



Ecological niche divergence between the brown recluse spiders *Loxosceles laeta* and *L. surca* (Sicariidae) in Chile

Andrés Taucare-Ríos ^a and William H. Piel ^{b,c}

^aFacultad de Ciencias, Universidad Arturo Prat, Iquique, Chile; ^bYale-NUS College, Singapore, Republic of Singapore; ^cDepartment of Biological Sciences, National University of Singapore, Singapore, Republic of Singapore

ABSTRACT

The laeta species group is the main source of *Loxosceles* species in Chile, a genus of medical importance due to the cytotoxic properties of its venom and the synanthropic habits of its dominant species, *Loxosceles laeta*. However, a poorly studied, cryptic, and putative sister species, *Loxosceles surca*, is also known to live in Chile at latitudes that overlap with *L. laeta*. In contrast to *L. laeta*, *L. surca* lives in natural areas away from humans. We used DNA sequences from *L. surca* to infer the phylogenetic history of this species and its congeners. Additionally, we used ecological niche modelling to define the ecology of this species in contrast to its sister species. Our results show that *L. surca* does, indeed, belong to the laeta species group, and is likely a sister species to *L. laeta*. Although these species are fairly cryptic with respect to each other, the substantial genetic divergence between them is consistent with other distinct sister species in this genus. The laeta group is also sister to the large reclusa group that radiated into the Caribbean, Central, and North America. The phylogeny further supports the contention that *L. diaguita* belongs in its own species group separate from laeta. Our ecological niche analysis shows that *L. surca* and *L. laeta* have distinctly different allopatric habitats, and we suggest that these differences explain why one species became synanthropic, while the other did not.

ARTICLE HISTORY

Received 9 March 2021
Accepted 27 May 2021



KEYWORDS

Venomous spider; ecological niche; phylogeny; sister species; synanthropic

Introduction

The family Sicariidae Keyserling, 1880 comprises two genera in South America: *Sicarius* Walckenaer, 1847 with 21 species and *Loxosceles* Heineken & Lowe, 1832, with 139 described species (Brescovit et al. 2017; Magalhães et al. 2017). Both genera have spiders of medical importance and their venoms are recognised as dangerous to humans; however, only *Loxosceles* bites have been documented in the Neotropical region (Manríquez and Silva 2009; Swanson and Vetter 2009; Taucare-Ríos and Piel 2020; Arán-Sekul et al. 2020).

Gertsch (1967) allocated South American *Loxosceles* to four groups: gaucho, laeta, spadicea and amazonica. The group with the greatest diversity is the laeta group

CONTACT Andrés Taucare-Ríos  antaucar@unap.cl
 Supplemental data for this article can be accessed [here](#).

© 2021 Informa UK Limited, trading as Taylor & Francis Group

(Brescovit et al. 2017) – both *Loxosceles laeta* (Nicolet, 1849) and *Loxosceles surca* (Gertsch, 1967) have been proposed to belong to this group (Gertsch 1967).

Recently Brescovit et al. (2017) carried out a taxonomic revision of the genus in Chile, documenting a total of six species. For these authors, the *laeta* group, which dominates the desert and semi-desert environments of the region, stands out for its endemism and restricted distribution, with the exception of *L. laeta*. The Chilean recluse spider *L. laeta* is distributed from Arica to Magallanes (Gertsch 1967; Brescovit et al. 2017; Carvajal and Faúndez 2017), lives mainly in synanthropic habitats (Schenone et al. 1970; Taucare-Ríos et al. 2013) and, as a consequence, is responsible for most dermonecrotic arachnid envenomation in this country (Schenone 2003). In northern of Chile, this species is found in great abundance in urban habitats between the coast and the 'Pampa del Tamarugal', in or around human habitations, and under rocks associated with the roots of the trunks of the tamarugos (*Prosopis tamarugo* Philipi and *Prosopis alba* Griseb., both Fabaceae) in the absolute desert and some towns in the foothills (Taucare-Ríos and Sielfeld 2013; Brescovit et al. 2017). At these latitudes, a second species is also found, *L. surca*, but is present in more natural area, under rocks and scrub in foothills over 2500 metres above sea level (Taucare-Ríos 2011; Brescovit et al. 2017).

In addition to their close geographic proximity, *L. laeta* and *L. surca* also share close morphological similarity, even in their genitalia (Gertsch 1967; Brescovit et al. 2017). However, *Loxosceles* taxonomy is notoriously difficult to infer due to high intraspecific variability and high morphological similarity among related species (Gertsch 1967; Brescovit et al. 2017; Carvajal and Faúndez 2017). Consequently, we have decided to use molecular phylogenetics to help confirm the putative sister relationship between these two species – an approach that is used with increasing frequency with this genus (e.g. Valdez-Mondragón et al. 2019).

Ecological model niche (EMN) methods combine observations of species with environmental variables and have been used to gain ecological and evolutionary insights and to predict species distributions (Elith and Leathwick 2009). This approach makes it possible to map areas of environmental suitability for a species based on the abiotic conditions, even when species distributions are known from more limited locality data (Pearson et al. 2007). Therefore, in the absence of complete distribution records, ecological niche modelling can provide valuable predictive information on the distributional range of taxa, especially in those cases where few records are available (Raxworthy et al. 2003).

EMN can also provide evidence for allopatry between populations and can detect divergent ecological niche or a niche conservatism between closely related species (Peterson et al. 1999; Graham et al. 2004; Raxworthy et al. 2007; Aguirre-Gutiérrez et al. 2015; Kurnaz and Yousefkhani 2020). In this sense, Wiens and Graham (2005) proposed two scenarios: first, where very close species have similar niches, with one species predicting the other species distribution (niche conservatism, Peterson et al. 1999), or else where niches are divergent (Raxworthy et al. 2007). If the ranges of sister taxa do not overlap, the mode of speciation is hypothesised to be allopatric, whereas if sister species are primarily syntopic, sympatric speciation is inferred (Barraclough et al. 1998; Graham et al. 2004; Kurnaz and Yousefkhani 2020). On the other hand, if allopatric sister species segregate in environmental space, then ecological selection may have a role in speciation. Finally, if allopatric sister species are occupying an identical environmental space, then ecological divergence is not important, suggesting divergence in isolation (Peterson et al. 1999; Graham et al. 2004; Raxworthy et al. 2007).

The spider *L. surca* is little known, there are few records of its presence in Chile, and there are no data related to its ecological niche and distribution. We inferred a molecular phylogeny of the genus to confirm the close evolutionary affinity between *L. surca* and *L. laeta* and used ecological niche modelling to better delimit their respective ecologies. Our prediction is that these species will be closely related and therefore should have similar climatic niches, they likely compete in the same habitats for the same resources, and that therefore there is no reason to think that *L. surca* is not expanding into human habitations like *L. laeta*.

Material and methods

Biological material

The new record of *L. surca* presented here was sampled on 7 January 2020. The environmental characteristics of the collection site were categorised as autochthonous, because the absence of human activities. The taxonomic identification was reached based on the diagnosis of *L. surca* proposed by Brescovit et al. (2017) and the specimens were analysed with the aid of a stereoscopic microscope. The specimens were collected and deposited in 100% ethanol for later molecular analysis.

Niche modelling

We compiled occurrence data for *L. surca* and *L. laeta* by searching the scientific publications available in Brescovit et al. (2017). We found a total of 30 records (excluding repeating records) for *Loxosceles laeta* and 10 records for *Loxosceles surca*. The map of the current distribution for these two species is shown in Figure 1. The bioclimatic variables were obtained from the Worldclim database (<http://www.worldclim.org>). This database includes a total of 19 bioclimatic variables (Hijmans et al. 2005). We used five climatic variables in the model for *Loxosceles surca*: Altitude (ALT), Precipitation of Wettest Month (BIO13), Precipitation Seasonality (Coefficient of Variation) (BIO15), Precipitation of Warmest Quarter (BIO18) and Precipitation of Coldest Quarter (BIO19), and only two climatic variables for *Loxosceles laeta* (*sensu* Canals et al. 2016): Precipitation of Warmest Quarter (BIO18) and Altitude (ALT). The potential distribution was modelled with Maxent Version 3.3.4 (Phillips et al. 2009) which produces results ranging from 0 to 1, indicating the relative suitability of a given cell (Hijmans and Graham 2006; Phillips et al. 2006). Models were built in Maxent using default settings with logistic output. We selected the option auto features that allow automatic limiting of feature types for small sample sizes. We used 75% of the occurrence points to generate the potential distribution model and 25% were used for model validation (Phillips et al. 2006). Specific options were a bootstrap subsampling with 10 replicates, random seeding and the mean of replicates as output. The potential distribution generated by Maxent was restricted using the 10th percentile of the threshold and the precision of the model was evaluated using the AUC index.

Ecological niche properties: niche breadth and overlap

We obtained the niche breadth for each species using the Levins' inverse concentration metric (Levins 1968). The niche breadth ranges from 0, when only one grid cell in the

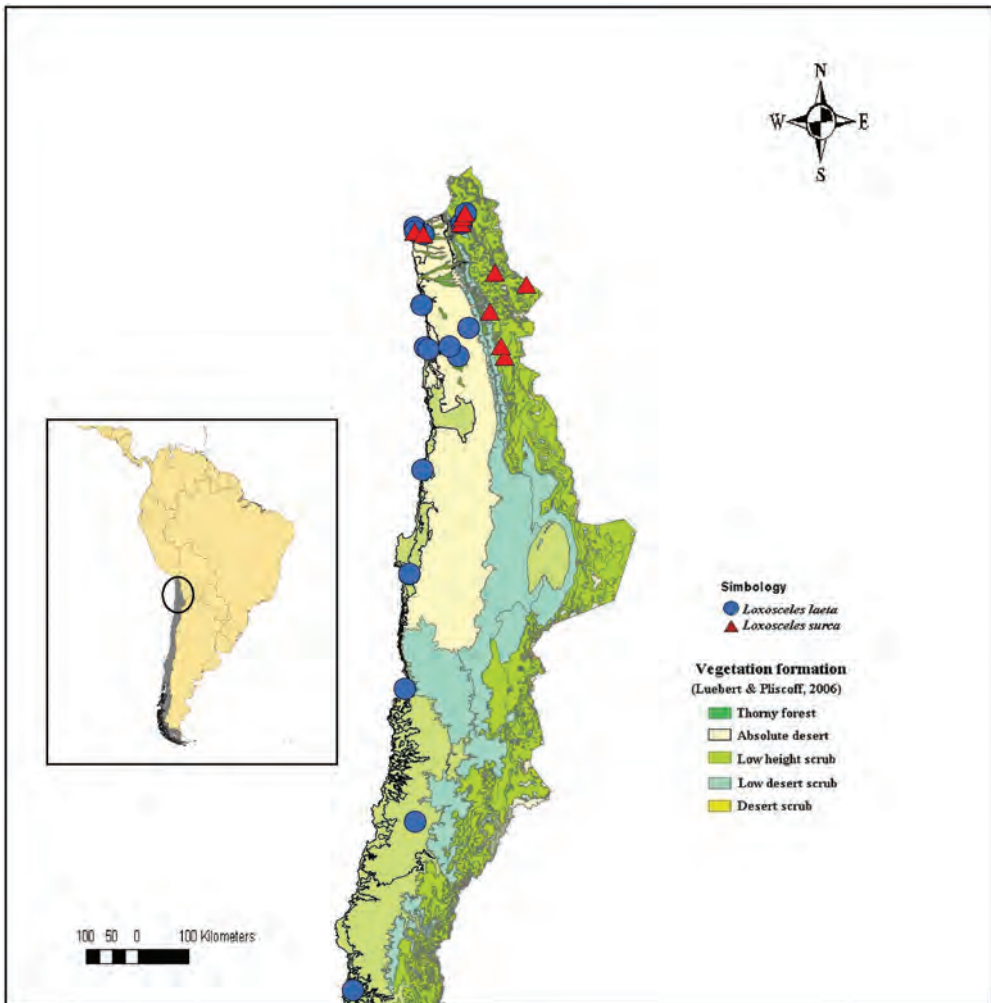


Figure 1. Location records for two species of *Loxosceles* showing the range overlap in northern of Chile; *L. laeta* (blue circles) and *L. surca* (red triangles).

geographical space has a non-zero suitability, to 1, when all grid cells are equally suitable, i.e. species with a wider environmental distribution render higher niche breadth values (Mandle et al. 2010). Niche overlap between the *Loxosceles* species was measured by two indices: a) firstly, we used the Schoener's D index which calculates the suitable range for a given species based on probability distributions for inhabiting a particular region (cells); b) finally, we used the Hellinger's-based I (Schoener and Gorman 1968) which compares probability distributions for both species in the environmental space. Both indices range from 0 (complete divergence/no overlap) to 1 (high similarity/complete overlap) (Warren et al. 2008, 2010; Aguirre-Gutiérrez et al. 2015; Kurnaz and Yousefkhani 2020). We compared the niche models for each species with a series of 100 pseudoreplicate models randomly generated (Warren et al. 2008). The Schoener's D and Hellinger's-based I of the true observed niche overlap were compared to the null distribution of these 100

replicates. If the observed niche overlap value is significantly smaller than the null distribution ($p < 0.05$), then the null hypothesis that the two species have similar ecological niches (niche conservatism) could be rejected (Warren et al. 2008). All these analyses were performed using ENMTools 1.3. (Warren et al. 2010).

Specimens collected

The following specimens were used in this study:

L. surca — Chile: Tarapacá region, Pozo Almonte, Road to Salar del Huasco, Altos de Pica, 1 ♀, 20°17'58.44"S 69°5'54.61"W, 3,540 m, 7. I.2020. W.H. Piel & A. Taucare-Ríos. Specimens were found under rocks associated with dry vegetation of high Andean grasses (Figure 2). The spiders likely feed on small epigeal insects, especially beetles that inhabit these environments. Near the foothills, these spiders coexists with other spider species, such as *Sicarius thomisoides* (Sicariidae) and *Odo patricius* (Xenoctenidae).

L. laeta — Chile: Tarapacá region: Iquique, Playa los Verdes, 1 ♂, 20°23'54"S 70°9'53"W, ~40 m, 13.ii.2016. W. H. Piel & A. Taucare-Ríos. Specimen recovered from a small cave under a boulder.

DNA extraction, amplification and sequencing

DNA extraction was performed on the leg from a *L. surca* specimen using a Quick-DNA Tissue/Insect Miniprep Kit (Zymo Research, Inc., Irvine, CA, USA).

Polymerase chain reaction amplification of the mitochondrial gene cytochrome C oxidase subunit I (COI) was performed using primers pairs LCO1490/C1-N-2191 and C1-J-2183/C1-N-2776 (Vidregar et al. 2014). Amplification of a portion of the nuclear ribosomal gene 28S was performed using primers 28SC/28SO (Hedin and Maddison 2001). Each PCR reaction used 2.5 µl of 10X ThermoPol® Reaction Buffer (New England BioLabs®), 0.125 µl of Taq DNA Polymerase (New England BioLabs®), 0.5 µl dNTP's (1st BASE dNTP Mix) (10 mM) and 1 µl of each primer (forward and reverse, 10 µM). The thermocycle programme included a denaturation step of 94°C, 35 cycles of 94°C for one minute, annealing at 40°C for one minute, and an extension at 72°C for one minute. PCR products were visualised on a 1% agarose gel stained with SYBR Safe (Invitrogen Corp., Carlsbad, CA, USA).

Amplicons were cleaned using Qiagen QIAquick PCR Purification Kit (Qiagen, Inc., Valencia, CA, USA) followed by quantification with a Thermo Scientific NanoDrop 2000 UV-VIS Spectrophotometer. Chain terminator Sanger sequencing was performed using BigDye® (Applied Biosystems) according to the manufacturer's thermocycle programme and with 10 µl reaction volumes. Each reaction included 2 µl of BigDye® Terminator 5X Sequencing Buffer, 0.5 µl of BigDye, 2 µl of primer (0.8 µM) and template with 50 ng of DNA. The products were subjected to the BigDye Ethanol-Sodium Acetate Clean-Up Protocol, and the sequences were obtained using an Applied Biosystems 96-capillary 3730/3730xl DNA Analyser. The resulting chromatograms were assembled and edited using Sequencher v. 4.9 (Gene Codes Corporation, Ann Arbor, MI, USA).

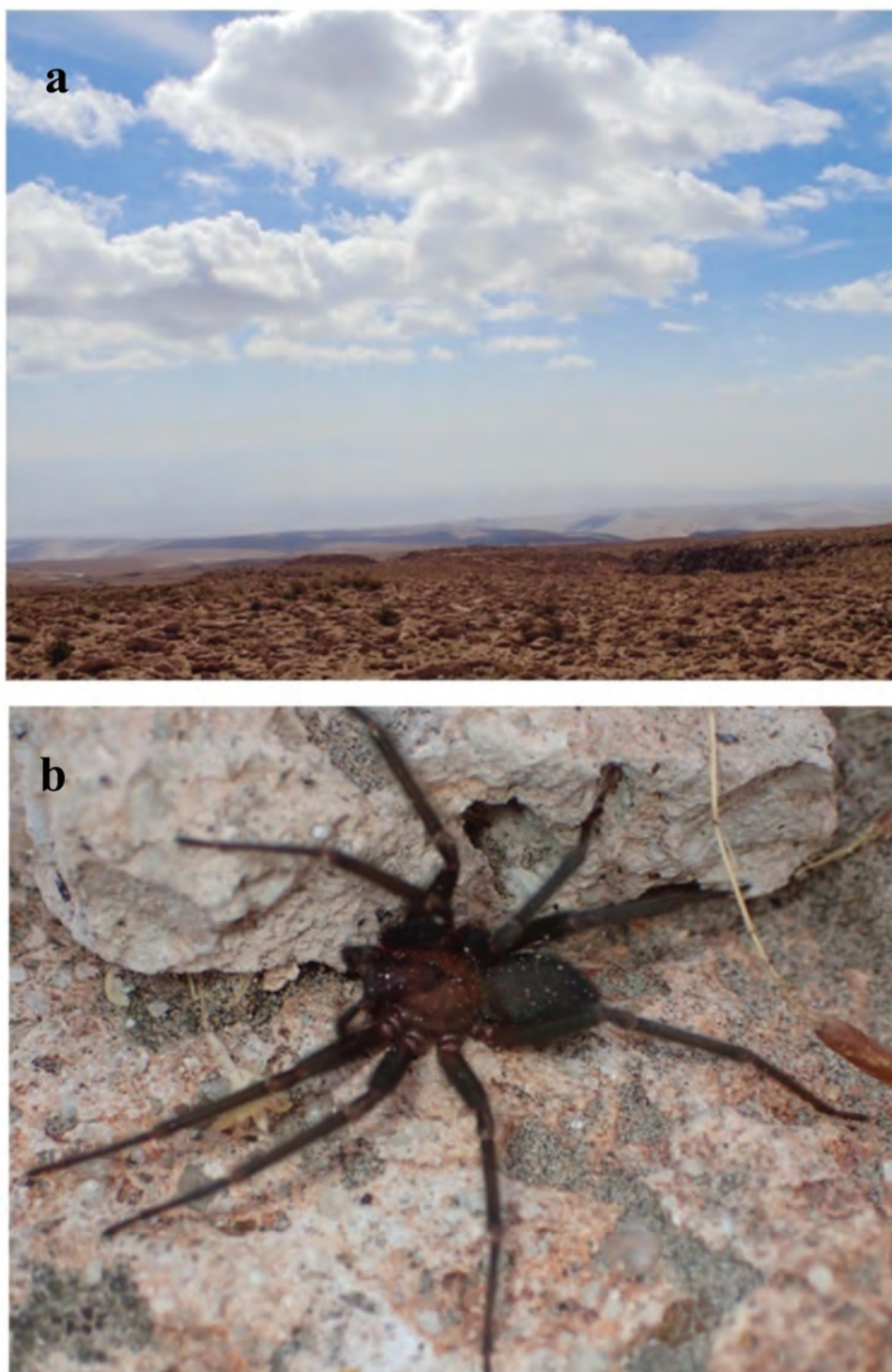


Figure 2. *Loxosceles surca* in northern of Chile. (a) Habitat where the spiders were found. (b) Live female specimen of the *Loxosceles surca*, Altos de Pica, Chile. (Photography: William H. Piel).

Phylogenetic analyses

The COI and 28S sequences of *L. surca* were queried against Genbank using BLASTN (Johnson et al. 2008), filtering the search results to the genus *Loxosceles*. Additionally, sequences were sourced from three species of *Sicarius* to serve as outgroups. Sequences for each matched species were assembled into alignments using Mesquite v. 3.61 (Maddison and Maddison 2019) and assisted by the MUSCLE programme. The alignment was pruned of all taxa with less than 550 bases in common with other taxa. A maximum likelihood search was performed on the alignment using RAxML (Stamatakis 2014), applying a GTR and gamma distributed substitution model, the data partitioned by gene and by codon, and with clade support estimated using 1,000 bootstrap replicates.

Results

DNA sequencing results

For each of *L. laeta* and *L. surca*, their four COI fragments assembled into sequences of length c. 1,285 bases and BLASTing against Genbank showed good correspondence with other known COI sequences sourced from *Loxosceles*. The two 28S fragments for *L. surca* assembled into a sequence of length 726. Subsequent BLASTing resulted in a 94% identity match with a *L. laeta* 28S sequence as expected; however, the alignment revealed three substantial INDELS of over 20 bases each, suggesting that we likely amplified a recent paralog. Paralogs of ribosomal subunits occasionally happen in spiders (e.g. Vink et al. 2011) and can potentially mislead phylogenetic results. As a result, we decided to exclude this sequence from our analysis.

Phylogenetic results

The assembled and pruned alignment was sourced from the Genbank accession numbers indicated in Table 1, which resulted in a matrix of 58 taxa and up to 1,860 sequences. The alignment and resulting phylogeny are deposited in TreeBASE with the URI <http://purl.org/phylo/treebase/phyloids/study/TB2:S27869>. The bootstrapped maximum likelihood result is indicated in Figure 3.

Ecological niche, habitat preferences and potential distribution

The most important environmental variables were precipitations and appear to be a limiting factor for the distribution of both species (Tables 2 and 3). The models have an excellent level of fit for *L. surca*: $AUC = 0.968 \pm 0,002$ and for *L. laeta*: $AUC = 0.91 \pm 0,002$. The model predicts a distribution restricted to the high Andean zone and foothills of the extreme north of Chile for *L. surca*, from Arica to Calama (Figure 4(a)). The greatest probabilities of occurrence for *L. surca* are found in the pre-Andean sector of Parinacota and Tarapaca, while the probabilities decrease towards the coast. This pattern is reversed for *L. laeta*, where the greatest probabilities of occurrence appear in arid coastal habitats in the north and centre of Chile (Figure 4(b)).

The corner spider *Loxosceles laeta*, seems to be adapted to more arid conditions (precipitation of warmest quarter: 0–58.8 mm; annual mean temperature: 14.4–17°C),

Table 1. Taxon labels, NCBI Genbank Accession Numbers, and published reference for the COI and 28S sequences used in this study.

Taxon Label	COI Accession	28S Accession	Reference Source
<i>Loxosceles</i> aff. <i>rufescens</i> Anti-Atlas	KF717007.1		Planas and Ribera 2014
<i>Loxosceles amazonica</i>	MN216037.1	EU817779.1	Binford et al. 2008
<i>Loxosceles apachea</i>	EU817665.1	EU817768.1	Binford et al. 2008
<i>Loxosceles arizonica</i>	EU817663.1	EU817769.1	Binford et al. 2008
<i>Loxosceles baja</i>	EU817661.1	EU817775.1	Binford et al. 2008
<i>Loxosceles blanda</i>	EU817664.1	EU817770.1	Binford et al. 2008
<i>Loxosceles caribbaea</i>	MF601287.1	MF600927.1	Petersen et al. 2021
<i>Loxosceles cf. spinulosa</i> GJB-2008	EU817686.1	EU817763.1	Binford et al. 2008
<i>Loxosceles chapadensis</i>	MN216038.1	MN219597.1	Magalhães et al. 2019
<i>Loxosceles chinateca</i>	EU817670.1		Binford et al. 2008
<i>Loxosceles colima</i>	EU817668.1	EU817777.1	Binford et al. 2008
<i>Loxosceles cubana</i>	MF601113.1	MF600811.1	Petersen et al. 2021
<i>Loxosceles deserta</i>	KY017913.1	EU817778.1	Binford et al. 2008
<i>Loxosceles diaguita</i>	MN216039.1	MN219598.1	Magalhães et al. 2019
<i>Loxosceles ericsoni</i>	MN216040.1	MN219599.1	Magalhães et al. 2019
<i>Loxosceles foutadjalloni</i>	GQ279238.1	GQ279187.1	Duncan et al. 2010
<i>Loxosceles gaucho</i>	FJ986178.1	GQ279184.1	Duncan et al. 2010
<i>Loxosceles hirsuta</i>	EU817678.1	EU817788.1	Binford et al. 2008
<i>Loxosceles hupalupa</i>		KP100147.1	Planas and Ribera 2014
<i>Loxosceles intermedia</i>	MN216041.1	MN219600.1	Magalhães et al. 2019
<i>Loxosceles jaca</i>	MN512428.1		Navarro-Rodríguez and Valdez-Mondragón 2020
<i>Loxosceles jamaica</i>	MF601298.1		Petersen et al. 2021
<i>Loxosceles jarmila</i>	MF601310.1		Petersen et al. 2021
<i>Loxosceles kaiba</i>	EU817662.1	EU817774.1	Binford et al. 2008
<i>Loxosceles lacta</i>	EU817672.1	EU817781.1	Binford et al. 2008
<i>Loxosceles laeta</i>	MW689929.1	GQ279183.1	Duncan et al. 2010
<i>Loxosceles malintzi</i>	MK936283.1		Navarro-Rodríguez and Valdez-Mondragón 2020
<i>Loxosceles misteca</i>	MK936276.1		Navarro-Rodríguez and Valdez-Mondragón 2020
<i>Loxosceles mrazig</i>	KF716998.1	GQ279185.1	Duncan et al. 2010
<i>Loxosceles nahuana</i>	MK936297.1		Navarro-Rodríguez and Valdez-Mondragón 2020
<i>Loxosceles persica</i>	MF467575.1		Tahami et al. 2017
<i>Loxosceles reclusa</i>	EU817669.1	EU817776.1	Binford et al. 2008
<i>Loxosceles sabina</i>	EU817666.1	EU817771.1	Binford et al. 2008
<i>Loxosceles similis</i>	MN216043.1	MN219601.1	Magalhães et al. 2019
<i>Loxosceles simillima</i>	MN216044.1		Magalhães et al. 2019
<i>Loxosceles</i> sp. 2 C1NR-2019	MK936306.1		Navarro-Rodríguez and Valdez-Mondragón 2020
<i>Loxosceles</i> sp. 2 GJB-2008	EU817694.1	EU817760.1	Binford et al. 2008
<i>Loxosceles</i> sp. 5 GJB-2008	EU817682.1	EU817765.1	Binford et al. 2008
<i>Loxosceles</i> sp. Fuerteventura-Lanzarote	KF669952.1		Planas and Ribera 2014
<i>Loxosceles</i> sp. Gran Canaria 1	KF669990.1		Planas and Ribera 2014
<i>Loxosceles</i> sp. La Gomera	KF670001.1		Planas and Ribera 2014
<i>Loxosceles</i> sp. RPD-2010 GC0101	GQ279111.1	GQ279112.1	Duncan et al. 2010
<i>Loxosceles</i> sp. RPD-2010 MA0201	GQ279226.1	GQ279195.1	Duncan et al. 2010
<i>Loxosceles</i> sp. Tenerife 2	KF669925.1		Planas and Ribera 2014
<i>Loxosceles</i> sp. Tenerife 3	KF669918.1		Planas and Ribera 2014
<i>Loxosceles spadicea</i>	EU817677.1	EU817787.1	Binford et al. 2008
<i>Loxosceles speluncarum</i>	EU817692.1	EU817751.1	Binford et al. 2008
<i>Loxosceles speluncarum</i>	EU817693.1	EU817754.1	Binford et al. 2008
<i>Loxosceles spinulosa</i>	EU817688.1	EU817756.1	Binford et al. 2008
<i>Loxosceles surca</i>	MW689930.1		This Study
<i>Loxosceles taino</i>	MF601103.1	MF600809.1	Petersen et al. 2021
<i>Loxosceles tenango</i>	MK936290.1		Navarro-Rodríguez and Valdez-Mondragón 2020

(Continued)

Table 1. (Continued).

Taxon Label	COI Accession	28S Accession	Reference Source
<i>Loxosceles tenochtitlan</i>	MK936280.1		Navarro-Rodríguez and Valdez-Mondragón 2020
<i>Loxosceles tolantongo</i>	MK936294.1		Navarro-Rodríguez and Valdez-Mondragón 2020
<i>Loxosceles variegata</i>	EU817675.1	EU817785.1	Binford et al. 2008
<i>Loxosceles vonwredei</i>	EU817681.1	EU817767.1	Binford et al. 2008
<i>Loxosceles zapoteca</i>	MK936302.1	MN525286.1	Navarro-Rodríguez and Valdez-Mondragón 2020
<i>Sicarius peruensis</i>	MN216099.1	MN219620.1	Magalhães et al. 2019
<i>Sicarius rugosus</i>	EU817706.1	EU817736.1	Binford et al. 2008
<i>Sicarius terrosus</i>	EU817704.1	EU817740.1	Binford et al. 2008

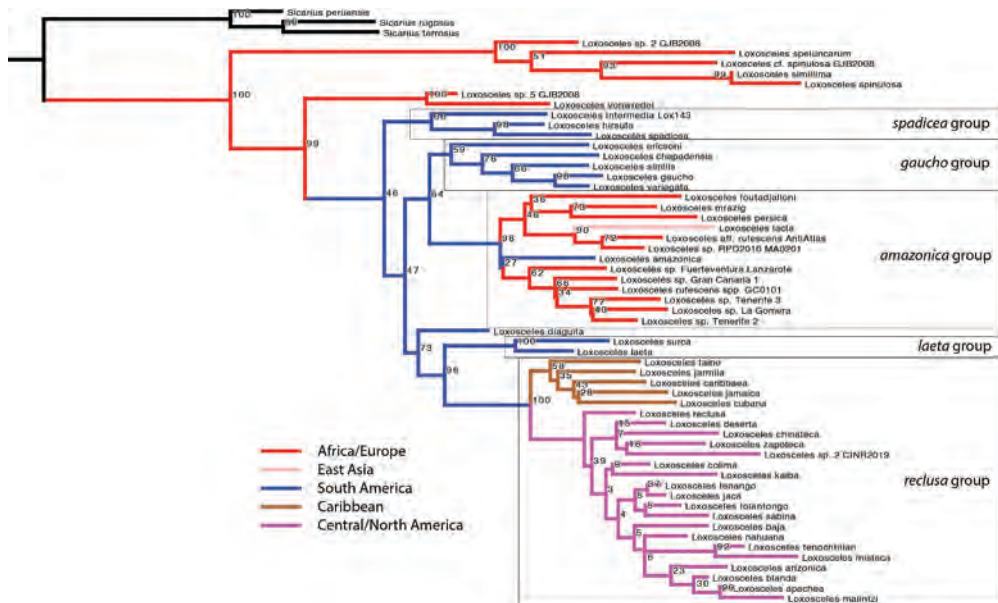


Figure 3. Maximum likelihood phylogeny of an alignment of COI and 28S sequences from *Loxosceles* species. The digits by each clade indicate percent bootstrap support based on 1,000 replicates. The species groups, as delineated by Gertsch (1967), are indicated by boxes enclosing clades. Continental biogeographic history is estimated using common-sense inference based on contemporary species distributions and is indicated in the figure using branch colours.

Table 2. Percentage contribution of the variables studied for *Loxosceles surca*.

Variable	Percent contribution (%)	Permutation importance (%)
Bio19	57.7	74.6
Bio15	20.8	6.7
Bio18	17.8	15.6
Bio13	2.5	3.1
Altitude	1.2	0.0

being present naturally in coastal scrub, thorn forest and in the absolute desert. On the other hand, the spider *Loxosceles surca* is restricted to medium and higher altitude environments with greater precipitation and low annual mean temperatures

Table 3. Percentage contribution of the variables studied for *Loxosceles laeta*.

Variable	Percent contribution (%)	Permutation importance (%)
Bio18	56	58
Altitude	44	42

(precipitation of warmest quarter: 154.4–193.6 mm; annual mean temperature: 6.5–9.6°C) (Figure 5), so it would be associated with high altitude scrub.

Niche breadth and overlap

The results from the niche breadth assessment showed a high variation in environmental suitability for *Loxosceles laeta* compared with *L. surca*. The highest niche breadth that we found was 0.392 for *L. laeta*, which also presented the broadest distribution of suitable habitat in Chile. The niche breadth of *Loxosceles surca* was low (0.105) and this species had a narrower distribution of suitable habitat. Although both spiders are closely related species, they occupy considerably different climatic niches and also differed in their niche space (niche overlap, $D = 0.11$; $I = 0.25$). In this sense, the identity test (niche similarity) indicated that the climatic niche overlap values were significantly smaller than the null distribution (Figure 6), supporting a pattern of niche divergence rather than niche conservatism between *L. laeta* and *L. surca* ($D_{H0} = 0.56 \pm 0.06$ vs. $D_{H1} = 0.11$ and $I_{H0} = 0.82 \pm 0.05$ vs. $I_{H1} = 0.25$; t-test, $df = 99$, $P < 0.05$).

Discussion

Our results show that (a) the two species are, indeed, in the same *laeta* species group and are likely to be sister species, and (b) while they overlap in latitude, they are allopatric and have distinctively different and non-overlapping climatic/ecological niches. Although they are very similar species, both their ecological niche and genetic differentiation suggest a process of allopatric speciation. The phylogeny also supports the contention that *L. diaguila* belongs in its own species group as hypothesised by Brescovit et al. (2017) but does not support their hypothesis that it is sister to the *spadicea* group. We confirm that *L. laeta* has a wider distribution with a large niche breadth (i.e. generalist species), is adapted to arid environmental conditions and is presently a mainly synanthropic species that lives mostly in coastal areas and shows low abundance in natural environments. By contrast, *L. surca* has a narrower niche and is found in natural environments at medium and high altitudes where temperatures are low and rainfall is higher than in coastal environments. For both species, rainfall seems to be a factor in their native distribution, and they only coexist in some intermediate altitude locations.

Relatively speaking, a very small number of spider species, known as synanthropics (Nuorteva 1963), have developed a close relationship with human settlements (Duran-Barrón et al. 2009; Taucare-Ríos et al. 2013). The degree of this relationship depends on the species, geographic and type of climates, as well as the characteristics of the habitat (Uribe-M et al. 2010; Taucare-Ríos et al. 2013). Gregor and Povolny (1958) classified synanthropy into three categories according to the abundance of each species in a determined area: 1) eusynanthropic, 2) hemisynanthropic, and 3) asynanthropic. In

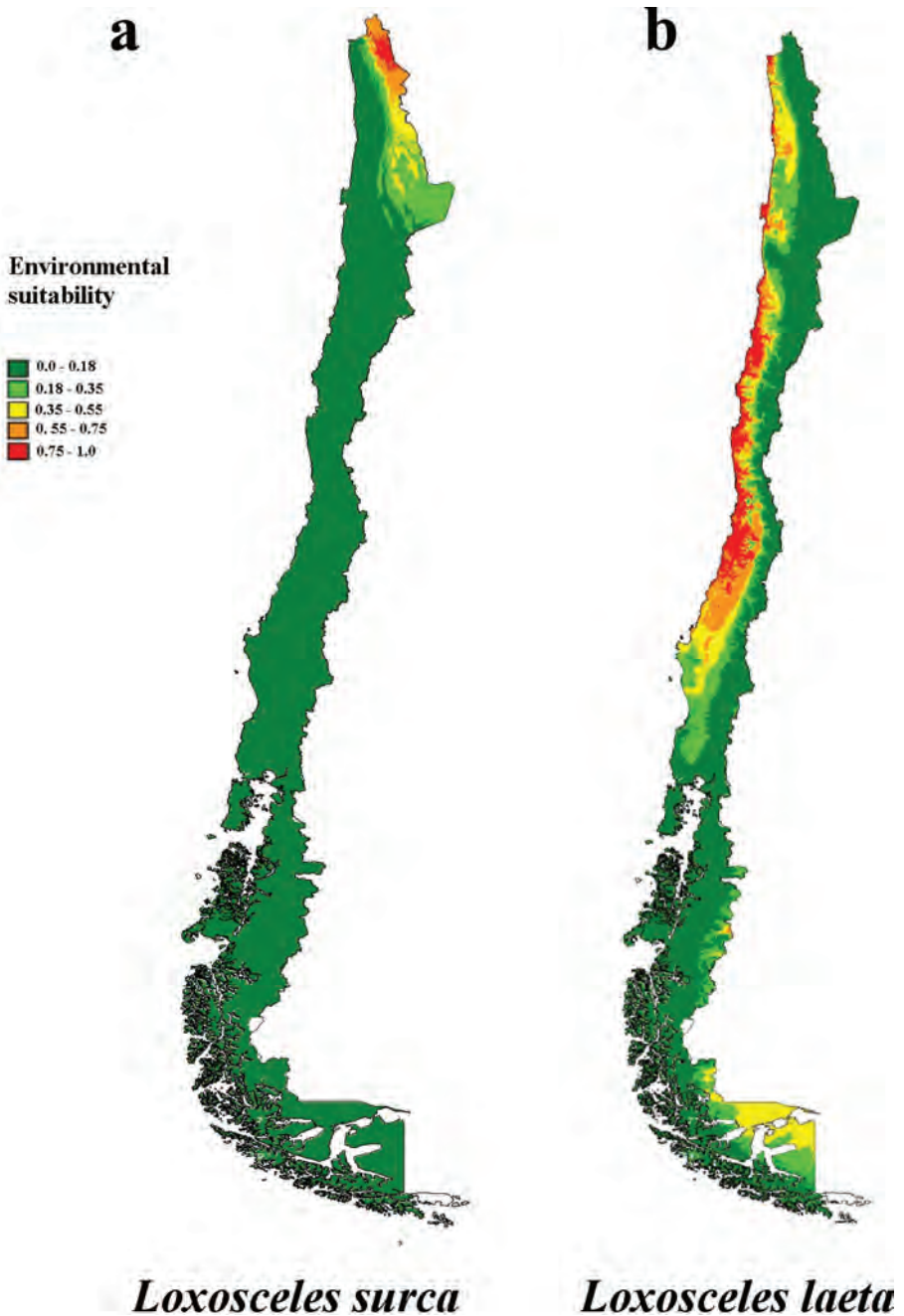


Figure 4. Environmental suitability map for *Loxosceles surca* and *Loxosceles laeta* under Maxent algorithm. Colours represent different ranges of probabilities of presence (high probability: 0.75–1.0). (a) Potential distribution of *Loxosceles surca*. (b) Potential distribution of *Loxosceles laeta*.

the case of the eusynanthropic species, they are typically urban and can be found mainly within human dwellings; hemisynanthropic species inhabit natural and urban areas alike; and asynanthropic species are very common in natural environments and less common in

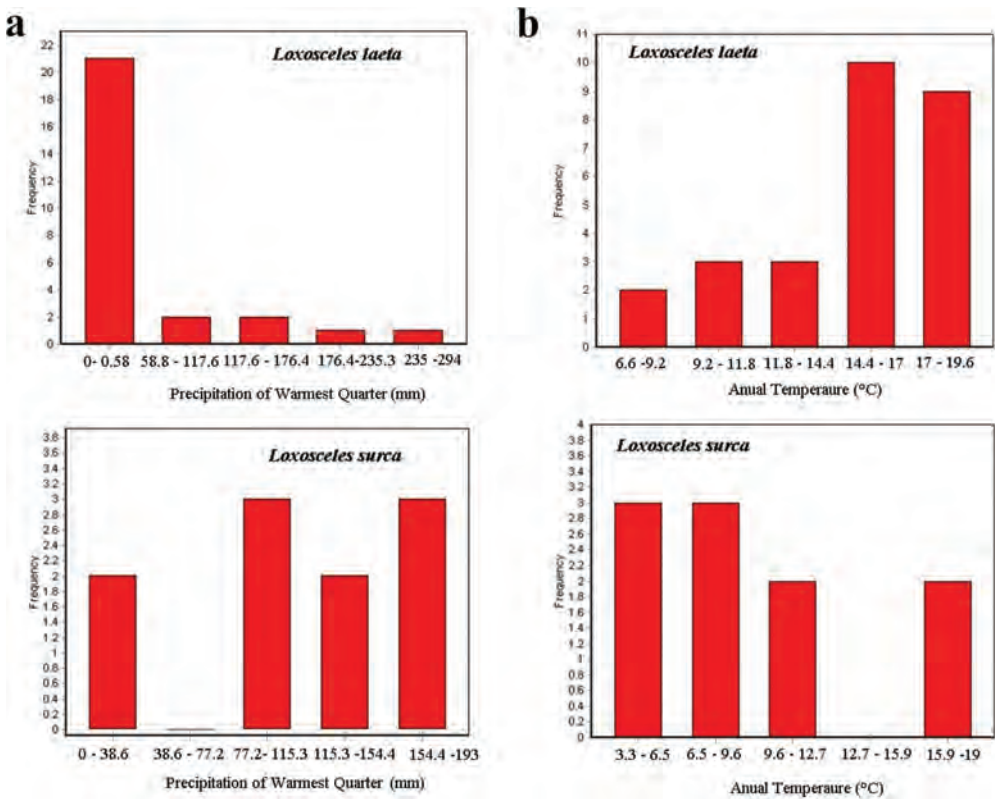


Figure 5. Precipitations and annual mean temperatures both *Loxosceles laeta* and *Loxosceles surca* records. (a) Histogram of the frequency of precipitation of warmest quarter period, constructed from the known distribution of both species. (b) Histogram of the frequency of annual mean temperature, constructed from the known distribution of both species.

urban areas. Some spider species like *Loxosceles laeta* become eusynanthropic under certain conditions (Duran-Barrón et al. 2009; Taucare-Ríos et al. 2013), such as having a generalist broad niche that brings them into contact with human habitations and having the plasticity to expand their niche to occupy new environments outside natural ones (novel niche hypothesis) (Shea and Chesson 2002).

Our study illustrates a notable contrast between two closely related species: *L. surca*, which has remained asynanthropic, and *L. laeta*, which has become eusynanthropic. As a consequence of this shift, *L. laeta* has vastly expanded its distribution and has emerged as a spider of medical importance because of its frequent contact with humans. This transition of *Loxosceles laeta* from natural to urban habitats could be facilitated by some aspects of its physiology. This species has great thermal tolerance, preferential temperatures between 16°C and 22°C (temperatures very common inside houses) and great tolerance to desiccation in comparison to another species (Alfaro et al. 2013; Canals et al. 2013). In addition, urban environments provide a constant availability of prey and stable ambient temperatures that match with their preferred temperatures and conditions would not be found in natural environments (Taucare-Ríos et al. 2013; Canals et al. 2016). On the other hand, the restricted distribution, habitat requirements, preference for

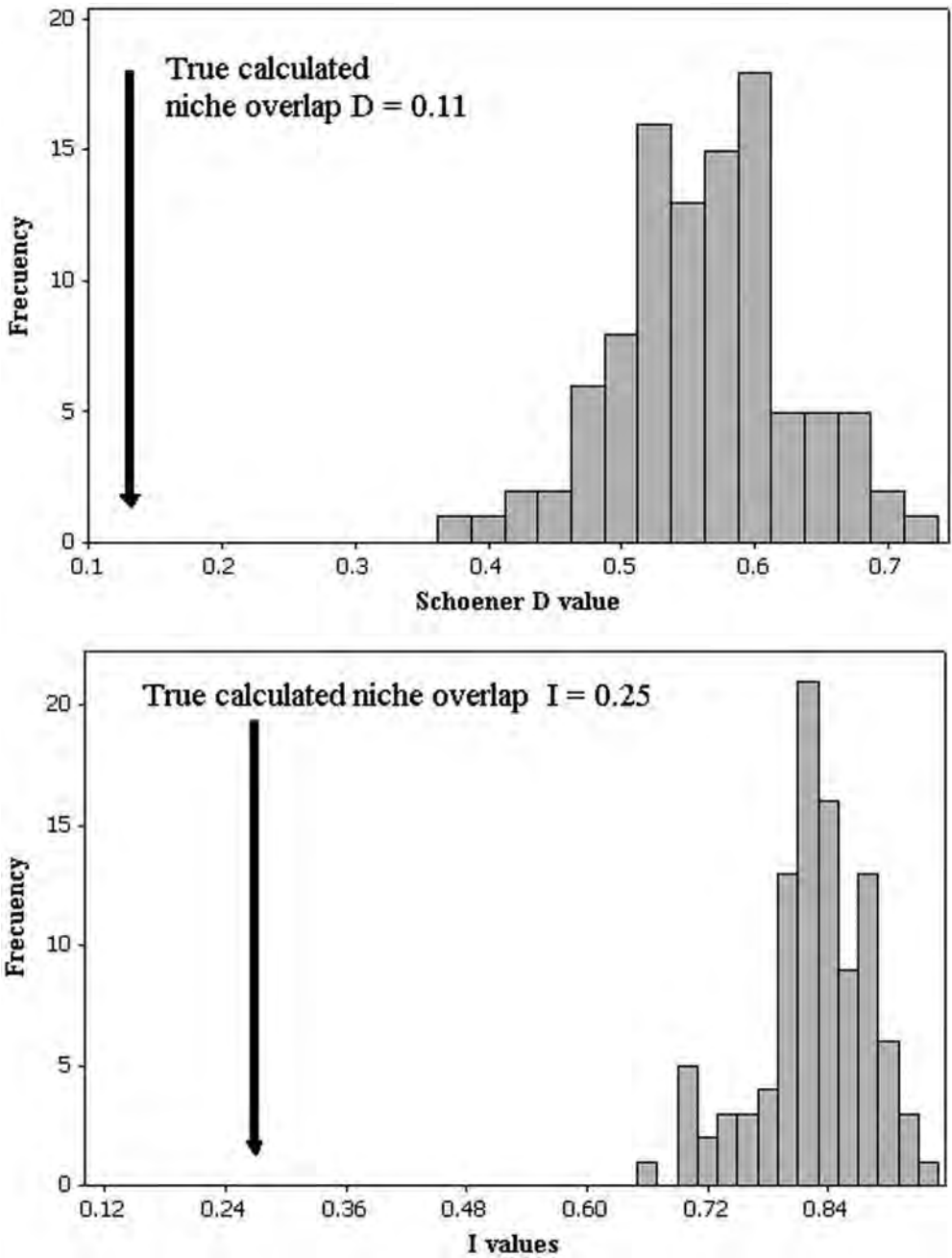


Figure 6. Identity test between *L. laeta* and *L. surca* in Chile. The expected niche area is significantly out of the observed niche between them.

low temperatures and low dispersal capacity (there are practically no human settlements where this spider lives) of *Loxosceles surca* could make it more difficult for it to colonise urban environments and expand its distribution.

One likely prerequisite for living in human habitations is a tolerance for xeric conditions, since neither rain nor dew falls inside the home. All sicariids of the Atacama region are, in this sense, exadapted to eusynanthropy because of their natural desert origins. Another likely prerequisite is whether the spiders' retreats or webs are amenable to human habitation. Among candidate sicariids, this requirement disfavors *Sicarius* species because they cannot climb slick vertical walls and they depend on a narrow rock-sand interface for brood rearing (Reiskind 1969; Magalhães et al. 2017, 2019). However, both *Loxosceles* species can build webbing in dark corners or under furniture much as they would build webbing under rocks or on the walls of caves, so we expect both species to be good candidates for acquiring eusynanthropy.

How is it, then, that *L. laeta* but not *L. surca* has become more synanthropic, and in so doing its distribution has greatly expanded much like *L. reclusa* has done in the Nearctic (reviewed in Vetter 2015). This synanthropic transition is important because it has also allowed *L. laeta* to become a 'tramp' species, having invaded distant regions such as U.S.A, Australia, and Finland (Canals et al. 2016; Brescovit et al. 2017; World Spider Catalog 2021), and to have become of medical concern because of its frequent contact with humans. Our ENM analysis suggests that the reason for the difference is that *L. surca* has a distinctly different and separate niche from *L. laeta*, restricting the former to a narrow climatic range at high elevations where humans are scarce, which contrasts with the far more populated coastal regions of the Atacama where *L. laeta* lives naturally. The constraining effect of limited rainfall on the populations of *Loxosceles laeta* would explain why it has adapted to urban indoor environments and is absent in natural environments of central and southern Chile (Schenone et al. 1970; Taucare-Ríos et al. 2013), where annual rainfall is widely higher than in the north of this country. Future studies could investigate whether other *Loxosceles* species, have the potential to become completely synanthropic species, especially in a scenario of climate change and the increasing desertification towards the south of this country. This information would be of medical relevance, since all the species of this genus are species recognised as potentially dangerous to humans.

Acknowledgements

We thank Antonio D. Brescovit and Guillermo D'Elía for useful comments in the manuscript.

Disclosure statement

No potential conflict of interest was reported by the author(s).

ORCID

Andrés Taucare-Ríos  <http://orcid.org/0000-0002-3850-2239>

William H. Piel  <http://orcid.org/0000-0002-0429-9797>

References

- Aguirre-Gutiérrez J, Serna-Chavez HM, Villalobos-Arambula AR, Rosa JAP, Raes N. 2015. Similar but not equivalent: ecological niche comparison across closely-related Mexican white pines. *Divers Distrib.* 21(3):245–257. doi:10.1111/ddi.12268.
- Alfaro C, Veloso C, Torres-Contreras H, Solís R, Canals M. 2013. Thermal niche overlap of the brown recluse spider *Loxosceles laeta* (Araneae; Sicariidae) and its possible predator, the spitting spider *Scytodes globula* (Scytodidae). *J Therm Biol.* 38:502–507. doi:10.1016/j.jtherbio.2013.08.003.
- Arán-Sekul T, Perčić-Sarmiento I, Valencia V, Olivero N, Rojas JM, Araya JE, Taucare-Ríos A, Catalán A. 2020. Toxicological Characterization and Phospholipase D Activity of the Venom of the Spider *Sicarius thomisoides*. *Toxins.* 12:702. doi:10.3390/toxins12110702.
- Barracough TG, Vogler AP, Harvey PH. 1998. Revealing the factors that promote speciation. *Proc R Soc B: Biol Sci.* 353:241–249.
- Binford GJ, Callahan MS, Bodner MR, Rynerson MR, Núñez PB, Ellison CE, Duncan RP. 2008. Phylogenetic relationships of *Loxosceles* and *Sicarius* spiders are consistent with Western Gondwanan vicariance. *Mol Phylogenet Evol.* 49(2):538–553. doi:10.1016/j.ympev.2008.08.003.
- Brescovit AD, Taucare-Ríos A, Magalhães ILF, Santos AJ. 2017. On Chilean *Loxosceles* (Araneae: Sicariidae): first description of the males of *L. surca* and *L. coquimbo*, new records of *L. laeta* and three remarkable new species from coastal deserts. *Eur J Taxon.* 388:1–20.
- Canals M, Alfaro C, Veloso C, Torres-Contreras H, Solís R. 2013. Tolerancia a la desecación y sobreposición del nicho térmico entre la araña del rincón *Loxosceles laeta* y un posible control biológico, la araña tigre *Scytodes globula*. *Rev Parasitología Latinoam.* 72:52–60.
- Canals M, Taucare-Ríos A, Brescovit AD, Peña-Gomez F, Bizama G, Canals A, Moreno L, Bustamante RO. 2016. Niche modelling of the Chilean recluse spider *Loxosceles laeta* and araneophagic spitting spider *Scytodes globula* and risk for loxoscelism in Chile. *Med Vet Entomol.* 30(4):383–391. doi:10.1111/mve.12184.
- Carvajal MA, Faúndez EI. 2017. Sobre la presencia de la araña de rincón *Loxosceles laeta* (Nicolet, 1849) (Araneae: Sicariidae) en Magallanes (Chile). *Archivos Entomoloxicos.* 18:355–359.
- Duncan RP, Rynerson MR, Ribera C, Binford GJ. 2010. Diversity of *Loxosceles* spiders in Northwestern Africa and molecular support for cryptic species in the *Loxosceles rufescens* lineage. *Mol Phylogenet Evol.* 55(1):234–248. doi:10.1016/j.ympev.2009.11.026.
- Duran-Barrón CG, Francke OF, Pérez-Ortiz TM. 2009. Diversidad de arañas (Arachnida: Araneae) asociadas a viviendas de la ciudad de México (Área metropolitana). *Rev Mex Biodivers.* 80:55–69.
- Elith J, Leathwick JR. 2009. Species distribution models: ecological explanation and prediction across space and time. *Annu Rev Ecol Syst.* 40:677–697. doi:10.1146/annurev.ecolsys.110308.120159.
- Gertsch WJ. 1967. The spider genus *Loxosceles* in South America (Araneae, Scytodidae). *Bull Am Mus Nat Hist.* 136:117–174.
- Graham CH, Ron SR, Santos JC, Schneider CJ, Moritz M. 2004. Integrating phylogenies and environmental niche models to explore speciation mechanisms in dendrobatid frogs. *Evolution.* 58:1781–1793. doi:10.1111/j.0014-3820.2004.tb00461.x.
- Gregor F, Povolny D. 1958. Versuch einer Klassifikation der synanthropen Fliegen. *J Hyg Epidemiol Microbiol Immunol.* 2:205–216.
- Hedin MC, Maddison WP. 2001. A combined molecular approach to phylogeny of the jumping spider subfamily Dendryphantinae (Araneae, Salticidae). *Mol Phylogenet Evol.* 18:386–403. doi:10.1006/mpev.2000.0883.
- Hijmans RJ, Graham CH. 2006. The ability of climate envelope models to predict the effect of climate change on species distributions. *Global Change Biol.* 12:1–10.
- Hijmans RJ, Guarino L, Jarvis A, O'Brien R, Mathur P, Bussink C, Cruz M, Barrantes I, Rojas E. 2005. DIVA-GIS. Version 5.4.0.1. [accessed 2021 Jan 7]. <http://www.diva-gis.org/>
- Johnson M, Zaretskaya I, Raytselis Y, Merezuk Y, McGinnis S, Madden TL. 2008. NCBI BLAST: a better web interface. *Nucleic Acids Res.* 36:W5–W9. doi:10.1093/nar/gkn201.
- Kurnaz M, Yousefkhani SSH. 2020. Ecological niche divergence between *Darevskia rudis* and *D. bithynica* (Lacertidae) in Turkey. *Biologia.* 75(9):1307–1312. doi:10.2478/s11756-019-00374-0.

- Levins R. 1968. Evolution in changing environments: some theoretical explorations. Princeton Univ. Press.
- Maddison WP, Maddison DR. 2019. Mesquite: a modular system for evolutionary analysis. Version 3.61. [accessed 2021 Jan 15]. <http://www.mesquiteproject.org>.
- Magalhães ILF, Brescovit AD, Santos AJ. 2017. Phylogeny of Sicariidae spiders (Araneae: Haplogynae), with a monograph on Neotropical *Sicarius*. Zool J Linn Soc. 179(4):767–864.
- Magalhães ILF, Neves DM, Santos FR, Vidigal THDA, Brescovit AD, Santos AJ. 2019. Phylogeny of Neotropical *Sicarius* sand spiders suggests frequent transitions from deserts to dry forests despite antique, broad-scale niche conservatism. Mol Phylogenet Evol. 140:106569. doi:10.1016/j.ympev.2019.106569.
- Mandle L, Warren DL, Hoffmann MH, Peterson AT, Schmitt J, von Wettberg EJ. 2010. Conclusions about niche expansion in introduced impatiens walleriana populations depend on method of analysis. Plos One. 5:e15297. doi:10.1371/journal.pone.0015297.
- Manríquez JJ, Silva S. 2009. Loxoscelismo cutáneo y cutáneo-visceral: revisión sistemática. Rev Chil Infectología. 26(5):420–432. doi:10.4067/S0716-10182009000600004.
- Navarro-Rodríguez CI, Valdez-Mondragón A. 2020. Description of a new species of *Loxosceles* Heineken & Lowe (Araneae, Sicariidae) recluse spiders from Hidalgo, Mexico, under integrative taxonomy: morphological and DNA barcoding data (CO1+ ITS2). Eur J Taxon. 704:1–30.
- Nuorteva P. 1963. Synanthropy of Blowflies (Diptera: Calliphoridae) in Finlandia. Ann Entomologicae Fennicae. 29:1–49.
- Pearson RG, Raxworthy CJ, Nakamura M, Peterson AT. 2007. Predicting species distributions from small numbers of occurrence records: a test case using cryptic geckos in Madagascar. J Biogeogr. 34:102–117. doi:10.1111/j.1365-2699.2006.01594.x.
- Petersen I, Agnarsson I, Coddington JA, Binford GJ. 2021. Biogeography of recluse spiders (*Loxosceles*) from Caribbean caves to continents. In prep.
- Peterson AT, Soberon J, Sánchez-Cordero V. 1999. Conservatism of ecological niches in evolutionary time. Science. 285:1265–1267. doi:10.1126/science.285.5431.1265.
- Phillips SJ, Anderson RP, Schapire RE. 2006. Maximum entropy modeling of species geographic distributions. Ecol Model. 190:231–259.
- Phillips SJ, Dudik M, Schapire RE. 2009. Maxent software for modeling species niches and distributions. [accessed 2021 Feb 15]. http://biodiversityinformatics.amnh.org/open_source/maxent/
- Planas E, Ribera C. 2014. Uncovering overlooked island diversity: colonization and diversification of the medically important spider genus *Loxosceles* (Arachnida: Sicariidae) on the Canary Islands. J Biogeogr. 41(7):1255–1266. doi:10.1111/jbi.12321.
- Raxworthy CJ, Ingram C, Rabibisoa N, Pearson R. 2007. Species delimitation applications for ecological niche modeling: a review and empirical evaluation using Phelsuma day Gecko Groups from Madagascar. Syst Biol. 56:907–923. doi:10.1080/10635150701775111.
- Raxworthy CJ, Martinez-Meyer E, Horning N, Nussbaum RA, Schneider GE, Ortega-Huerta MA, Peterson AT. 2003. Predicting distributions of known and unknown reptile species in Madagascar. Nature. 426:837–841. doi:10.1038/nature02205.
- Reiskind J. 1969. Stereo typed burying behavior in *Sicarius*. Am Zool. 9(1):195–200. doi:10.1093/icb/9.1.195.
- Schenone H. 2003. Cuadros tóxicos producidos por mordeduras de araña en Chile: latroductismo y loxoscelismo. Rev Médica Chile. 131:437–444. doi:10.4067/S0034-98872003000400013.
- Schenone H, Rojas A, Villarreal F, Suarez G. 1970. Prevalence of *Loxosceles laeta* in houses in central Chile. Am J Trop Med Hyg. 16:564–567. doi:10.4269/ajtmh.1970.19.564.
- Schoener TW, Gorman GC. 1968. Some niche differences in three lesser Antillean lizards of the genus *Anolis*. Ecology. 49:819–830. doi:10.2307/1936533.
- Shea K, Chesson P. 2002. Community ecology theory as a framework for biological invasions. Trends Ecol Evol. 17:170–176. doi:10.1016/S0169-5347(02)02495-3.
- Stamatakis A. 2014. RAxML version 8: a tool for phylogenetic analysis and post-analysis of large phylogenies. Bioinformatics. 30(9):1312–1313. doi:10.1093/bioinformatics/btu033.
- Swanson DL, Vetter RS. 2009. Loxoscelism. Clin Dermatol. 24:213–221. doi:10.1016/j.clindermatol.2005.11.006.

- Tahami MS, Zamani A, Sadeghi S, Ribera C. 2017. A new species of *Loxosceles* Heineken & Lowe, 1832 (Araneae: Sicariidae) from Iranian caves. *Zootaxa*. 4318(2):377–387. doi:[10.11646/zootaxa.4318.2.10](https://doi.org/10.11646/zootaxa.4318.2.10).
- Taucare-Ríos A. 2011. *Loxosceles surca* (Gertsch, 1967) (Araneae: Sicariidae) en el norte de Chile. *Bol Biodivers Chile*. 5:45–49.
- Taucare-Ríos A, Brescovit A, Canals M. 2013. Synanthropic spiders (Arachnida: Araneae) from Chile. *Rev Ibérica Aracnología*. 23:49–56.
- Taucare-Ríos A, Piel WH. 2020. Predation on the gecko *Phyllodactylus gerrhopygus* (Wiegmann) (Squamata: Gekkonidae) by the six-eyed sand spider *Sicarius thomisoides* (Walckenaer) (Araneae: Sicariidae). *Rev Soc Entomol Argent*. 79(2):48–51. doi:[10.25085/rsea.790207](https://doi.org/10.25085/rsea.790207).
- Taucare-Ríos A, Sielfeld W. 2013. Arañas (Arachnida: Araneae) del extremo norte de Chile. *Bol Museo Nacional Hist Nat*. 62:7–27.
- Uribe-M N, Wolff M, de Carvalho CJ. 2010. Synanthropy and ecological aspects of Muscidae (Diptera) in a tropical dry forest ecosystem in Colombia. *Revista Bras Entomol*. 54(3):462–470. doi:[10.1590/S0085-56262010000300018](https://doi.org/10.1590/S0085-56262010000300018).
- Valdez-Mondragón A, Navarro-Rodríguez CI, Solís-Catalán KP, Cortez-Roldán MR, Juárez-Sánchez AR. 2019. Under an integrative taxonomic approach: the description of a new species of the genus *Loxosceles* (Araneae, Sicariidae) from Mexico City. *Zookeys*. 892:93–133. doi:[10.3897/zookeys.892.39558](https://doi.org/10.3897/zookeys.892.39558).
- Vetter RS. 2015. The brown recluse spider. Ithaca (NY): Cornell University Press.
- Vidergar N, Toplak N, Kuntner M. 2014. Streamlining DNA barcoding protocols: automated DNA extraction and a new *cox1* primer in arachnid systematics. *PLoS One*. 9(11):e113030. doi:[10.1371/journal.pone.0113030](https://doi.org/10.1371/journal.pone.0113030).
- Vink CJ, Dupérré N, McQuillan BN. 2011. The black-headed jumping spider, *Trite planiceps* Simon, 1899 (Araneae: Salticidae): redescription including cytochrome c oxidase subunit 1 and paralogous 28S sequences. *NZ J Zool*. 38(4):317–331. doi:[10.1080/03014223.2011.613939](https://doi.org/10.1080/03014223.2011.613939).
- Warren D, Glor R, Turelli M. 2010. ENMTools: a toolbox for comparative studies of environmental niche models. *Ecography*. 33:607–611.
- Warren DL, Glor RE, Turelli M. 2008. Environmental niche equivalency versus conservatism: quantitative approaches to niche evolution. *Evolution*. 62:2868–2883. doi:[10.1111/j.1558-5646.2008.00482.x](https://doi.org/10.1111/j.1558-5646.2008.00482.x).
- Wiens JJ, Graham CH. 2005. Niche conservatism: integrating evolution, ecology, and conservation biology. *Annu Rev Ecol Evol Syst*. 36:519–539. doi:[10.1146/annurev.ecolsys.36.102803.095431](https://doi.org/10.1146/annurev.ecolsys.36.102803.095431).
- World Spider Catalog. 2021. World Spider Catalog. Version 22.0. Natural History Museum Bern. [accessed 2021 Feb 15]. <http://wsc.nmbe.ch>.