Biol Invasions (2023) 25:251–265
https://doi.org/10.1007/s10530-022-02904-5

ORIGINAL PAPER

Species distribution models and climatic niche comparisons provide clues on the geographic origin of a spider invasion in the Americas

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Received: 28 May 2021 / Accepted: 28 August 2022 / Published online: 15 September 2022

Abstract Identifying the source population of alien species is important to assess the distribution and potential effects in the invaded area. The araneid spider *Cyrtophora citricola* is widely distributed in Europe, Asia, and Africa; however, in the last 26 years, it has been reported in several countries across the Americas. To date, the geographic origin of the populations established in the Americas remains unclear, but considering the successful colonization after its recent arrival, assessing climatic similarities between the invaded and native geographic ranges could be useful to address this question. In this study, we used a combination of Species Distribution Models and Ordination Methods to assess the climatic match between the invaded region (the Americas) and two potential origins (southern Africa and the Mediterranean) aiming to determine the more likely origin for the populations established in the Americas. We found that the American populations of *C. citricola* occupy sites with climatic conditions more similar to those occupied by southern African populations, than to those occupied by the Mediterranean populations. Therefore, our results suggest a southern African rather than a Mediterranean origin for the populations established in America. In addition, our results also show that populations in America are spreading into sites that differ in climate conditions from those occupied by native populations. Further studies assessing intrinsic (e.g., physiological tolerances, plasticity, behavior, reproduction) and extrinsic (physical barriers, predator release) factors could provide further information to disentangle the mechanisms behind the geographic and climatic niche expansion of this species.

Keywords Species distribution modeling · Biogeography · *Cyrtophora citricola* · Araneidae · Mediterranean · Africa

Introduction

Intercontinental translocation of species, mediated primarily by human activities, has increased steadily over the last decades (Lockwood et al. 2013; Ricciardi 2013; Pyšek et al. 2020). The establishment success of long-distance invading species in a recipient area

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Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s10530-022-02904-5.

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is a synergetic process that depends primarily on the species' dispersal capacity, the propagule pressure, and the environmental similarity between original and recipient areas (Brown et al. 1996; Peterson 2003; Lockwood et al. 2013). Most research on long-distance invading species has centered on plants and vertebrates (Mollot et al. 2017), while information on other groups, such as spiders, is scant (Nentwig et al. 2017; Řezáč et al. 2021).

Successful invasions depend on several extrinsic and intrinsic features of each species (Kolar and Lodge 2001; Bellard et al. 2016). For instance, the abiotic environment represents an important filter in the establishment success of invasive species (Soberón 2007; Bomford et al. 2009; Broennimann et al. 2021); therefore, species would likely be more successful in sites with similar climatic characteristics to those occupied in their native range (Peterson 2003; Wiens and Graham 2005). For long-distance dispersal species, other factors, such as tolerance to long periods of starvation and desiccation, high reproductive rate, and high dispersal capacity, are also relevant for a successful invasion (Lockwood et al. 2013; Jeschke and Heger 2018). Some spiders have these features (Foelix 2011; Nedvěd et al. 2011), making them well-suited for invading new and distant geographical areas, particularly through human-mediated long-distance jumps.

There are few reports of trans-oceanic spider invasions in the Neotropics (Garb et al. 2004; Laborda and Simó 2008), and the most recent corresponds to the tent-web spider *Cyrtophora citricola* (Forsskål 1775) (sensu lato). *Cyrtophora citricola* is reported to have a discontinuous native distribution, but is restricted to the tropics and subtropics (Blanke 1972). It is found in southern and northern Africa, southwestern Asia (Afghanistan, Saudi Arabia, and India), and southern Europe (around the Mediterranean sea) (Blanke 1972), where it is often associated with coastal habitats (Blanke 1972). This species has recently invaded the Americas, with the first report in 1996 in Colombia (Levi 1997). Then it was recorded, chronologically, in the Dominican Republic (Alayón-García et al. 2001), Florida (Edwards 2006; Mannion et al. 2002), Costa Rica (Víquez 2007), Cuba (Alayón-García 2003; Sánchez-Ruiz and Teruel 2006; Martín-Castejón and Sánchez-Ruiz 2010; Teruel et al 2014), Brazil (Soares-Álvares and De-Maria 2004) and Haiti (Starr 2005).

Invasive species have a pervasive negative impact on ecosystems, communities, and populations, and thus, on the biodiversity in the recipient areas (Gurevitch and Padilla 2004; Ehrenfeld 2010). Although research has focused on plants and vertebrates, arthropod invader species are also known to affect the abundance and diversity of local species (Snyder and Evans 2006; Vonshak et al. 2010; Tilman et al. 2017). A major issue with the negative impact of invasive species is that when the problem is noted, it is difficult—if not impossible—to eradicate the species or at least manage it appropriately (Simberloff et al. 2013). Prevention has been argued to be the best approach to reduce the impact of alien species in the recipient area, and knowing the environmental characteristics of the native distribution, as well as those of the occupied area in the invaded region, is one of the essential factors required to limit the negative impact of alien species (Latombe et al. 2017). Hence, evidence of the climatic characteristics on the native region of *C. citricola* would provide relevant information on the potential expansion of the species in the Americas, and which native species could be likely affected.

The specific region from which *C. citricola* migrated to the Americas remains unknown. Previous evidence shows that recent invaders tend to occupy similar climatic conditions to those in their native range (Gillard et al. 2020; Liu et al. 2020a). Moreover, habitat suitability models, which compare the native and invaded climatic conditions, have successfully predicted the spreading of different invasive species of animals and plants in non-native regions (Iguchi et al. 2004; Ficetola et al. 2007; Jarnevich and Reynolds 2011). Given the climatic differences between the regions composing the disjunctive native distribution of *C. citricola* (Cowling et al. 1996; Köppen et al. 2011; Peel et al. 2007), comparing their climatic match with invasive populations could help identify the most likely geographic origin of the American populations.

Considering that many populations of *C. citricola* in the Mediterranean and southern African regions occur near coastal areas (Blanke 1972), and that the species constructs long-lasting webs, there is a high chance that it was introduced to the Americas via merchant marine vessels (Hulme 2009). In its native range, *C. citricola* occupies open areas with seasonal climates (Blanke 1972). In the Americas, the species has been reported in urban or highly altered habitats in seasonal areas (Víquez 2007), suggesting that the spider tends to establish in sites that share similarities with native habitats. However, while preliminary molecular phylogenetic analyses suggest a closer relationship between the American and the southern African populations (Agnarsson et al. unpublished), the morphology and behavior of American populations seem more similar to the Mediterranean populations (Y. Lubin pers. comm.). Incorporating climatic information could help to better understand this contradictory scenario and track the potential origin of the populations of *C. citricola* in the Americas.

In this study, we describe the realized climatic niche of *C. citricola* in the Americas and provide quantitative support for the most likely geographic origin of its invasion in the Americas. Using a combination of species distribution models (SDMs) and ordination techniques we (1) tested which of the realized niches of the Mediterranean or southern African populations predict more accurately the current distribution of this spider in the Americas, and (2) quantified with different metrics the match between the climate of each native region and the invaded regions in the Americas. Considering that the invasion of *C. citricola* in the Americas is very recent (it has been less than 30 years since it was first reported), we expected that established populations occupy habitats with similar climatic niches to those of the native region (Peterson 2003, 2011; Zhang et al. 2020). Therefore, the climate niche of the *C. citricola* in the Americas should have a higher overlap with the most probable source region of the two native ranges, and this should be supported by the consensus of the multiple tests performed here.

Methods

Species occurrences

We compiled 2795 geo-referenced occurrence points of *C. citricola* from five different sources. We obtained 258 data points from the Global Biodiversity Information Facility (GBIF.org; accessed on March 28th 2018, https://doi.org/10.15468/dl.hi6ahq), 18 from SpeciesLink (http://splink.cria.org.br/, accessed on April 4th, 2018), and 662 from the Royal Museum of Central Africa database. We also obtained 78 records from different literature sources (Online Resource 1) and collected 13 points in the field in Costa Rica that we geo-referenced using Google Earth. Additionally, our colleague Angela Chuang kindly provided 1574 data points from the USA, collected as part of her research.

Before conducting the analyses, we first removed duplicates and discarded erroneous records from the database using QGIS (version 3.0.1-1). We checked all records individually, excluding those points located on the ocean or outside the city mentioned in the locality description. In such cases, we also checked for missing or incorrect signs in the coordinates and misplacements of the decimal separator that may generate erroneous occurrences. If those changes still did not match the described locality, we discarded the respective occurrence. Finally, we filtered the remaining data using the R package *spThin* (Aiello-Lammens et al. 2015) to remove all data points having less than a distance of 5 km from any other point and guarantee one record maximum per cell according to the resolution of our climatic layers. After this procedure, we gathered 32 data points for South Africa and southeastern Mozambique (hereafter, the southern African region), 108 for the Mediterranean region and 122 for the Americas (Fig. 1).

Climatic information

To quantify climatic conditions throughout *C. citricola*'s distribution range, we used data from the WorldClim database Version 2 (Fick and Hijmans 2017, http://www.worldclim.org) at a 2.5 arcmin resolution. We used a subset of the 19 WorldClim bioclimatic variables for all analyses. We also constructed a Maximum Annual Wind Speed (hereafter wind speed) layer by extracting the maximum speed values for each cell layer within the monthly layers of wind speed, also provided by the WorldClim database Version 2. We included this last variable since newborn spiderlings of this species disperse by wind (Johannesen et al. 2012), and wind speed conditions affect the direction and distance at which spiders disperse (Sheldon et al. 2017).

For the analyses described below, we selected six climatic variables by prioritizing (1) a reduction in multicollinearity and (2) the biological relevance of the variable considering the species' life history (Saupe et al. 2012; Brandt et al. 2017). To do so, we

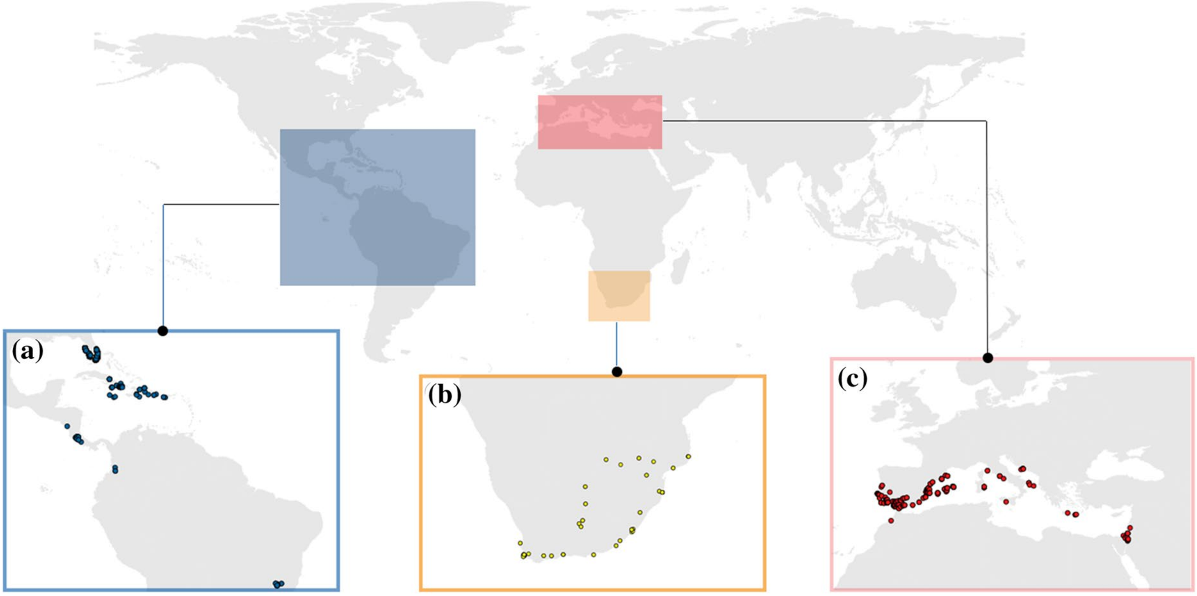


Fig. 1 Invaded and native distributions of the araneid *Cyrtophora citricola,* defined as study regions (**a**–**c**) to run the SDM: **a** represents the occurrences recorded in the Americas, **b** the occurrences in the southern African region and **c** the occurrences for the Mediterranean region

built a Pearson correlation matrix and assessed which variables were highly correlated (|r|> 0.7) across the studied regions. We then counted the number of variables that were highly correlated with each other (e.g., Bio 12 was highly correlated with other 11 variables, while Bio 1 was highly correlated with only four) (Dormann et al. 2013). Considering that this species lives for several months (Yip and Lubin 2016), we decided to focus on variables that better represent temperature or precipitation extremes for more extended periods (e.g., quarterly averages were preferred over monthly averages). Therefore, we chose Bio 10 (mean temperature of the warmest quarter), Bio 16 (precipitation of the wettest quarter), and Bio 17 (precipitation of the driest quarter). These variables were highly correlated with different sets of other excluded variables, but not among them. We maintained Bio 2 (mean diurnal range) and Bio 15 (precipitation seasonality), as they were not strongly correlated ($R < 0.7$) with any other variables. We also kept wind speed that, as explained above, relates to this species' dispersal mechanism.

Species distribution models

To estimate potential distributions for the native and invasive populations of *C. citricola*, we created three sets of candidate SDMs using Maxent v3.4.3 (Phillips et al. 2017): one set for each of the two potential native regions (southern Africa, Mediterranean) and one for the invaded region (the Americas). We generated sets of models with different model complexity in the R package *ENMeval* v2 (Kass et al. 2021). For this, we used variations of two different parameters: (1) regularization multipliers that penalize complexity and result in simple models with fewer predictor variables (see Elith et al. 2011; Phillips et al. 2017) (we selected values ranging from 1 to 4, at intervals of 0.5) and (2) different feature classes (transformations of the values of the climatic variables, see Elith et al. (2011)) including Linear (L), Quadratic (Q), Hinge (H), and their combinations (Phillips et al. 2006, 2017; Phillips and Dudík 2008).

We calibrated all candidate models by delimiting an area of 50 km around the presence points of each region (as other web-building spiders have been recorded to disperse up to 30 km, Thomas et al. 2003), and used 10,000 background points, a number used often in the literature (Phillips et al. 2009;

Barbet-Massin et al. 2012). Therefore, the calibration area would include enough information to adequately sample the climate available for the species and to contrast with those conditions in which the species occur. To improve independence between validation and training points in each region, we spatially partitioned the data using the Checkerboard 2 method (default aggregation factor). This method divides the data into four spatial bins and facilitates the inclusion of isolated occurrences without altering the geographical size of the bin (Muscarella et al. 2014). Therefore, we considered this method appropriate for the scattered occurrences in the studied regions. To select the model with the optimal settings from each set of candidate models, we prioritized those with (1) the highest average Area under the Curve for the validation points ($AUC_{val.avg}$) and (2) the lowest value of the 10% omission rate (OR_{10}) following the listed order; for details regarding these criteria, see Muscarella et al. (2014) and Kass et al. (2021).

The selected models for each native region were projected to the invaded region. To evaluate how accurately these models predicted the species distribution in the invaded range, we projected the models to the Americas and estimated the Continuous Boyce Index (CBI, Boyce et al. 2002; Hirzel et al. 2006). This metric evaluates model transferability using presence-only data to quantify how different the model predictions are from a random distribution of observed presences across the prediction gradient (Hirzel et al. 2006). Positive values indicate that the model accurately predicts the distribution of presence data, while negative values predict low suitability in areas where presences are frequent, and values near-zero indicate models that do not differ from random models (Hirzel et al. 2006). This analysis was performed using the *ecospat* package (Di Cola et al. 2017). In addition, we conducted a Multivariate Environmental Similarity Surface (MESS; Elith et al. 2010) analysis using the *dismo* R package (Hijmans et al. 2021) to identify areas where each model is extrapolating and that should be interpreted with caution (included in the Supplementary materials). For this analysis we used the same variables used to train the SDMs.

Niche overlap and niche margin index estimation

To quantify and compare the two native niches with the invaded niche in the climatic space, we followed the protocols and metrics used in studies of climatic niche dynamics (Guisan et al. 2014) that measures centroid shifts, overlap, unfilling and expansion (COUE scheme; Guisan et al. 2014). First, we used the PCA-env approach described by Broennimann et al. (2012) based on the same six variables selected to build the SDMs. This is an ordination method that represents the climatic space of the species niche using kernel densities of the climatic variables extracted from the species occurrences (Broennimann et al. 2012).

With the PCA-env, we performed tests of niche equivalency and niche similarity (Warren et al. 2008). Both tests estimate differences between a measured niche and null model niches within a given background area: while niche similarity assesses whether the niches are more or less similar than expected by chance, niche equivalency informs if two niches are equivalent (Di Cola et al. 2017). From the PCA-env, we also estimated "stability", "expansion" and "unfilling". "Stability" estimates the proportion of climatic conditions shared between two regions (Petitpierre et al. 2012), in our case the invaded versus each of the two native regions. "Expansion" estimates the proportion of conditions in which the species is present in the invaded range but not in the native range; and "unfilling" estimates the proportion of the native niche that does not overlap with the niche occupied in the new range (Petitpierre et al. 2012). All these analyses were performed using functions available in the *ecospat* package in R (Di Cola et al. 2017).

Additionally, we complemented our COUE analysis using the n-dimensional hypervolume approach of Blonder et al. (2014). This approach decomposes the climatic niche, and estimates shared and unshared niches between two or more species in n-hypervolume climatic space. We compared the niches of the two native populations (southern Africa and the Mediterranean) and the invasive population (the Americas). For hypervolume estimation, we used the same climatic variables used to train the SDMs. All layers were standardized to z-scores by subtracting the layer mean from each cell value and dividing the resulting value by the layer variance. We extracted the value of the standardized layers for each occurrence and with them, ran a principal component analysis (PCA). We selected the first five PCA axes, which explained 99% of the variance of the entire dataset. Using the PCA-scores of each population, we generated hypervolumes with the *hypervolume* R package (Blonder and Harris 2018), using the Gaussian kernel density estimation and the rest of the parameters with the values established by default; we used the "Silverman" method to estimate the bandwidth (Blonder et al., 2018). We evaluated the similarity between populations using the *kernel.similarity* function of the *BAT* R package (Cardoso et al. 2021). We chose the pairwise centroid distance and the minimum distance to evaluate the spatial relatedness between the hypervolume populations. To assess the overlap between hypervolume populations, we used the intersection and Sorensen-Dice similarity indices (Cardoso et al. 2021). We also decomposed the niches to estimate the total niche differentiation (H_{total}) and the shared volume ($H_{overlap}$) between populations using the function *kernel.beta* of the same package (Cardoso et al. 2021). We report the hypervolumes in niche units as the standard deviations to the power of the number of niche dimensions used (5).

Finally, we computed the Niche Margin Index (NMI, Broennimann et al. 2021) for all occurrences in the Americas to quantify their niche matching with each native climatic niche (NCN) of the potential regions of origin (i.e., Mediterranean and southern Africa). NMI is a recently proposed niche metric based on the distance to niche margins by estimating a standardized distance between a given locality and the species' NCN margin (Broennimann et al. 2021). The obtained values range between $-\infty$ and $+1$, where negative values represent sites outside the NCN, zeroes correspond to sites in the niche margin, and positives to sites inside the NCN. We ran this analysis using the functions provided in the supplementary material of Broennimann et al. (2021) and the same bioclimatic variables used in the previous analyses.

Results

The evaluation metrics of the three models selected showed an overall good performance when projected to the same region where they were trained. Evaluation with cross-validation showed omission rates below 0.1 (OR_{MTP}: Southern Africa = 0.05, Mediterranean and the Americas = 0.01), and AUC around 0.7 (Southern Africa and Mediterranean = 0.69, the Americas = 0.75) (see Table 1, Supp. Fig. S1).

When projecting the models trained in the native regions to the Americas, the southern African model predicted broader areas of high climatic suitability for *C. citricola* across the invaded region compared to the prediction obtained from the Mediterranean model (Fig. 2), which coincided with the results from our MESS, that showed that southern Africa is more similar to the Americas as well (Supp. Fig. S2). Using the invasion occurrences as an independent evaluation set, we found a higher CBI in the southern African model (CBI = 0.756) than in the Mediterranean model (CBI = 0.126).

We found that climatic niche overlap between the southern African and the Americas regions is

Table 1 Parameters and evaluation metrics of the models selected for each region analyzed

Region	Southern Africa	Mediterranean	Americas
Data partition method	Checkerboard 2	Checkerboard 2	Checkerboard 2
Feature Classes	Linear	Quadratic	Quadratic
Regularization multipliers	1	1	1
OR_{MTP} (sd)[a]	0.05 (0.06)	0.01 (0.01)	0.01 (0.01)
$AUC_{VAL.AVG}$ (sd)[b]	0.69 (0.17)	0.69 (0.06)	0.75 (0.05)
OR_{10} (sd)[c]	0.07 (0.08)	0.10 (0.01)	0.09 (0.04)
Parameters	4	6	6

The standard deviation for each value is included in parentheses

[a] OR_{MTP}: Minimum training presence omission rate

[b] $AUC_{VAL.AVG}$: Average Area Under the Curve Across 5 CV training–testing sets (four bins and one all training–testing)

[c] OR_{10}: 10% Training omission rate

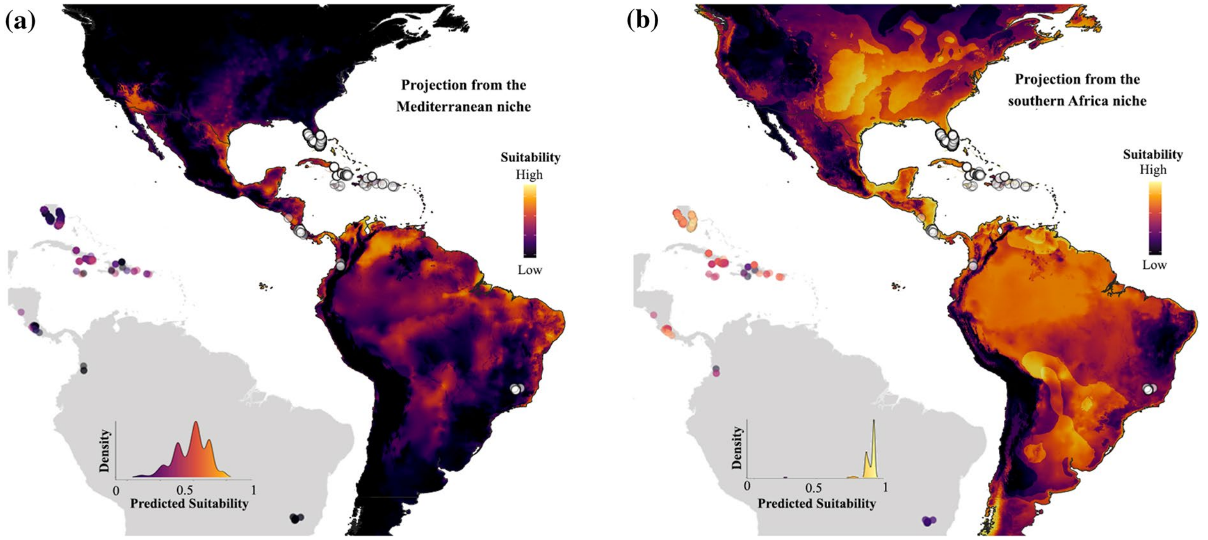


Fig. 2 Predictions of the distribution of *Cyrtophora citricola* in the Americas projected from the two native niche models. The gray maps in each panel show the distribution of suitability values assigned by the respective model to each occurrence

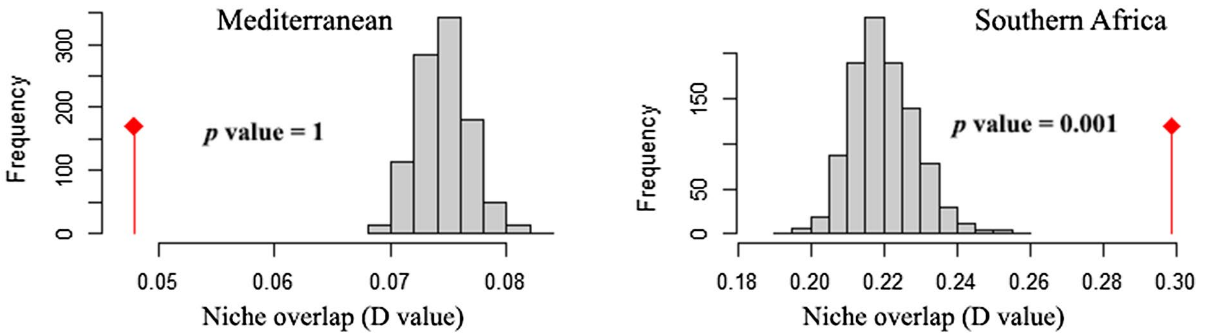
moderate to low (D = 0.3) but is higher than the overlap between the Mediterranean region and the Americas (D = 0.05). The niche equivalency test was significant only for the southern Africa region, suggesting that the compared southern African and the Americas niches are equivalent when compared with the random overlaps generated for the null model. (Fig. 3). The niche similarity tests were also significant when comparing the American and southern African niches, suggesting that the southern African and American niches are more similar than expected by chance (Fig. 3).

According to the PCA-env analysis, the climatic niche of *C. citricola* in southern Africa had a greater overlap (Stability 85%) with the climatic niche in the Americas than with that in the Mediterranean range (Stability 7%) (Fig. 4). This result also indicates that this spider has occupied new climatic conditions (analog niche expansion) in the Americas when compared to those in the native range: 15% based on the southern African model and 93% based on the Mediterranean Model. The species has also expanded to areas with completely new climatic niches not available in its native distribution (Fig. 4).

Our n-dimensional hypervolume approach also supported these results; the American population shared a higher climatic niche volume with the southern African population ($H_{overlap} = 3.608$) than with the Mediterranean one ($H_{overlap} = 1.379$). The total differentiation of volumes was higher between the American and the Mediterranean populations ($H_{total} = 0.918$) than between the American and the southern African populations ($H_{total} = 0.862$). The American population had a closer centroid and higher similarity (Intersection and Sorensen similarity index) of hypervolumes with the southern African population than with the Mediterranean population (Table 2, Supp. Fig. S3). However, based on the minimum distance between hypervolumes, the Mediterranean population was closer to the American population (Table 2).

The NMIs estimated for each occurrence in the alien range were consistent with higher similarity between the invaded region and the southern African native climatic niche (Fig. 5.A). This analysis also showed many sites that fall outside the Mediterranean and southern African climatic niches. However, we found a significant difference in NMI values between regions ($F_{(1,\ 3346)} = 1215$, $p = < 2e-16$), providing evidence of higher climatic niche matching between the alien occurrences and the southern African niche (Fig. 5B).

(a) **Equivalency tests**



(b) **Similarity tests**

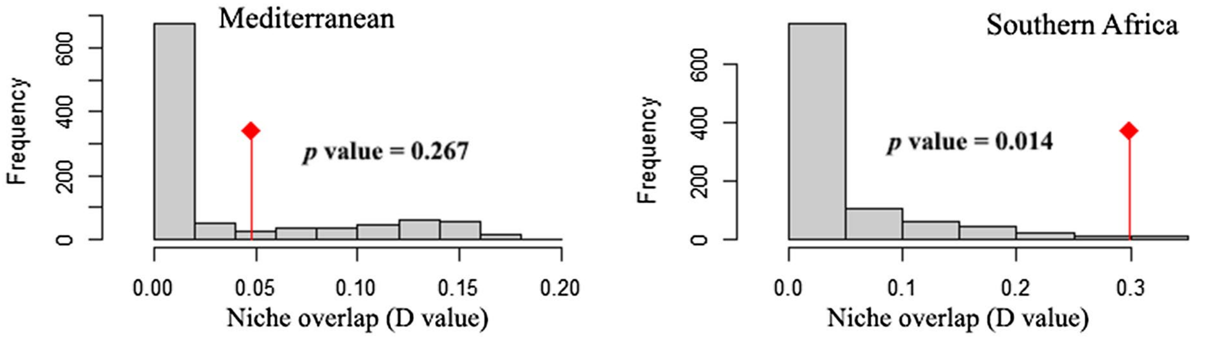


Fig. 3 Overlap tests for both native regions. **a** Equivalency tests showing that the niches of the Americas and southern Africa are equivalent, but the Mediterranean and American niches are not. **b** Similarity test results for both native regions projected to the Americas. Southern Africa is more similar to the Americas than what would be expected by chance, while the Mediterranean is not. Red lines in the plots show the observed value of overlap (Schoener´s D), gray bars show the distribution of D values for 1000 simulated comparisons

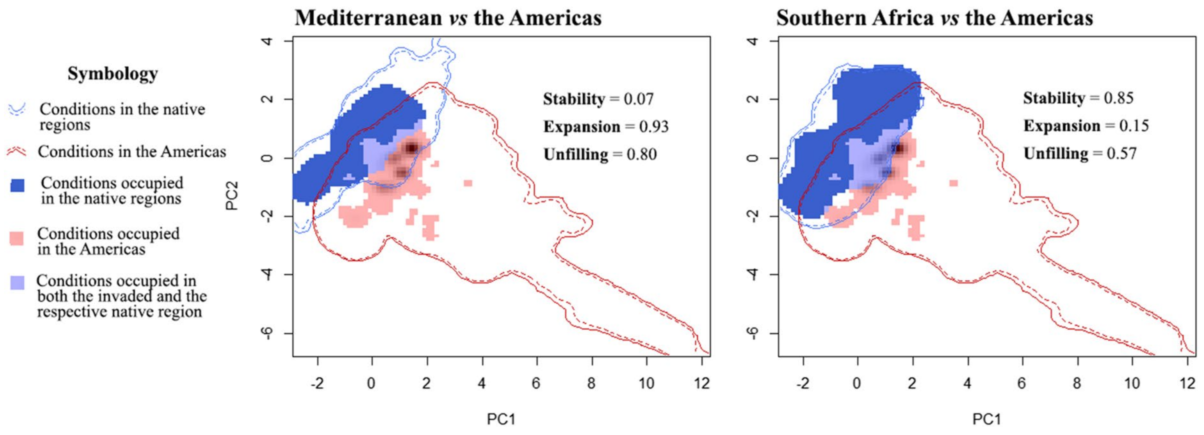


Fig. 4 Representation of overlap between native and invaded niches of *C. citricola* in the climatic multivariate space using the PCA-env method

Table 2 Distance values and similarity indices between the hypervolumes of three populations of the spider *Cyrtophora citricola*

Distance			Minimum distance	
		Americas	Mediterranean	Southern Africa
	Americas		*0.08*	*0.12*
Distance between centroids	Mediterranean	1.97		*0.07*
	Southern Africa	1.79	0.65	
Similarity		Sorensen' similarity		
	Americas		*0.14*	*0.22*
Intersection	Mediterranean	1.29		*0.31*
	Southern Africa	3.36	3.71	

In the distance matrix: the above diagonal (italic) values represent the minimum distance between hypervolume borders of two populations; below diagonal values correspond to the distance between hypervolume centroids. In the similarity matrix: the above diagonal (italic) values represent Sorensen' similarity index and below the diagonal are the volume of the intersection values of two volumes

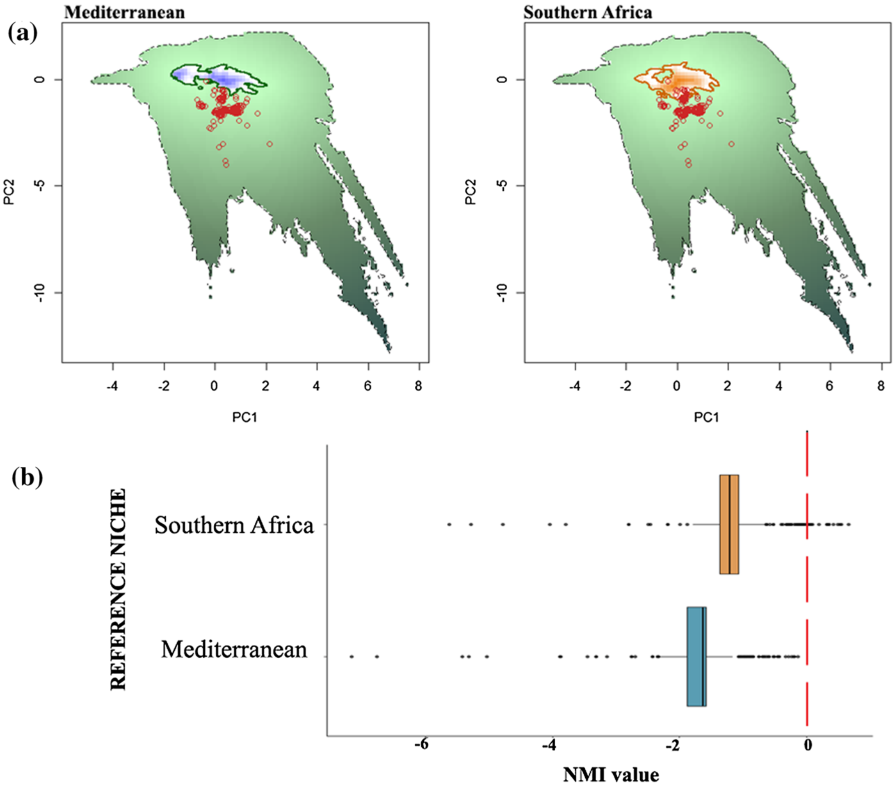


Fig. 5 Niche Margin Index (NMI) analysis for the alien occurrences of *Cyrtophora citricola* in relation to the potential native climatic niches (NCNs). **A** In green, the global available climatic space; each native niche (Mediterranean in blue and Southern African in orange) was estimated with a kernel density estimator and the alien occurrences in the Americas (red points). **B** Boxplots comparing the NMI values assigned to each of the alien occurrences (N = 1720) in relation to the reference NCNs. The dotted red line crosses the zero value, which represents the margin of the NCNs, with positive values being inside and negative values outside each NCN

Discussion

In this study, we aimed to identify the possible geographic origin of the invasion of *C. citricola* in the Americas by determining which of the two potential native distributions shared more climatic conditions with the invaded region. We used a variety of niche comparison methods and found strong consistency between our results that the climatic conditions occupied by *C. citricola* in the Americas, which are more similar to those in the southern African region than those occupied by this species in the Mediterranean region.

The successful establishment of a given species in a new geographic area is largely determined by the biotic and abiotic features of the recipient area and species-specific life-history traits, such as dispersal capability, demographic structure (e.g., sex ratio), and adaptability to different environmental conditions and novel biotic interactions (e.g., a new set of predators and parasites) (Brown et al. 1996; Guisan and Zimmermann 2000). After arrival, the climatic conditions could play a fundamental role in species establishment (Nuñez and Medley 2011; Peterson 2003; van Wilgen and Richardson 2012). Species arriving to places with similar conditions to those of the native area are more likely to succeed in their establishment than species arriving at sites with a different combination of climatic conditions (Brown 1989; Peterson 2003; Hayes and Barry 2008; Liu et al. 2020a; Broennimann et al. 2021). Given that the invasion of *C. citricola* is very recent, the significantly higher similarity of the climatic conditions between American and southern African populations found in this study supports the hypothesis that this species dispersed from the southern African region to the Americas. Such a result is congruent with preliminary genetic data suggesting a southern African origin for the American populations (Agnarsson et al. unpublished).

Interestingly, our analyses also showed that *C. citricola* occupies novel sets of climatic conditions in the Americas, not present in the native regions analyzed (i.e., non-analog niche shift, Fig. 4). This finding provides evidence for either a realized niche shift into environmental conditions not available in the native ranges, or a true shift in the fundamental niche. In the Americas, *C. citricola* could be occupying new environmental combinations not accessible in the native ranges but compatible with the species' intrinsic physiological tolerance (Sagarin et al. 2006). It is also possible that this species experienced a realized niche shift through phenotypic plasticity, either by physiological (e.g., thermal tolerances) or behavioral (e.g., spider orientation in the web, Marice and Agnes 2010) responses. Finally, the observed expansion to non-analog climatic conditions could be an example of a rapid adaptation that has led to a fundamental niche shift in the American population of *C. citricola*. Rapid adaptations have been observed in multiple recent invasions (Yoshida et al. 2007), and they offer a unique opportunity to understand invasion ecology from an evolutionary perspective. Evidence of intraspecific adaptation to different climatic conditions has been found in other spiders (Tanaka 1996; Krehenwinkel and Tautz 2013). Future studies elucidating the factors behind the niche shift in *C. citricola* could be highly informative in discerning whether this is a case of phenotypic plasticity or rapid adaptation.

Niche shifts recorded for recently invading species (Liu et al. 2020a) pose a particular challenge to the transferability of SDMs for the risk assessment of biological invasions (e.g., Atwater et al. 2018; Liu et al. 2020b; Pili et al. 2020; Nguyen and Leung 2022). However, our focus here was to contrast the similarity between two potential native regions and the known distribution of the species in the invaded range. Then, while it is possible for *C. citricola* to expand its niche soon after arrival to the Americas (as reported for other terrestrial ectotherms, Liu et al. 2020a), we consider this species would overall share more niche similarities to its potential source population's region than other regions. However, we acknowledge that this limitation of correlative approaches requires further empirical studies to discern between the role of niche conservatism and the possibility of a rapid niche expansion in driving the establishment of the species in the Americas.

Similar to other invasive species, *C. citricola* has several traits that facilitate its rapid spread and establishment in the Americas. This spider is a generalist predator, so the diet is not a major limitation (Chauhan et al. 2009). It has a long annual reproductive season and a high reproductive rate: one female can produce several egg sacs during a single reproductive season (Chauhan et al. 2009; Leborgne et al. 1998). It has a dispersal method (ballooning) that allows a rapid establishment into new areas (Teruel et al. 2014), and the species is also highly tolerant of disturbed environments—favoring its establishment in open areas around cities (Nedvěd et al. 2011; Sánchez-Ruiz and Teruel 2006; Teruel et al. 2014). For instance, in Costa Rica we have observed that if conditions are suitable for an effective dispersal (e.g., open fields and mild seasonal climate), the species could rapidly occupy new areas including some with distinct conditions to those first occupied in the recipient region. In this country, *C. citricola* was first reported in dry, seasonal sites and progressively invaded more wet and less seasonal habitats, with the most recent report at the edge of Caribbean forests (GB unpublished). Thus, this species has apparently rapidly adapted to more humid and less seasonal climates but is always associated with open fields. However, dense tropical forested areas apparently limit the expansion of this spider species. Several non-systematic samplings in forested areas conducted close to sites where the species has been observed over three years, showed that the species is rare at the edge of tropical dry and rain forests (Sandoval and Barrantes unpublished).

The present study is, to our knowledge, the first to combine different methods comparing climatic conditions to assess the possible origin of an invasive species. This idea has been previously proposed (Steiner et al. 2008), but this is the first study that deduces the more likely invasion source by comparing climatic similarities between the potential native and invaded regions. However, we are aware that this approach has some drawbacks. A general limitation in our results is that the predictions are based on long-term means, extremes, and variances, which might not be representative of the niche for dynamic populations (Elith et al. 2010; Elith and Leathwick 2009), and this could affect the precision of the predictions obtained (Elith et al. 2010; Guisan and Zimmermann 2000). The limitations of SDMs (e.g., biases in occurrence sampling and the predictors used, uncertainty in model evaluation approaches) have also been addressed before (Araujo and Guisan 2006; Elith et al. 2010), and, particularly, the projections of our SDMs based on the native regions need to be interpreted with caution.

All our analyses indicate that the most likely region of origin of this recent *C. citricola* invasion is the southern African region, given its greater climatic matching with the invaded region. We recognize that although our results are appealing, they are correlative, and support from complementary analyses to determine, for example genetic affinities between the whole range of the alien populations and those of the native regions, could certainly provide additional insights into the origin of the studied invasion (Cristescu 2015; Guillemaud et al. 2010). Due to the widespread distribution of *C. citricola* and the contradictory morphological, behavioral and molecular information, there is also the possibility that the invasion of *C. citricola* has multiple sources (e.g., that some portion of the American populations arrived from both the Mediterranean and southern Africa) and/or introduction events (i.e., the arrival to the Americas did not happen only once). Though, to be able to discern if any of these scenarios are true, molecular analyses addressing these specific questions need to be conducted. Therefore, we consider our study an accessible approach that could be implemented as a first step to direct further research, mainly when resources to conduct fieldwork or molecular studies might be limited.

In conclusion, the analyses conducted here support the hypothesis that the invaded populations of *C. citricola* originated from southern Africa, based on the assumption that the source region should have a more similar climate to the invaded region. Our results also provide evidence of the expansion of *C. citricola* into a completely new set of climatic conditions in the Americas, which could represent a realized niche shift (reflecting species plasticity) or a fundamental niche shift (due to rapid evolution). Further studies focusing on physiological performance, adaptation strategies, and biological constraints for *C. citricola* in native and invasive populations may help us reach a better understanding of the processes driving its rapid expansion in the tropical areas of the invaded region.

Acknowledgements We would like to thank Dr. Angela Chuang and Dr. Ren Chu Cheng for providing information about the occurrence of this species in the United States and Africa, Dr. Ingi Agnarsson for sharing the preliminary results of the phylogenetic analysis of *Cyrtophora*, and Dr. Yael Lubin for the guidance and valuable information about this spider's natural history. We thank the Vicerrectoría de Investigación of the Universidad de Costa Rica (project C0-252) for providing financial support to GB. We also thank Dr. Jamie Kass for guiding an enriching editorial process as well as Dr. Stefano Mammola and an anonymous reviewer, who provided valuable feedback on the submission of this manuscript.

Authors contribution All authors developed the concept, LSH, AGR and ECM performed the analyses, LSH wrote the first draft of the manuscript and all authors provided revisions for the final version.

Funding GB was supported by the Vicerrectoría de Investigación of the Universidad de Costa Rica (project C0-252).

Availability of data and material and code availability The data used is available as Online Supplementary Material (Online Resource 1) and in online databases (GBIF.org; http://splink.cria.org.br/); the code used is available on GitHub: https://github.com/Garcia-Rodriguez/Cyrtophora_Invasion.

Declarations

Conflict of interest The authors declare that they have no conflict of interest.

References

Aiello-Lammens ME, Boria RA, Radosavljevic A, Vilela B, Anderson RP (2015) spThin: An R package for spatial thinning of species occurrence records for use in ecological niche models. Ecography 38:541–545. https://doi.org/10.1111/ecog.01132

Alayón-García G (2003) *Cyrtophora citricola* (Araneidae), registro nuevo de araña para Cuba. Cocuyo 13:14

Alayón-García G, Armas LF, Abud AJ (2001) Presencia de *Cyrtophora citricola* (Forskal, 1775) (Araneae: Araneidae) en las Antillas. Revista Ibérica De Aracnología 4:9–10

Araujo MB, Guisan A (2006) Five (or so) challenges for species distribution modelling. Biogeography 33:1677–1688. https://doi.org/10.1111/j.1365-2699.2006.01584.x

Atwater DZ, Ervine C, Barney JN (2018) Climatic niche shifts are common in introduced plants. Nat Ecol Evol 2:34–43. https://doi.org/10.1038/s41559-017-0396-z

Barbet-Massin M, Jiguet F, Albert CH, Thuiller W (2012) Selecting pseudo-absences for species distribution models: how, where and how many? Methods Ecol Evol 3:327–338

Bellard C, Leroy B, Thuiller W, Rysman JF, Courchamp F (2016) Major drivers of invasion risks throughout the world. Ecosphere 7:e01241

Blanke R (1972) Field Studies on the ecology and ethology of *Cyrtophora citricola* Forskal (Araneidae) in Andalusia. Forma Et Function 5:125–206

Blonder B, Harris DJ (2018) hypervolume: High dimensional geometry and set operations using kernel density estimation, support vector machines, and convex hulls. R package version 2.0.11. 2:. https://CRAN.R-project.org/package=hypervolume

Blonder B, Lamanna C, Violle C, Enquist BJ (2014) The *n* -dimensional hypervolume. Glob Ecol Biogeogr 23:595–609. https://doi.org/10.1111/geb.12146

Blonder B, Morrow CB, Maitner B, Harris DJ, Lamanna C, Violle C, Enquist BJ, Kerkhoff AJ (2018) New approaches for delineating n-dimensional hypervolumes. Methods Ecol Evol 9:305–319. https://doi.org/10.1111/2041-210X.12865

Bomford M, Kraus F, Barry SC, Lawrence E (2009) Predicting establishment success for alien reptiles and amphibians: a role for climate matching. Biol Invasions 11:713–724

Boyce MS, Vernier PR, Nielsen SE, Schmiegelow FKA (2002) Evaluating resource selection functions. Ecol Modell 157:281–300. https://doi.org/10.1016/S0304-3800(02)00200-4

Brandt LA, Benscoter AM, Harvey R, Speroterra C, Bucklin D, Romañach S, Watling JI, Mazzotti FJ (2017) Comparison of climate envelope models developed using expert-selected variables versus statistical selection. Ecol Model 345:10–20. https://doi.org/10.1016/j.ecolmodel.2016.11.016

Broennimann O, Fitzpatrick MC, Pearman PB, Petitpierre B, Pellissier L, Yoccoz NG, Thuiller W, Fortin MJ, Randin C, Zimmermann NE, Graham CH, Guisan A (2012) Measuring ecological niche overlap from occurrence and spatial environmental data. Global Ecol Biogeogr 21:481–497. https://doi.org/10.1111/j.1466-8238.2011.00698.x

Broennimann O, Petitpierre B, Chevalier M, González-Suárez M, Jeschke JM, Rolland J, Gray SM, Bacher S, Guisan A (2021) Distance to native climatic niche margins explains establishment success of alien mammals. Nat Commun 12:1–8

Brown JH (1989) Patterns, modes and extents of invasions by vertebrates. In: Di Castri F, Groves RH, Kruger FJ, Williamson M (eds) Biological invasions: a global perspective. Wiley, pp 85–110

Brown JH, Stevens GC, Kaufman DM (1996) The geographic range: size, shape, and internal structure. Annu Rev Ecol Syst 27:597–623. https://doi.org/10.1146/annurev.ecolsys.27.1.597

Cardoso PM, Mammola S, Rigal F, Carvalho J (2021) BAT-Biodiversity Assessment Tools. R package version 2.7.1. https://CRAN.R-project.org/package=BAT

Chauhan R, Sihag V, Singh NP (2009) Distribution and biocontrol potential of chosen spiders. J Biopest 2:151–155

Cowling RM, Rundel PW, Lamont BB, Arroyo MK, Arianoutsou M (1996) Plant diversity in mediterranean-climate regions. Trends Ecol Evol 11:362–366. https://doi.org/10.1016/0169-5347(96)10044-6

Cristescu ME (2015) Genetic reconstructions of invasion history. Mol Ecol 24:2212–2225. https://doi.org/10.1111/mec.13117

Di Cola V, Broennimann O, Petitpierre B, Breiner FT, D'Amen M, Randin C, Engler R, Pottier J, Pio D, Dubuis A, Pillissier L, Mateo RG, Hordijk W, Salamin N, Guisan A (2017) ecospat: an R package to support spatial analyses and modeling of species niches and distributions. Ecography 40:774–787. https://doi.org/10.1111/ecog.02671

Dormann CF, Elith J, Bacher S, Buchmann C, Carl G, Carré G, García Marquéz JR, Gruber B, Lafourcade B, Leitão PJ, Münkemüller T, McClean C, Osborne PE, Reineking B, Schröder B, Skidmore AK, Zurrell D, Lautenbach S (2013) Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. Ecography 36:27–46. https://doi.org/10.1111/j.1600-0587.2012.07348.x

Edwards GB (2006) *Cyrtophora citricola* (Araneae: Araneidae): a colonial tentweb orbweaver established in Florida. Entomol Circ 411:5–8

Elith J, Kearney M, Phillips S (2010) The art of modelling range-shifting species. Methods Ecol Evol 1:330–342. https://doi.org/10.1111/j.2041-210X.2010.00036.x

Elith J, Leathwick JR (2009) Species Distribution Models: ecological explanation and prediction across space and time. Annu Rev Ecol Evol S 40:677–697. https://doi.org/10.1146/annurev.ecolsys.110308.120159

Elith J, Phillips SJ, Hastie T, Dudík M, Chee YE, Yates CJ (2011) A statistical explanation of MaxEnt for ecologists.

Divers Distrib 17:43–57. https://doi.org/10.1111/j.1472-4642.2010.00725.x

Ehrenfeld JG (2010) Ecosystem consequences of biological invasions. Annu Rev Ecol Evol Syst 41:59–80. https://doi.org/10.1146/annurev-ecolsys-102209-144650

Ficetola GF, Thuiller W, Miaud C (2007) Prediction and validation of the potential global distribution of a problematic alien invasive species—The American bullfrog. Diversity Distrib 13:476–485. https://doi.org/10.1111/j.1472-4642.2007.00377.x

Fick SE, Hijmans RJ (2017) WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. Int J Climatol 37:4302–4315. https://doi.org/10.1002/joc.5086

Foelix RF (2011) Biology of Spiders (3rd editon). Oxford University Press, New York

Garb JE, González A, Gillespie RG (2004) The black widow spider genus *Latrodectus* (Araneae: Theridiidae): phylogeny, biogeography, and invasion history. Mol Phylogenet Evol 31:1127–1142. https://doi.org/10.1016/j.ympev.2003.10.012

Gillard MB, Drenovsky RE, Thiébaut G, Tarayre M, Futrell CJ, Grewell BJ (2020) Seed source regions drive fitness differences in invasive macrophytes. Am J Bot 107:749–760

Guillemaud T, Beaumont MA, Ciosi M, Cornuet J-M, Estoup A (2010) Inferring introduction routes of invasive species using approximate Bayesian computation on microsatellite data. Heredity 104:88–99. https://doi.org/10.1038/hdy.2009.92

Guisan A, Petitpierre B, Broennimann O, Daehler C, Kueffer C (2014) Unifying niche shift studies: insights from biological invasions. Trends Ecol Evol 29:260–269. https://doi.org/10.1016/j.tree.2014.02.009

Guisan A, Zimmermann NE (2000) Predictive habitat distribution models in ecology. Ecol Model 135:147–186. https://doi.org/10.1016/S0304-3800(00)00354-9

Gurevitch J, Padilla DK (2004) Are invasive species a major cause of extinctions? Trends Ecol Evol 19:470–474. https://doi.org/10.1016/j.tree.2004.07.005

Hayes KR, Barry SC (2008) Are there any consistent predictors of invasion success? Biol Invasions 10:483–506

Hijmans RJ, Phillips S, Leathwick J, Elith J (2021) dismo: Species Distribution Modeling. R package version 1.3-5. https://CRAN.R-project.org/package=dismo

Hirzel AH, Le Lay G, Helfer V, Randin C, Guisan A (2006) Evaluating the ability of habitat suitability models to predict species presences. Ecol Model 199:142–152. https://doi.org/10.1016/j.ecolmodel.2006.05.017

Hulme PE (2009) Trade, transport and trouble: Managing invasive species pathways in an era of globalization. J Appl Ecol 46:10–18

Iguchi K, Matsuura K, McNyset KM, Peterson AT, Scachetti-Pereira R, Powers KA, Vieglais DA, Wiley EO, Yodo T (2004) Predicting invasions of North American basses in Japan using native range data and a genetic algorithm. Trans Am Fish Soc 133:845–854. https://doi.org/10.1577/T03-172.1

Jarnevich CS, Reynolds LV (2011) Challenges of predicting the potential distribution of a slow-spreading invader: a habitat suitability map for an invasive riparian tree. Biol Invasions 13:153–163. https://doi.org/10.1007/s10530-010-9798-4

Jeschke JM, Heger T (2018) Invasion biology: hypotheses and evidence (vol 9). CABI, Oxfordshire

Johannesen J, Wennmann JT, Lubin Y (2012) Dispersal behaviour and colony structure in a colonial spider. Behav Ecol Sociobiol 66:1387–1398. https://doi.org/10.1007/s00265-012-1394-4

Kass JM, Muscarella R, Galante PJ, Bohl CL, Pinilla-Buitrago GE, Boria RA, Soley-Guardia M, Anderson RP (2021) ENMeval 2.0: Redesigned for customizable and reproducible modeling of species' niches and distributions. Methods Ecol Evol 12:1602–1608

Kolar CS, Lodge DM (2001) Progress in invasion biology: predicting invaders. Trends Ecol Evol 16:199–204

Köppen W, Volken E, Brönnimann S (2011) The thermal zones of the Earth according to the duration of hot, moderate and cold periods and to the impact of heat on the organic world. Meteorol Z 20:351–360. https://doi.org/10.1127/0941-2948/2011/105

Krehenwinkel H, Tautz D (2013) Northern range expansion of European populations of the wasp spider *Argiope bruennichi* is associated with global warming–correlated genetic admixture and population-specific temperature adaptations. Mol Ecol 22:2232–2248. https://doi.org/10.1111/mec.12223

Laborda A, Simó M (2008) First South American records of *Holocnemus pluchei* (Scopoli, 1763) and *Spermophora senoculata* (Dugés, 1836) (Araneae: Pholcidae). Gayana (concepc) 72:261–265. https://doi.org/10.4067/S0717-65382008000200013

Leborgne R, Cantarella T, Pasquet A (1998) Colonial life versus solitary life in *Cyrtophora citricola* (Araneae, Araneidae). Insectes Soc 45:125–134. https://doi.org/10.1007/s000400050074

Levi HW (1997) The American orb weavers of the genera *Mecynogea*, *Manogea*, *Kapogea* and *Cyrtophora* (Araneae: Araneidae). Bull Museum Comparat Zool 155:215–255

Liu C, Wolter C, Xian W, Jeschke JM (2020a) Most invasive species largely conserve their climatic niche. Proc Natl Acad Sci USA 117:23643–23651. https://doi.org/10.1073/pnas.2004289117

Liu C, Wolter C, Xian W, Jeschke JM (2020b) Species distribution models have limited spatial transferability for invasive species. Ecol Lett 23:1682–1692. https://doi.org/10.1111/ele.13577

Lockwood JL, Hoopes MF, Marchetti MP (2013) Invasion ecology, 2nd edn. Wiley, West Sussex

Latombe G, Pyšek P, Jeschke JM, Blackburn TM, Bacher S, Capinha C, Costello MJ, Fernández M, Gregory RD, Hobern D, Hui C, Jetz W, Kumschick S, McGrannachan C, Pergl J, Roy HE, Scalera R, Squires ZE, Wilson JRU, Winter M, Genovesi P, McGeoch MA (2017) A vision for global monitoring of biological invasions. Biol Conserv 213:295–308. https://doi.org/10.1016/j.biocon.2016.06.013

Mannion C, Amalin D, Peña J, Edwards GB (2002) A new spider in Miami-Dade County: *Cyrtophora citricola*. Hort Newsletter, University of Florida Extension 2:3

Marice PV, Agnes AM (2010) Influence of light on spatial orientation and web construction of *Cyrtophora citricola* (Araneae, Araeneidae). J Ecobiol 27:179–186

Martín-Castejón Y, Sánchez-Ruiz A (2010) Registros más occidentales de *Cyrtophora citrícola* (Forskal, 1775) (Araneae: Araneidae) en Cuba. Novitates Caribaea 3:83–84

Mollot G, Pantel JH, Romanuk TN (2017) The effects of invasive species on the decline in species richness: a global meta-analysis. In: Bohan DA, Dumbrell AJ (eds) Advances in ecological research. Academic Press, pp 161–178

Muscarella R, Galante PJ, Soley-Guardia M, Boria RA, Kass JM, Uriarte M, Anderson RP (2014) ENMeval: An R package for conducting spatially independent evaluations and estimating optimal model complexity for Maxent ecological niche models. Methods Ecol Evol 5:1198–1205. https://doi.org/10.1111/2041-210X.12261

Nedvěd O, Pekár S, Bezděčka P, Líznarová E, Řezáč M, Schmitt M, Sentenská L (2011) Ecology of Arachnida alien to Europe. Biocontrol 56:539–550. https://doi.org/10.1007/s10526-011-9385-3

Nentwig W, Paolo Pantini P, Vetter RS (2017) Distribution and medical aspects *of Loxosceles rufescens*, one of the most invasive spiders of the world (Araneae: Sicariidae). Toxicon 132:19–28. https://doi.org/10.1016/j.toxicon.2017.04.007

Nguyen D, Leung B (2022) How well do species distribution models predict occurrences in exotic ranges? Glob Ecol Biogeogr 31:1051–1065. https://doi.org/10.1111/geb.13482

Nuñez MA, Medley KA (2011) Pine invasions: Climate predicts invasion success; something else predicts failure. Divers Distrib 17:703–713. https://doi.org/10.1111/j.1472-4642.2011.00772.x

Peel MC, Finlayson BL, McMahon TA (2007) Updated world map of the Köppen–Geiger climate classification. Hydrol Earth System Sciences 11:1633–1644. https://doi.org/10.5194/hess-11-1633-2007

Peterson AT (2003) Predicting the geography of species' invasions via ecological niche modeling. Q Rev Biol 78:419–433. https://doi.org/10.1086/378926

Peterson AT (2011) Ecological niche conservatism: a time-structured review of evidence. J Biogeogr 38:817–827. https://doi.org/10.1111/j.1365-2699.2010.02456.x

Petitpierre B, Kueffer C, Broennimann O, Randin C, Daehler C, Guisan A (2012) Climatic niche shifts are rare among terrestrial plant invaders. Science 335:1344–1348. https://doi.org/10.1126/science.1215933

Phillips SJ, Anderson RP, Dudík M, Schapire RE, Blair ME (2017) Opening the black box: an open-source release of Maxent. Ecography 40:887–893. https://doi.org/10.1111/ecog.03049

Phillips SJ, Anderson RP, Schapire RE (2006) Maximum entropy modeling of species geographic distributions. Ecol Model 190:231–252. https://doi.org/10.1016/j.ecolmodel.2005.03.026

Phillips SJ, Dudík M (2008) Modeling of species distribution with Maxent: new extensions and a comprehensive evalutation. Ecography 31:161–175. https://doi.org/10.1111/j.0906-7590.2008.5203.x

Phillips SJ, Dudík M, Elith J, Graham C, Lehmann A, Leathwick J, Ferrier S (2009) Sample selection bias and presence-only distribution models: implications for background and pseudo-absence data. Ecol Appl 19:181–197

Pili AN, Tingley R, Sy EY, Diesmos MLL, Diesmos AC (2020) Niche shifts and environmental non-equilibrium undermine the usefulness of ecological niche models for invasion risk assessments. Sci Rep 10:7972. https://doi.org/10.1038/s41598-020-64568-2

Pyšek P, Hulme PE, Simberloff D, Bacher S, Blackburn TM, Carlton JT, Dawson W, Essl F, Foxcroft LC, Genovesi P, Jeschke JM, Kühn I, Liebhold AM, Mandrak NE, Meyerson LA, Pauchard A, Pergl J, Roy HE, Seebens H, van Kleunen M, Vilà M, Wingfield MJ, Richardson DM (2020) Scientists' warning on invasive alien species. Biol Rev 95:1511–1534. https://doi.org/10.1111/brv.12627

Řezáč M, Růžička V, Hula V, Dolanský J, Machač O, Roušar A (2021) Spiders newly observed in Czechia in recent years—Overlooked or invasive species? BioInvas Rec 10:555–566. https://doi.org/10.3391/bir.2021.10.3.05

Ricciardi A (2013) Invasive species. In: Leemans R (ed) Ecological systems: selected entries from the Encyclopedia of Sustainability Science and Technology. Springer, New York, pp 161–178. https://doi.org/10.1007/978-1-4614-5755-8_10

Sagarin RD, Gaines SD, Gaylord B (2006) Moving beyond assumptions to understand abundance distributions across the ranges of species. Trends Ecol Evol 21:524–530

Sánchez-Ruiz A, Teruel R (2006) Acerca de la presencia de *Cyrtophora citricola* (Forskål, 1775) (Araneae: Araneidae) en Cuba. Boletin De La Sociedad Entomológica Aragonesa 38:335–336

Saupe EE, Barve V, Myers CE, Soberón J, Barve N, Hensz AT, Peterson AT, Owens HL, Lira-Noriega A (2012) Variation in niche and distribution model performance: the need for a priori assessment of key causal factors. Ecol Model 237–238:11–22. https://doi.org/10.1016/j.ecolmodel.2012.04.001

Sheldon KS, Zhao L, Chuang A, Panayotava I, Miller L, Bourouiba, (2017) Revisiting the physics of spider ballooning. In: Layton AT, Miller LA (eds) Women in mathematical biology. Springer, Cham, pp 163–178

Simberloff D, Martin JL, Genovesi P, Maris V, Wardle DA, Aronson J, Courchamp F, Galil B, García-Berthou E, Pascal M, Pyšek P, Sousa R, Tabacchi E, Vilà M (2013) Impacts of biological invasions: what's what and the way forward. Trends Ecol Evol 28:58

Snyder WE, Evans EW (2006) Ecological effects of invasive arthropod generalist predators. Annu Rev Ecol Evol Syst 37:95–122. https://doi.org/10.2307/annurev.ecolsys.37.091305.30000

Soares-Álvares ES, De María M (2004) First record of Cyrtophora *citricola* (Forskål) in Brazil (Araneae: Araneidae) Rev. Brasileira Zool 21:155–156

Soberón J (2007) Grinnellian and Eltonian niches and geographic distributions of species. Ecol Lett 10:1115–1123

Starr ChK (2005) Observaciones sobre *Cyrtophora citricola* (Araneae: Araneidae) en Haití. Cocuyo 15:15

Steiner FM, Schlick-Steiner BC, VanDerWal J, Reuther KD, Christian E, Stauffer C, Suarez AV, Williams SE, Crozier RH (2008) Combined modelling of distribution and niche in invasion biology: a case study of two invasive

Tetramorium ant species. Divers Distrib 14:538–545. https://doi.org/10.1111/j.1472-4642.2008.00472.x

Tanaka K (1996) Seasonal and latitudinal variation in supercooling ability of the house spider, *Achaearanea tepidariorum* (Araneae: Theridiidae). Funct Ecol 10:185–192. https://doi.org/10.2307/2389842

Teruel R, Martín-Castejón Y, Cala F, García GA, Rodríguez-Cabrera TM (2014) Actualización de la distribución de *Cyrtophora citricola* (Forskal, 1775) (Araneae: Araneidae) en Cuba y las Antillas. Revista Ibérica De Aracnología 25:27–32

Thomas CFG, Brain P, Jepson PC (2003) Aerial activity of linyphiid spiders: modelling dispersal distances from meteorology and behaviour: Dispersal distances of ballooning spiders. J Appl Ecol 40:912–927. https://doi.org/10.1046/j.1365-2664.2003.00844.x

Tilman D, Clark M, Williams DR, Kimmel K, Polasky S, Packer C (2017) Future threats to biodiversity and pathways to their prevention. Nature 546:73–81. https://doi.org/10.1038/nature22900

van Wilgen NJ, Richardson DM (2012) The roles of climate, phylogenetic relatedness, introduction effort, and reproductive traits in the establishment of non-native reptiles and amphibians. Conserv Biol 26:267–277. https://doi.org/10.1111/j.1523-1739.2011.01804.x

Víquez C (2007) First record of *Cyrtophora citricola* (Forskål) from Costa Rica, with notes on some related species (Araneae: Araneidae). Boletin De La Sociedad Entomológica Aragonesa 1:385–388

Vonshak M, Dayan T, Ionescu-Hirsh A, Freidberg A, Hefetz A (2010) The little fire ant *Wasmannia auropunctata*: a new invasive species in the Middle East and its impact on the local arthropod fauna. Biol Invasions 12:1825–1837. https://doi.org/10.1007/s10530-009-9593-2

Warren DL, Glor RE, Turelli M (2008) Environmental niche equivalency versus conservatism: quantitative approaches to niche evolution. Evolution 62:2868–2883. 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. https://doi.org/10.1146/annurev.ecolsys.36.102803.095431

Yip EC, Lubin Y (2016) Effects of diet restriction on life history in a sexually cannibalistic spider. Biol J Linn Soc 118:410–420. https://doi.org/10.1111/bij.12730

Yoshida T, Goka K, Ishihama F, Ishihara M, Kudo S (2007) Biological invasion as a natural experiment of the evolutionary processes: introduction of the special feature. Ecol Res 22:849–854. https://doi.org/10.1007/s11284-007-0435-3

Zhang Z, Mammola S, McLay CL, Capinha C, Yokota M (2020) To invade or not to invade? Exploring the niche-based processes underlying the failure of a biological invasion using the invasive Chinese mitten crab. Sci Total Environ 728:138815