

Matching global and regional distribution models of the recluse spider *Loxosceles rufescens*: to what extent do these reflect niche conservatism?

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Abstract. The Mediterranean recluse spider, *Loxosceles rufescens* (Dufour, 1820) (Araneae: Sicariidae) is a cosmopolitan spider that has been introduced in many parts of the world. Its bite can be dangerous to humans. However, the potential distribution of this alien species, which is able to spread fairly quickly with human aid, is completely unknown. Using a combination of global and regional niche models, it is possible to analyse the spread of this species in relation to environmental conditions. This analysis found that the successful spreading of this species varies according to the region invaded. The majority of populations in Asia are stable and show niche conservatism, whereas in North America this spider is expected to be less successful in occupying niches that differ from those in its native region and that do not support its synanthropic way of living.

Key words. Alien spider, biological invasions, loxoscelism, niche conservatism, regional niche.

Introduction

The spread of alien spiders beyond their native environments has increased significantly in the last decades as a result of the global transportation of people and goods (Kobelt & Nentwig, 2008; Nentwig, 2015). As generalist predators, alien spiders have the potential to affect native arthropod species assemblages and, as venomous animals, can also affect human health (Nyffeler *et al.*, 1986; Gruner, 2005; Taucare-Ríos *et al.*, 2016; Nentwig *et al.*, 2017).

The genus *Loxosceles* currently consists of 133 species, of which only one species, *Loxosceles rufescens*, has a more or less global distribution (World Spider Catalog, 2018). *Loxosceles* spiders in general are of medical importance because their bites may cause necrotic skin lesions that indicate a

condition known as ‘loxoscelism’ (Vetter, 2008; Nentwig *et al.*, 2017). Recent reviews of medical aspects of *Loxosceles* bites revealed that despite frequent publications, only 11% of reported bites are considered as verified bites. In half of the verified cases, systemic effects (such as fever or nausea) appeared, and in three-quarters of cases skin necrosis developed, of which roughly half healed spontaneously and half required surgical debridement. No verified *L. rufescens* bite had a fatal issue (Stuber & Nentwig, 2016; Nentwig *et al.*, 2017).

The spider *L. rufescens* originated in North Africa, probably in Morocco, and has spread by its own means and by human transport for more than 5000 years within the Mediterranean basin, to the Near East and to Iran and Afghanistan (Duncan *et al.*, 2010; Planas *et al.*, 2014; Nentwig *et al.*, 2017). In fact, *Loxosceles* spiders have a high affinity for human buildings,

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which facilitates their spread by human activities (Nentwig, 2015; Canals *et al.*, 2016). In this sense, *Loxosceles* species are even better than average alien spiders: they hide in small sites, where they can remain motionless for long periods, and can survive for 3–5 months without food or water (Cramer, 2008).

Species distribution models (SDMs) could be used to predict the potential distribution of an invasive species assuming that climatic niches do not change [niche conservatism *sensu* (Wiens & Graham, 2005)] and also to hypothesize stages and the dynamic of invasions (Gallien *et al.*, 2012; Taucare-Ríos *et al.*, 2016). Such models can be defined as ‘statistical methods that combine observations of species occurrence with environmental variables’, and have been used to predict potential distributions, especially in invasive species (Elith & Leathwick, 2009; Vink *et al.*, 2011; Kumar *et al.*, 2015; Taucare-Ríos *et al.*, 2016). All studies, in which invasion ranges can be predicted with occurrences from the native range, assume niche conservatism in alien species (Peterson & Vieglais, 2001; Broennimann *et al.*, 2007). However, niche shift may result from changes in either the fundamental niche (Holt *et al.*, 2005), or the realized niche of the species (i.e. the fundamental niche constrained by biological interactions) (Chase & Leibold, 2003; Broennimann *et al.*, 2007), thus reflecting environmental changes and evolutionary adaptations.

Making comparisons between global and regional SDMs can be a good method of inferring invasion processes (Gallien *et al.*, 2012) and has already been used to analyse the invasion of alien spiders (Taucare-Ríos *et al.*, 2016). Initially the global model was constructed by using all occurrences collected for the species worldwide and could be viewed as a proxy of the species’ fundamental niche (Vetaas, 2002). By contrast, a regional niche is the realized niche of the species in native or invaded regions (Gallien *et al.*, 2012), which can be documented using abiotic conditions, biotic interactions and dispersal ability (Soberon & Peterson, 2005; Wilson *et al.*, 2007; Taucare-Ríos *et al.*, 2016).

The combination of both can help to predict invasion processes in different parts of the world (Gallien *et al.*, 2012). The present study used this comparison to obtain four theoretical scenarios of potential distribution: (a) when most observed species records fall within an area predicted to be suitable by both the global and the regional model, such populations can be considered as stabilized; in some way these values represent the proportion of populations that conserve their niches; (b) when most observed records fall within the global, but outside the regional, model predictions, this can be considered as ongoing regional colonization; (c) when populations occur within regional predictions but not within global predictions, these populations can be considered as adapting to their new environment (e.g. local adaptations or facilitation), and (d) when records fall outside suitable areas predicted by both models, the observed populations should be considered as sink populations (Gallien *et al.*, 2012; Cabra-Rivas *et al.*, 2015; Taucare-Ríos *et al.*, 2016).

Firstly, the global distribution of *L. rufescens* was analysed by comparing the global and regional models. Secondly, possible conservation or niche differentiation in the invaded regions was evaluated by comparing the native and global models. The

different invasion histories of North and South America (common vs. absent) and Africa south of the Sahara (uncommon) vs. Asia (common), including the possible ecological mechanisms related to such different invasion processes, are discussed.

Materials and methods

Occurrences

The Global Biodiversity Information Facility (GBIF; <http://www.gbif.org/>) was used to assess the current global distribution of *L. rufescens*. Records from the published literature were collected (Nentwig *et al.*, 2017). This process identified 191 records around the world that showed occurrences on every continent, with the exception of Antarctica (Fig. 1).

Global and regional distribution models

Species distribution models were developed using Maxent software, which evaluates the probability distribution of a species using a function of maximum entropy (Phillips *et al.* 2006). Two invaded ranges (North America and Asia) and the native area (North Africa) were used to construct regional models. A global model was constructed using all regions in which the species has been recorded. Bioclimatic variables were obtained from the database Worldclim (<http://www.worldclim.org/>), to a spatial resolution of 2.5 arc seconds. The climatic variables were the same as those used by Taucare-Ríos *et al.* (2016): annual mean temperature (Bio1); mean diurnal range of temperature (Bio2); annual precipitation (Bio12), and precipitation seasonality (Bio15). To build the SDMs, 75% of the data were used to develop the model, and the remaining 25% were used for testing. An average model obtained from 50 replicates was selected. To regulate an excess of parameterization, parameter $b = 1$ was used (Phillips & Dudik, 2008). The projection used deactivating clamping and extrapolation in Maxent, avoiding model predictions in environments not available (Anderson, 2013; Merow *et al.*, 2013).

DivaGis Version 7.5.0 (<http://www.diva-gis.org/download>) was used to define the four scenarios in geographic space. Potential distributions obtained from Maxent software were used. Following Gallien *et al.* (2012), a threshold of 0.5 was used to define suitable (>0.5) and unsuitable (<0.5) habitats to ensure that at least half of the models agreed. Thus, the overlap between the global and regional model predictions concerns stabilized populations; an occurrence within an area predicted only by the regional model refers to locally adapted populations; an occurrence within an area predicted only by the global model represents the colonization phase of a population, and, finally, occurrences outside the global and regional models’ predictions represent sink populations (Cabra-Rivas *et al.*, 2015; Taucare-Ríos *et al.*, 2016).

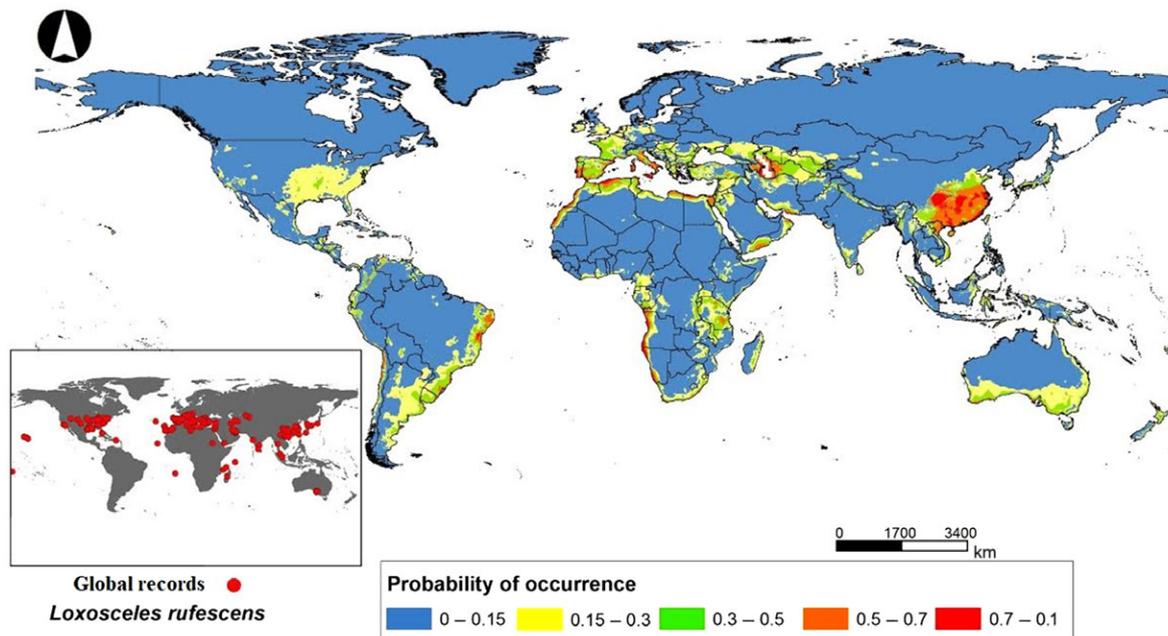


Fig. 1. Global species distribution model for the recluse spider *Loxosceles rufescens*, projected from the global climatic niche. Colours represent different ranges of occurrence probability. Dots represent records from the present authors' initial database. [Colour figure can be viewed at wileyonlinelibrary.com].

Results

For all models, the importance of temperature over precipitation is emphasized. The highest contribution to the global model came from 'annual mean temperature' (Bio1, 68.1%). For the regional models (including that for the native area), 'mean diurnal range' (Bio2) was the most important variable (Table 1). Each model demonstrated good performance: North America: area under the curve (AUC) = 0.834 ± 0.004 ; Asia: AUC = 0.88 ± 0.002 ; native area: AUC = 0.907 ± 0.005 , and global model: AUC = 0.94 ± 0.005 .

In the global model, the highest probability of presence (0.7–1.0) could be calculated for the Mediterranean region of North Africa (native area) and for Europe. In addition, the global model predicted high probabilities of presence in the invaded areas in Asia (e.g. China and Japan). However, the model demonstrated low and medium probabilities of presence in the warmer climates of the U.S.A. (Florida) and southeastern Brazil (Fig. 1).

For the native area in the Mediterranean region, the highest proportion of the predicted presences falls within the stabilized population areas (51.7%) and within the sink population areas (30.6%) (Fig. 2). For the Asian invaded area, the highest proportion falls within the stabilized area (75.5%) and only a few of the predicted presences are outside this (Fig. 3). Finally, in the American invaded area, the model shows that the highest proportions of predicted presences fall within the local adaptation region (57.6%) or in the sink population regions (26.9%) (Fig. 4).

Table 1. Contributions of the bioclimatic variables selected for the global and regional *Loxosceles rufescens* distribution models.

Variables	Contribution, %
Global model	
Annual mean temperature (Bio1)	68.1
Annual precipitation (Bio12)	5.8
Mean diurnal range (Bio2)	24.7
Precipitation seasonality (Bio15)	1.4
Regional model (Asia)	
Annual mean temperature (Bio1)	9.6
Annual precipitation (Bio12)	4.3
Mean diurnal range (Bio2)	78.6
Precipitation seasonality (Bio15)	8.1
Regional model (North America)	
Annual mean temperature (Bio1)	0.5
Annual precipitation (Bio12)	2.4
Mean diurnal range (Bio2)	92.4
Precipitation seasonality (Bio15)	2.2
Native region (Mediterranean region)	
Annual mean temperature (Bio1)	12.6
Annual precipitation (Bio12)	14.7
Mean diurnal range (Bio2)	67.5
Precipitation seasonality (Bio15)	5.1

Discussion

The global invasion of the recluse spider *L. rufescens* is a complex and dynamic process in which populations in different stages of invasion have been identified in America and Asia. The present results suggest source–sink dynamics from the native

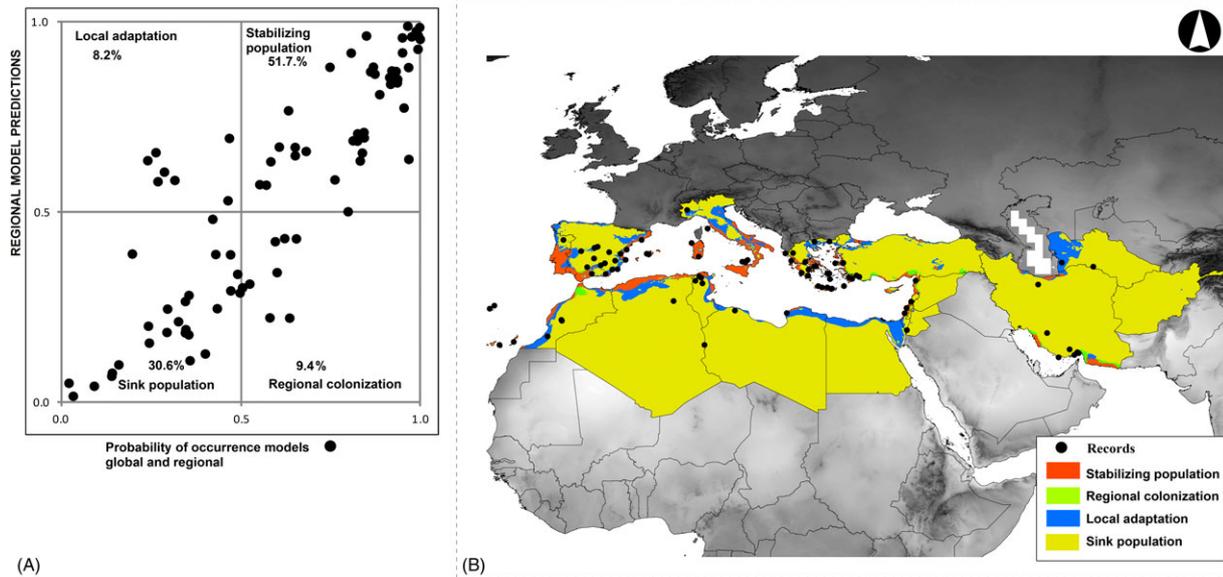


Fig. 2. Invasion stages for the recluse spider *Loxosceles rufescens* in the Mediterranean region (regional niche) with (A) niche and (B) geographic space. A threshold occurrence probability of ≥ 0.5 was used in the mapping of both distribution models, following Gallien *et al.* (2012). [Colour figure can be viewed at wileyonlinelibrary.com].

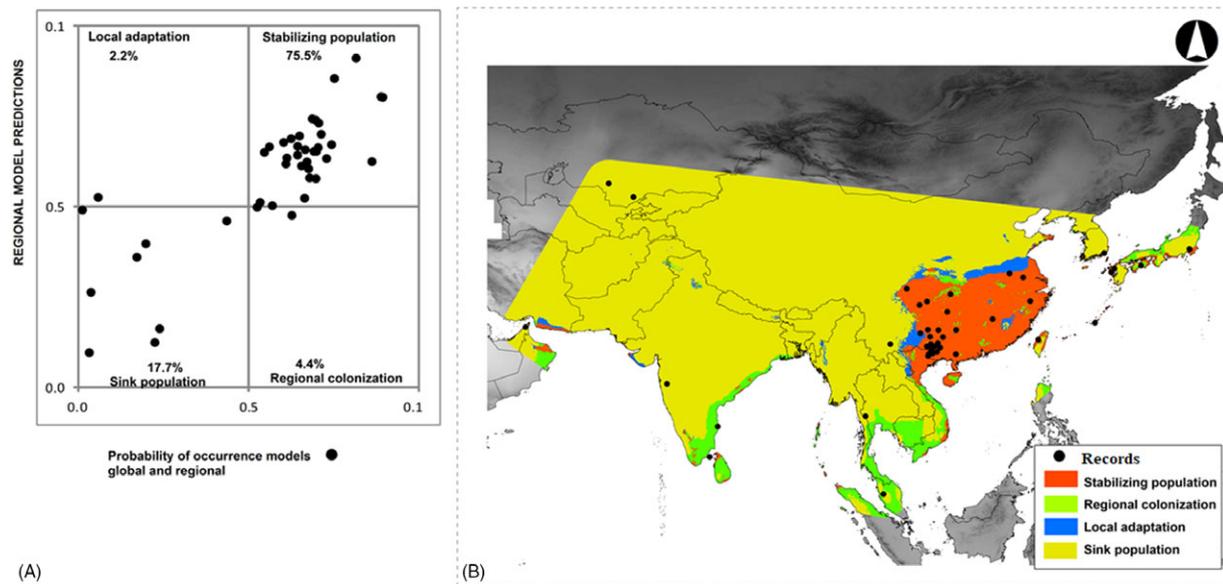


Fig. 3. Invasion stages for the invasive spider *Loxosceles rufescens* in Asia (regional niche) with (A) niche and (B) geographic space. A threshold occurrence probability of ≥ 0.5 was used in the mapping of both distribution models, following Gallien *et al.* (2012). [Colour figure can be viewed at wileyonlinelibrary.com].

area to invaded areas. The results emphasize low probabilities of occurrence of the species in major parts of the Americas, Africa south of the Sahara and Australia. As expected, probabilities of occurrence in the Mediterranean region and adjacent western parts of temperate Asia, where this species is native, were high (Planas *et al.*, 2014; Nentwig *et al.*, 2017). However, it is clear that the current model of global distribution does not perfectly match the known distribution of this spider. This suggests that

the species' current distribution is not limited primarily by abiotic factors, but instead reflects the much greater involvement of human aid in spreading this highly invasive species beyond its initial natural boundaries. The native vs. global model comparison shows niche conservatism in the invaded areas, where the ecological requirements of the species are maintained despite the climatic differences. Only in the U.S.A. does the species appear to occupy new niches (high proportions of

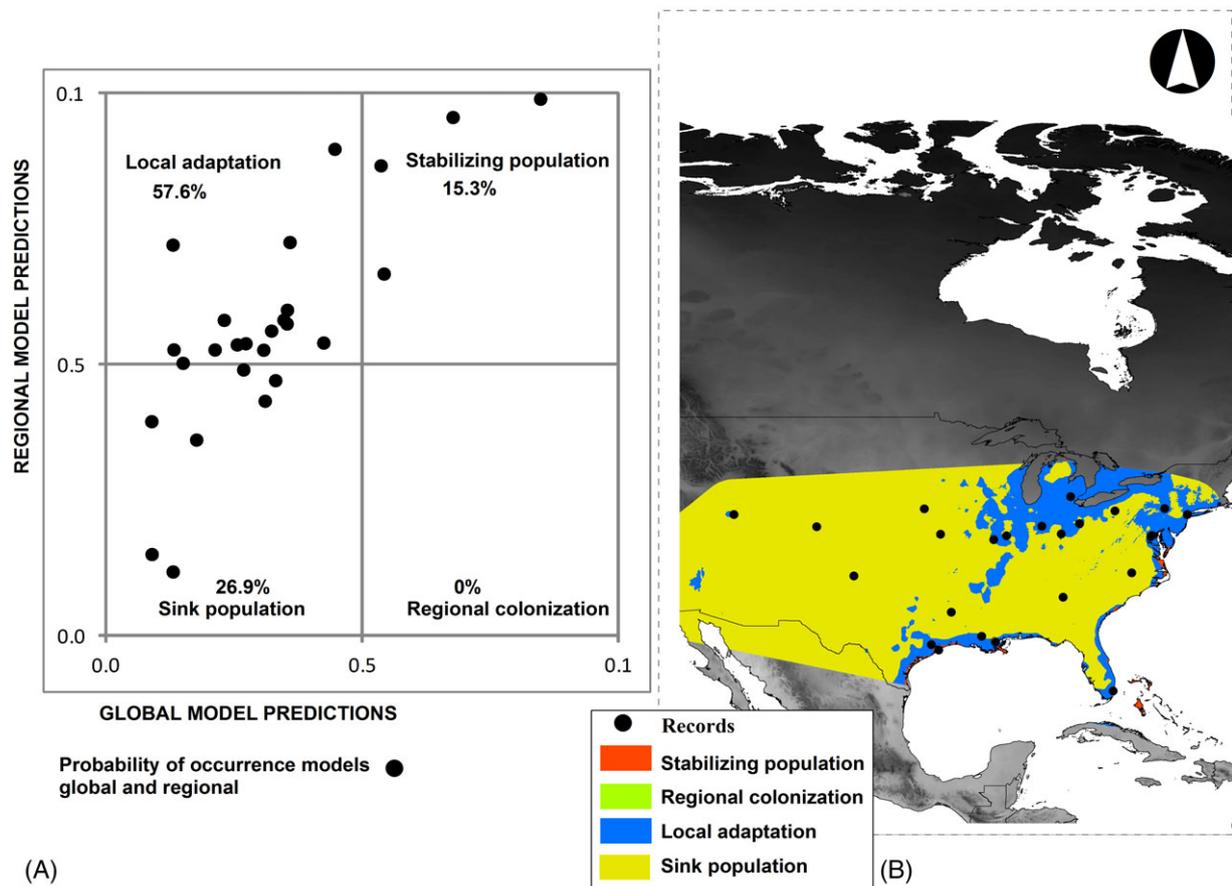


Fig. 4. Invasion stages for the invasive spider *Loxosceles rufescens* in the U.S.A. (regional niche) with (A) niche and (B) geographic space. A threshold occurrence probability of ≥ 0.5 was used in the mapping of both distribution models, following Gallien *et al.* (2012). [Colour figure can be viewed at wileyonlinelibrary.com].

populations adapt to new climates), which may be determined by human facilitation and urbanization that generates new microenvironments favourable to the species. In fact, only in this invaded region is the species totally synanthropic (Vetter, 2005), whereas in the Mediterranean region (native area) it is able to live in natural environments (Nentwig *et al.*, 2017). Another aspect to consider is that reclusive spiders are strongly limited in their ability to disperse because they are not capable of ballooning (Bell *et al.*, 2005). In invaded areas, these spiders live in synanthropic habitats and their dispersal capacity is mediated by human activity, which allows them to colonize urban environments they could otherwise not invade because of their low dispersion capacity (Vetter, 2005; Zamani & Rafinejad, 2014).

Temperature proved to be the most important of the variables examined to define the potential distribution of this species; the present study confirms earlier publications on *Loxosceles* species (Saupe *et al.*, 2011; Canals *et al.* 2015, 2016). Clearly, *L. rufescens* is able to establish easily in temperate climates in North America and Asia, probably as a result of these areas' similarities in climate with its area of origin. In addition, the current analysis indicates that the climates of Asia are more

susceptible to future *L. rufescens* invasions, given the climatic niche requirements of this spider. Both global and regional niche models predict the highest probabilities of occurrence in China, which is likely to show a high proportion of stable populations and fewer sinks compared with North America. In this sense, current distributions in the U.S.A., China and Japan show how a first arrival in a major port is followed by further spread within the country (Vetter, 2005; Nentwig *et al.*, 2017). Most populations were shown to be genetically quite homogeneous, which is a strong indication of a recent introduction (Luo & Li, 2015), and the same pattern can be considered for the U.S.A. (Vetter, 2005; Nentwig *et al.*, 2017).

Sink populations were found in areas with deserts and cold climates, which represent stressful and extreme temperatures. It may be that these regions offer habitats unsuitable for this species, compared with other areas around the world. However, in most parts of the areas it invades, *L. rufescens* lives synanthropically (i.e. in buildings). The species is usually found on ground floors and in cellars and thus avoids thermally stressful environments (Vetter, 2005; Greene *et al.*, 2009; Zamani & Rafinejad, 2014; Nentwig *et al.*, 2017). Such a synanthropic way of life, however, also raises the question of whether the current

modelling approach can be applied to a spider that is found in nature under stones and in microcaves and, in invaded areas, in buildings designed for human use, and is therefore only peripherally exposed to the major weather components used in the model. This also refers to limitations of the Maxent software, as discussed below.

Most continental records of *L. rufescens* come from the U.S.A. and China, and the species seems to be still absent from Central and South America (Gertsch, 1967; Nentwig *et al.*, 2017). Although distribution models predict the presence of the species in certain areas in South America, its absence may be attributable to three circumstances. Firstly, it is possible that the spider has not yet arrived in South America or that invading populations were too small to establish, despite the fact that European colonization of Central and South America predates that of North America by around 100 years. The second possible circumstance refers to competition (biotic resistance) by native species of the same genus. The genus *Loxosceles* evolved in the Americas with 58 species in Mexico and Central America, six in the West Indies, and 30 in South America. The majority of these live in desert and semi-desert environments, and only a few species have become synanthropic (Gertsch, 1967; Vetter, 2005; World Spider Catalog, 2018). The presence of a large number of phylogenetically closely related native species, thus, would make it difficult for *L. rufescens* to establish (Duncan & Williams, 2002). Thirdly, *L. rufescens* and other *Loxosceles* species are poor in distinctive patterns. Therefore, the identification of *L. rufescens* and its separation from similar species may be difficult (Greene *et al.*, 2009; Vetter, 2015; Nentwig *et al.*, 2017). Hence, a cryptic invasion without due taxonomic recognition is possible, although the present authors are not convinced of its likelihood.

Finally, the current work found several populations in a stage of local adaptation, occupying new climatic niches in the U.S.A. Many studies have documented climate niche shifts for other invasive species, such as insects, spiders and plants (e.g. Broennimann *et al.*, 2007; Fitzpatrick *et al.*, 2007; Guisan *et al.*, 2014; Kumar *et al.*, 2015; Taucare-Ríos *et al.*, 2016). Local adaptation of an introduced species in a new area can occur in different ways (Gallien *et al.*, 2012; Kumar *et al.*, 2015). For example, climatic niche shifts may be assigned either to shifts in both the fundamental and the realized niches (Pearman *et al.*, 2008) or to shifts in the realized niche only, usually as a result of the relaxation of biotic constraints (Rödder & Lötters, 2009). Local disturbance, such as urbanization, creates new niches for invasive species, often free of natural enemies (Sax *et al.*, 2005). This may be especially relevant in the case of spiders colonizing urban environments and thus living synanthropically in the areas they invade (Vink *et al.*, 2011; Taucare-Ríos *et al.*, 2016). In this scenario, *L. rufescens* might occupy an area with climatic conditions that are absent in its native area (niche realized), but are within its fundamental niche (see global model), as has been found previously (Kumar *et al.*, 2015; Taucare-Ríos *et al.*, 2016).

The present study finds that the success of this species' invasion varies depending on the region invaded. The majority of populations in Asia are stable, showing climatic niche conservatism in the species, whereas in North America this spider is likely to be less successful in occupying niches that differ from those in its native region without its synanthropic

way of living. It is also important to consider the limitations of Maxent software in predicting the distribution of invasive species, which refer to the resolution of abiotic variables, multicollinearity and failure to account for biotic processes (Syfert *et al.*, 2013; Kumar *et al.*, 2015; Taucare-Ríos *et al.*, 2016). However, the differences found in the present study between invaded regions may account for local microscale processes that have not been considered so far. Thus, the results of this study are important and useful for the control and management of this spider in invaded areas, but future studies are required to analyse local population dynamics in both this species' native and invaded regions.

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