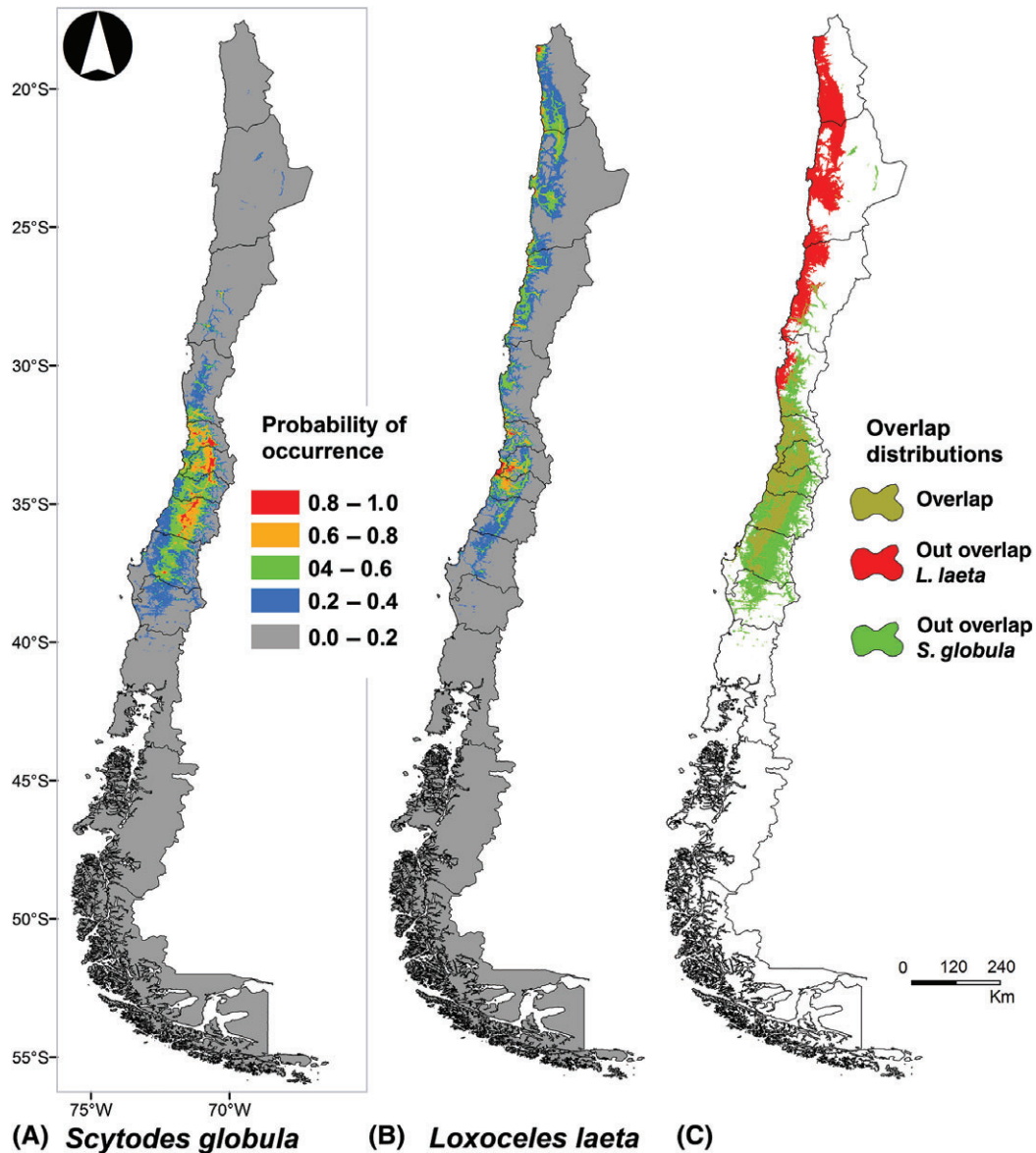
The species analysed in the current study differed in all relevant bioclimatic variables and in the human footprint. The principal components explaining global variability were similar in the two species: the first was associated positively with temperatures and negatively with precipitation; the second was associated with altitude, and the third with variability in temperature. *Loxosceles laeta* was associated with high temperatures and low levels of precipitation, whereas although *S. globula* was also associated with high temperatures, it was associated with a higher level of precipitation. The niche breadth of both species was narrow, showing a clear climatic dependence similar to that reported for *L. reclusa* (Saupe *et al.*, 2011). The niche overlap was  $J=0.26$ , which is lower than those reported previously by ecophysiological estimations, such as the value of 0.852 for thermal preferences (Alfaro *et al.*, 2013; Canals *et al.*, 2013). This may be explained by the fact that the present study was conducted at a climatic scale (macro

scale), whereas previous studies were performed at a micro scale. Microclimatic preferences detected in the laboratory may be poor predictors of geographic distribution, but may be appropriate to extrapolating preferences in human dwellings or particular habitats. The niche and distribution estimated in the laboratory from ecophysiological characteristics may differ from those estimated at a climatic scale. For example, in the laboratory, the spider *Dysdera crocata* (Araneae: Dysderidae) shows a very narrow niche, with a preferred temperature near 9 °C in central Chile; however, this is a cosmopolitan species (Sepúlveda *et al.*, 2014). Under the assumption of niche fidelity, this may be explained by the ability of this species to find appropriate micro environments, but may also refer to local adaptation (i.e. phenotypic plasticity) (Wiens *et al.*, 2010).

Discriminant analysis showed that the niche differences between the species examined herein were associated with mean temperatures and their variability, precipitation level and the human footprint. Although both species preferred high temperatures, the temperature and temperature variability scores are positively associated with the niche of *L. laeta*, suggesting that this species prefers xeric environments and zones of Mediterranean climate, in agreement with previously reported data (Alfaro *et al.*, 2013; Canals *et al.*, 2013). However, although *S. globula* prefers high temperatures, the extreme temperatures of northern Chile appear to constrain its distribution in this zone. By contrast, precipitation is negatively associated with the distribution of *L. laeta* and positively associated with the distribution of *S. globula*.

Although the presence of predators might be expected to reduce the niche of their prey (Putman & Wratten, 1984), the current investigations did not find a predation effect of *S. globula* on the niche breadth of *L. laeta* in the two main principal components of the niche. Further, in the third component the effect was contrary: the niche breadth of *L. laeta* was wider when the predator (*S. globula*) was present. This may be explained by the fact that *S. globula* is a polyphagous predator and *L. laeta* is not a limiting resource, and thus predation pressure is low, or may indicate that predation does not shape distribution at a wide level, whereas climate variables do.

Maxent modelling with all variables demonstrated a good fit with the empirical distributions of both species and showed that the main variable associated with the distribution of *L. laeta* is the human footprint, which is consistent with the niche analysis. The distribution of *L. laeta* was mainly associated with low altitudes and low levels of precipitation. Its distribution was associated with xeric semi-desert formations such as 'el monte', 'el espinal', pampas and steppes, characteristics of this area at latitudes of 18–30 °S (arid diagonal) and a more Mediterranean zone at 30–40 °S. The dependence of *L. laeta* on temperature agrees with the good fit of a model that used only temperatures to predict its distribution (Canals *et al.*, 2015d). In addition, the human footprint correlated strongly with all temperature-related variables (B1–B11) and not with precipitation-related variables, which may suggest an indirect effect of this variable in the temperature axis. The main factors that explain the distribution of *S. globula* were precipitation level and the negative effect of variability in temperature. *Scytodes globula* had a clear central–southern distribution in Chile with Mediterranean influence, which is associated with a higher level



**Fig. 4.** Modelling of the potential distributions of (A) *Scytodes globula*, (B) *Loxosceles laeta* and (C) their overlap based on bioclimatic variables and the human footprint.

of precipitation than the northern zone, and shared only this area with *L. laeta*. Its northern limit ( $\approx 30^\circ\text{S}$ ) coincides with the southern limit of the arid diagonal and the blocking effect of atmospheric masses imposed by the Andes Range. This explains why the use of only temperatures to predict the distribution of this species leads to poor predictions (Canals *et al.*, 2015d). Its southern limit ( $\approx 40^\circ\text{S}$ ) coincides with the latitude at which temperature falls and precipitation increases.

*Loxosceles laeta* showed a distribution with a southern limit at the Los Lagos region ( $40\text{--}44^\circ\text{S}$ ), which coincides with high precipitation levels and low temperatures. This is similar to that reported for *L. reclusa*, a species in which lower critical temperatures impose a limit to its distribution (Cramer & Maywright, 2008; Saupe *et al.*, 2011). The potential distribution

of *L. laeta* in Chile also agrees with the distribution of cases of loxoscelism in the country. For example, Ríos *et al.* (2007) reported cases distributed from Arica and Parinacota to the Los Lagos region.

The human footprint was associated mainly with *L. laeta*, which agrees with the recognized synanthropy of this species, whereas *S. globula* is found in human dwellings and is also relatively frequent in natural environments (Taucare-Ríos *et al.*, 2013). The human footprint explained 20.6% of the distribution of *S. globula* and 48.6% of the distribution of *L. laeta*; the latter value is very high compared with the average of 21% (Gallardo *et al.*, 2015) reported for terrestrial invaders. This indicates that this species may be considered as highly invasive, like other *Loxosceles* species such as *Loxosceles rufescens*

(Luo & Li, 2015), and agrees with reports of its introduction into North America, Central America, Finland and Australia (Gonçalves-de-Andrade & Tambourgi, 2003). The presence of a species is associated with: (a) local conditions that allow its persistence and reproduction; (b) its interaction(s) with other species, and (c) its dispersion capability (Hirzel & Le Lay, 2008). It is relevant in an epidemiological sense that in the case of *L. laeta* humans contribute to its distribution by providing suitable local conditions such as human dwellings, construction areas and land cover, and also by facilitating its dispersion by various means of transport and routes of human access such as roads and railway lines. Occasional popular observations of this species in southern Chile, outside its distribution range, in human dwellings, do not necessarily imply invasion but indicate potential increases in the species' colonization and in the range of loxoscelism.

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