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En busca de la fuente: definiendo el origen de *Cyrtophora citricola* (Araneae: Araneidae), una especie invasora en América utilizando comparaciones ambientales.

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RESUMEN

Conocer el origen de las invasiones biológicas es de vital importancia para evaluar los posibles impactos de la especie invasora en los sitios donde se establece y tomar las medidas de mitigación correspondientes. *Cyrtophora citricola* es una especie recientemente introducida en América, pero, tanto las causas de su introducción, así como el sitio de origen de donde los individuos emigraron hacia América no son claros. Hasta ahora, se ha considerado que la especie tiene un amplio rango nativo que se extiende por Europa, África y parte de Asia. Sin embargo, análisis filogenéticos muestran diferencias considerables entre las poblaciones nativas, siendo las poblaciones de Suráfrica las más emparentadas con las americanas. Por otro lado, similitudes en morfología y comportamiento entre las poblaciones del Mediterráneo y las americanas, así como la gran cantidad de intercambio comercial que se da entre estas dos regiones, apoyan la hipótesis de un origen mediterráneo de esta invasión por vía marítima. Con el objetivo de dilucidar el origen de la invasión de *C. citricola*, utilicé Modelos de Nicho Ecológico, en conjunto con Análisis de Componentes Principales Ambiental, para comparar las características ambientales entre los dos posibles sitios de origen considerados (Sur de África y la región Mediterránea), con las características ambientales de los sitios donde la especie se ha registrado en América. Dado que es una invasión reciente (tanto solo 20 años desde su primer registro), se prevé que las poblaciones establecidas en América ocurren en sitios con características ambientales similares al sitio de donde provienen. Por lo tanto, al contrastar las características ambientales de las poblaciones americanas con aquellas de las dos regiones nativas, la región nativa con mayor similitud ambiental puede ser considerada como el sitio de origen de la invasión.

Mis resultados sugieren consistentemente que la región con mayor similitud ambiental con respecto a los sitios invadidos en América es el Sur de África. Esto concuerda con los resultados del análisis filogenético, por lo tanto, probablemente dicha invasión proviene del Sur de África. Estos resultados brindan un camino a seguir en la investigación de los impactos que esta especie podría tener en los sitios invadidos, pues al delimitar su origen se pueden enfocar esfuerzos de investigación comparando los aspectos de la historia natural en dicha región que pueden ser relevantes para su estudio y control en América.

PALABRAS CLAVE: Modelos de nicho ecológico, biogeografía, invasiones biológicas, América, Mediterráneo, Suráfrica.

ABSTRACT

In the study of biological invasions, it is important to know the origin of each invasion in order to assess the possible impacts the foreign organism might have on the new regions, as this aids to take the necessary measures to minimize said impacts. *Cyrtophora citricola* is a species that was recently introduced to the American continent, however, it is unknown the way in which this species came to the continent nor the place where the invasion came from. Until now, it has been considered that the species has a broad native distribution – Europe, Africa and the East of Asia-, however, molecular analyses show considerable differences between the native populations, as well as they show that the South African populations are more similar to the populations in America. On the other hand, similarities in both morphology and behaviour between the Mediterranean and American populations, alongside the high commercial trade

between the two regions, support that this species might have arrived from the Mediterranean region. In order to elucidate the origin of the invasion of *C. citricola*, I used Ecological Niche Models, alongside Environmental Principal Component Analysis, to compare the environmental conditions of the two origin sites considered (South of Africa and the Mediterranean) to those of the sites where the species have been reported in the invaded region. As it is a recent invasion (just 20 years have passed since its first report), it is considered that the American populations will occur in sites with similar environmental conditions to those of the region where the species came from. Therefore, when comparing the environmental conditions associated to the American populations with those of the populations in both native regions, the native region with higher environmental similarity can be considered as the region of origin of the invasion.

My results consistently support that the the South of Africa is the region with higher environmental similarity in comparison to the invaded sites in America. This agrees with the molecular analyses, and we conclude that it is highly possible the species migrated from the South of Africa. This results open the door to studies focused in assessing the possible impacts this species might have in the invaded sites, because knowing the natural history of the populations where the species came from allows us to assess the risks based on the aspects and interactions this species has in its own native habitat.

KEYWORDS: Ecological Niche Modeling, biogeography, biological invasion, America, Mediterranean Basin, South Africa.

INTRODUCTION

The study of biological invasions has gained interest in the scientific community over the last two decades (Lowry et al., 2013). Numerous species have arrived and continue arriving, to regions all around the world (Loiselle et al., 2003; Lowry et al., 2013; Valéry, Fritz, Lefeuvre, & Simberloff, 2008; Williamson 1996). Some of the main impacts invasive species have presented are competitive exclusion and predation on native species (Manchester & Bullock, 2000), transmission of pathogens (Manchester & Bullock, 2000), hybridization (Manchester & Bullock, 2000), economic losses (Andersen *et al.*, 2004; Cook *et al.*, 2007; Stone, 2005), and health issues (Andersen *et al.*, 2004). However, the factors responsible for biological invasions, as well as the impacts the invaders have on the new communities, vary widely across species (Blackburn et al., 2011; Valéry et al., 2008).

The arrival and establishment of a particular species on a recipient area is a process that depends primarily on the species dispersal capacity, the propagule pressure (Simberloff, 2009), and the environmental similarity between both the original and the recipient area (Brown, Stevens, & Kaufman, 1996; Peterson, 2003). In general, the probability of an arriving species to establish on the recipient area increases with the similarity of the environmental conditions between the original and new areas (Peterson, 2003; Wiens & Graham, 2005). At the recipient area, the interaction with the native biota is unpredictable, but knowing the interactions and ecological requirements of the original population could provide useful insights on the possible effects a particular species may have in the newly invaded region (Peterson, 2003; Wiens & Graham, 2005).

Even though biological invasions are common in nature, long-distance dispersal is rare, since it is often restricted by climatic and physical barriers (Diamond, 1984; Peterson, 2003; Wiens & Graham, 2005). However, human transportation – whether intentionally or not – has rapidly increased the rate of such long-distance events in recent times (Brown et al., 1996; Kobelt & Nentwig, 2008; Peterson, 2003). In order to successfully establish in a new area – especially one that could be impossible to reach under more natural conditions -

Invasive species share some general traits that favor their expansion in new habitats, such as tolerance to long periods of starvation and desiccation periods, high reproductive rate, and high dispersal capacity (Foelix, 2011; Nedvěd et al., 2011). These are traits that some spider species possess (Foelix, 2011) and make them well suited for invading new and distant geographical areas. Invasive spider species are generally associated with synanthropic conditions and altered natural habitats (Baird & Stoltz, 2002; Kobelt & Nentwig, 2008; Laborda & Simó, 2008; Nedvěd et al., 2011). Information on invasive spider species coming from other continents to the Neotropics is scarce (Garb, González, & Gillespie, 2004; Laborda & Simó, 2008) with the exception of the recently documented invasion of *Latrodectus geometricus* from South Africa to the Neotropics (Garb et al., 2004; Taucare-Ríos, Bizama, & Bustamante, 2016) and the araneid *Cyrtophora citricola* (Forsskål, 1775) (*sensu lato*), which is the focus of the present study (Levi, 1997).

Cyrtophora citricola is reported as native to northern Africa, southeastern Europe, and the Middle East (Mediterranean region here after), and in southern Africa (Peel, Finlayson, & McMahon, 2007), with extensive desert regions separating each group of populations. However,

the specific region from which this species migrated to America remains unknown. Considering the disjunct native distribution of this species, we hypothesize the South African region and the Mediterranean region as the two possible origins for the invasion to America. Phylogenetic evidence places *Cyrtophora* spiders from America closer to those of South Africa (I. Agnarsson unpubl.data). However, we do not discard the possibility that this spider might have arrived to America from the Mediterranean region on commercial vessels traveling between these two regions. Particularly, considering the intense maritime, commercial trade between the Mediterranean region and America (38542 Twenty-foot Equivalent Units (TEU) in 2016; the American Association of Port Authorities -AAPA) compared with South African trading (2770 TEU, ~7% the Mediterranean trade). Additionally, many populations of *C. citricola* occur near coastal areas in the Mediterranean region (Blanke 1972), which increases the probability of being transported by merchant marine vessels. The morphology and behavior of the Mediterranean *C. citricola* also resemble those of American spiders rather than those of southern Africa (Y. Lubin pers. comm.).

To provide support for the possible origin of the invasion of *Cyrtophora* in the Americas, we evaluated the combination of environmental variables that best explain the distribution of *C. citricola* spiders in the Mediterranean and southern African regions. To this end we applied different geographic and environmental approaches to test which of these combinations predict more precisely the current distribution of this spider in America. Considering that the invasion of *Cyrtophora* in America is very recent – specifically it was first registered in 1996 (Levi, 1997) – we expect that newly established populations occupy habitats with similar environmental

conditions to those of the native region (Peterson, 2003). Therefore, the environmental variables of the region occupied by *Cyrtophora citricola* in America will have a higher overlap with the set of variables from the native region than with the non-native region.

METHODS

Study species

Cyrtophora citricola is a gregarious species that has been observed in both colonial and solitary webs, built on diverse plant species and human constructed structures (Chauhan, Sihag, & Singh, 2009; Johannesen, Wennmann, & Lubin, 2012; Lubin, 1980; Madrigal-Brenes, 2012; Rypstra, 1979; Teruel, Martín-Castejón, Cala, García, & Rodríguez-Cabrera, 2014). Colonies can be massive and often cover the entire crown of bushes and medium-size trees (Barba-Díaz, Alegre-Barroso, & de la Torre, 2014; Chauhan et al., 2009; Edwards, 2006; Martín-Castejón & Sánchez-Ruiz, 2010; Rao & Lubin, 2010).

The distribution of *Cyrtophora citricola* was originally restricted to Asia, Africa, and the southeastern portion of Europe (Blanke 1972), but recently the species has been recorded in several countries of the Americas, ranging from Brazil to Florida in the United States (Alayón García, 2003; Edwards, 2006; Levi, 1997; Martín-Castejón & Sánchez-Ruiz, 2010; Sánchez-Ruiz & Teruel, 2006; Viquez, 2007).

Species occurrences

For this study, we compiled 2795 geo-referenced data 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 29th,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 (See Mat. Suppl. Table S.2), 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 own research.

We removed duplicated and inaccurate data points (e.g. points that fell in the ocean) from the database prior to conduct the analyses by projecting all points in a global map. Then we filtered the remaining data using the R package spThin (Aiello-Lammens, Boria, Radosavljevic, Vilela, & Anderson, 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. This procedure generated 32 data points for South Africa and the Southeastern part of Mozambique (hereafter, the South African region), 108 for the Mediterranean Region and 122 for America (Fig.1).

Environmental information

The Mediterranean region's climate is seasonal with warm-dry summers, and cold-wet winters (Cowling, Rundel, Lamont, Arroyo, & Arianoutsou, 1996). The Western Cape of South Africa has similar climatic conditions to those of the Mediterranean region (Cowling et al.,

1996), but the climate varies markedly in other South African areas (Köppen, Volken, & Brönnimann, 2011; Peel et al., 2007). It ranges from oceanic, subtropical and semi-arid climates in the coastal areas to hot and cold semi-arid, or cold and hot desert climates further in mainland (Köppen et al., 2011; Peel et al., 2007).

We used the 19 bioclimatic variables available at WorldClim data base Version 2, in a 2.5 arcmin resolution (approximately 20 km² near the Equator, Fick & Hijmans, 2017, <http://www.worldclim.org>) for all analyses. This set of variables comprises means of climatic information from 1970 to 2000, obtained as interpolation of data from weather stations all over the world by using thin-plate splines (Fick & Hijmans, 2017). Additionally, we constructed three more layers using the layers of monthly precipitation, minimum temperature and wind speed available in this second version of Worldclim. With the mean value obtained from the monthly precipitation layers, we calculated the Average Annual Precipitation (hereafter AAP). We extracted the minimum temperature value for each cell within the 12 monthly layers of minimum temperature to get the Minimum Annual Temperature (hereafter MAT). Finally, we constructed a Maximum Annual Wind Speed (hereafter MWS) layer, by extracting the maximum speed values for each cell layer within the monthly layers of wind speed. We included this last variable as this species is known to disperse by wind (Johannesen et al., 2012).

Analyses

Model calibration

To elucidate the possible native region of the American *C. citricola* we created three sets

of independent ecological niche models (ENM's): one for each of the for the two potential native regions (South African and Mediterranean) and one for the invaded region. One of the "Native models" based on the environmental conditions from the South Africa region, and the other based on the environmental conditions of the populations around the Mediterranean region. To determine the accuracy with which each native model predicted the real known occurrences of spiders in the invaded region, we projected both models prediction on America (Fig. 1). Then we created a third model calibrated on the invaded environmental conditions and projected it onto the two possible native regions, to cross validate the accuracy of our native models. We calibrated all models by delimiting an area of 1000 km around the presence points of each region (Fig. 1), so that the calibration area would include enough background area containing both, environments were the species could be present and other where the species is likely absent.

For each region we generated several candidate ENM's with different parameterizations using the ENMeval R package (Muscarella et al., 2014). Each model was constructed using variations of two different parameters: (1) regularization multipliers that generate penalty values which help to select more simple models (see Elith et al., 2011; Phillips, Anderson, Dudík, Schapire, & Blair, 2017) (these values range from 0.5 to 5, at intervals of 0.5) and (2) different feature classes (transformations of the environmental variables values, see Elith et al., 2011): Linear (L), Quadratic-Linear(QL), Hinge (H), and their combinations with Product and Threshold (LQHP y LQHPT) (Phillips, Anderson, & Schapire, 2006; Phillips & Dudík, 2008). To avoid the spatial autocorrelation between testing and training points we used two different data partitioning methods implemented by Muscarella et al., 2014. For the South African Model,

we used the Blocks method, which divides the data in four bins with equal amount of occurrences but allows bins to vary in geographic size (Muscarella et al., 2014). This method has been recommended in cases where spatial extrapolation is needed (Muscarella et al., 2014) such as the case of this region which presents few occurrences that besides tend to be grouped (Fig. 1). For the Mediterranean and American models, we used the Checkerboard 2 partitioning method, which, as the blocks method, divides the data in four bins, but facilitates the inclusion of isolated occurrences without altering the geographical size of the bin (Muscarella et al., 2014). We considered this method appropriate for the scattered occurrences we have for these two regions. Initially, we used the same partitioning method (Checkerboard 2) for all three models, however, we decided to use the Blocks partitioning method for the South African model because the Checkerboard 2 method showed an overfitted prediction in this region and the model had considerably less occurrence points than the models of the other two regions (See Suppl. Mat, Table S.1, Fig. S.1).

To evaluate the performance of each set of models created and select the best fitted for each native region, we used four selection criteria with the following priority order: (1) the lowest ‘Minimum training presence’ omission rate (OR_{MTP}), (2) the highest Area Under the Curve (AUC_{TEST}), (3) the lowest value of 10% Training omission rate (OR_{10}), and (4) the lowest number of parameters. For details regarding these parameters, see Muscarella et al. (2014). The model that best fitted the criteria mentioned, was selected as the model to run the posterior projections and analyses.

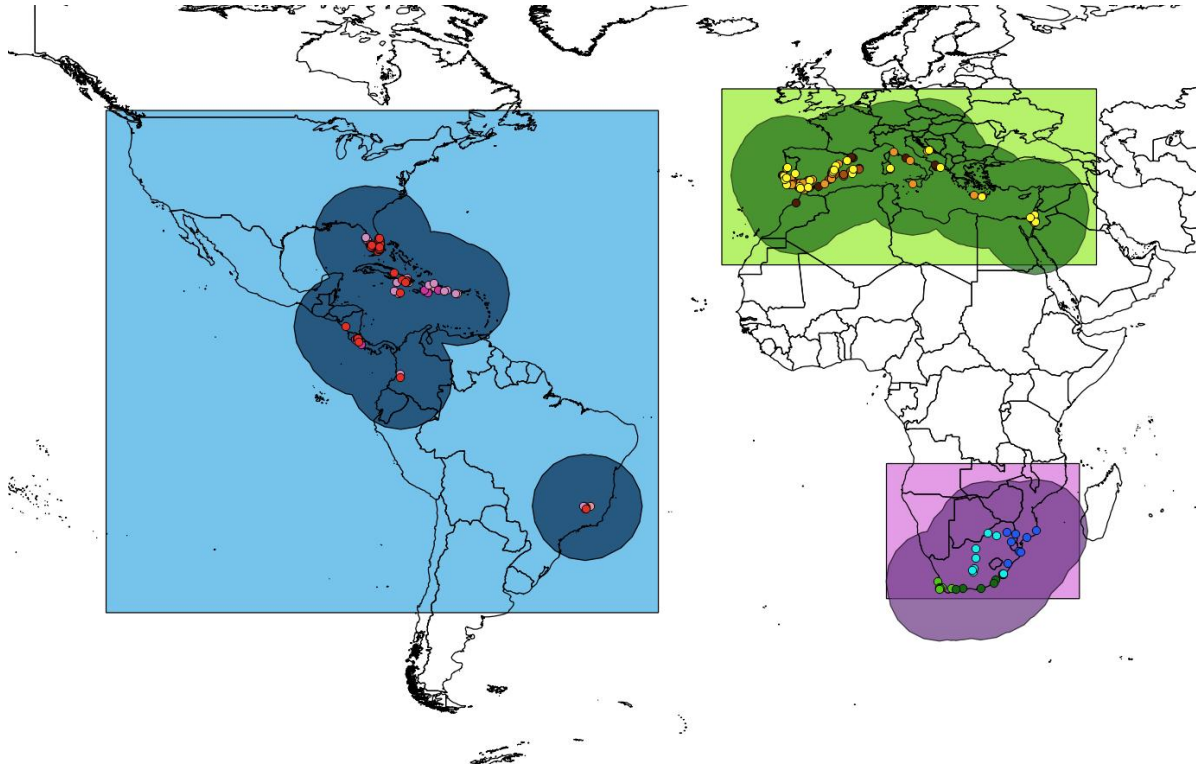


Figure. 1. Invaded and native regions defined as study regions to run the niche models. An area of 1000 km around the occurrences for each region was used to calibrate the models (represented in dark green in the Mediterranean, dark purple in South Africa and dark blue in America). The rectangular areas represent the areas in which the models were projected: in light blue, the area covered by the projections of both native models in America, the light purple and light green the areas in which the American model was projected in the Mediterranean and South African region, respectively. The different colors for the occurrences represent the bins in which the occurrences were split according to the partitioning method used. All models were constructed using the information available only for the terrestrial area within the regions shown in this figure.

Environmental comparisons

We extracted the suitability values assigned by each selected native model to the occurrences of *C. citricola* in America. These values are generated by each model for each cell in the region where it was projected, after correlating and fitting the environmental variables to the occurrences included for the region used for calibration (Warren & Seifert, 2011). We compared the suitability values of both native models using a T-test.

We also converted the predictions of the selected native models to binary maps depicting suitable and unsuitable regions in order to determine the number of occurrences in America that each model omitted. We used three different threshold criteria to define this binarization: the Minimum training presence logistic threshold (MTP), the 10th percentile training presence logistic threshold (P10), and the Maximum training sensitivity plus specificity logistic threshold value (MSS) (Liu, White, & Newell, 2013). We obtained these threshold values as part of the output of each native model (Tables 2-3). Each American occurrence with a suitability value lower than each threshold was considered environmentally unsuitable for the species (therefore, an absence), and every value above each threshold was considered environmentally suitable for *C. citricola* (therefore, the species is considered present in the area). We followed the same procedure when the American model was projected onto each native region.

We also calculated the environmental niche overlap using a PCA-env, following the approach designed by Broennimann et al. (2012). This approach allowed us to compare the environmental conditions of the American region with those present in each native region. Broennimann's environmental PCA provides three measures of climatic similarity: Unfilling,

Stability and Expansion. The first one indicates the proportion of environmental conditions in which the species is found in the native region but that are not associated with the distribution of the species in the invaded region (Petitpierre et al., 2012). Stability measures the proportion of environmental conditions shared between two regions (Petitpierre et al., 2012), in our case the invaded region versus each of the two native regions. And Expansion corresponds to the proportion of environmental conditions in which the species has been observed in the invaded region that are different from the conditions in which the population have been documented in its native region (Petitpierre et al., 2012).

Geographic comparison

To analyze the geographic overlap between the native model projected in the invaded region we used Schoener's D index (Schoener, 1968) and Hellinger's I index (Warren, Glor, & Turelli, 2008). We applied these indices to compare the predictions of each native model projected into America, to the predictions of another model created in America and projected in America as well. These indices ranges from 0 (no niche overlap) to 1 (total niche overlap). We used the same criteria proposed by Rodder and Engler (2011) to interpret the index obtained: values between 0-0.2 indicate no or limited overlap, 0.2-0.4 indicates low overlap, 0.4-0.6 for moderate overlap, 0.6-0.8 represents high overlap and 0.8-1 very high overlap.

RESULTS

The parameters and evaluation metrics of the three models selected are presented in Table 1. For the South African model, Precipitation of Driest Quarter, Isothermality and the

Minimum Annual Temperature were the three variables that had the largest contribution. Precipitation of Wettest Month, Mean Temperature of Coldest Quarter and Temperature Seasonality showed the highest contribution for the Mediterranean model. Maximum Annual Wind Speed, the Mean Temperature of Wettest Quarter and Mean Temperature of Driest Quarter had the highest contributions in the American Model (Suppl. Mat, Table S.3).

The projection of the South African model predicted more precisely the current distribution of *C. citricola* in America than the Mediterranean model. This second model predicted only a few isolated suitable regions for the species, but failed in predicting most of the current distribution of the spider in the invaded region (Fig. 2).

The suitability values obtained for the occurrence points in America from the South African model were higher (0.87 ± 0.10 SD), than those obtained from the Mediterranean model ($0.31 \text{ SD} \pm 0.26$) ($t = -21.87$, $g1 = 154.28$, $p < 0.0001$). Thus, the South African model estimates higher suitability values for the occurrence sites already occupied by *C. citricola* in America (Fig. 3.A).

When the values of each model were binarized into suitable and unsuitable sites, the South African model predicted all but one of the current occurrence points of *C. citricola* in America (Table 2, Fig. 4, Suppl. Mat. Fig. S.2). On the contrary, the Mediterranean model, predicted only a few of the actual American occurrences (Table 2, Fig. 4, Fig. Suppl. Mat. Fig. S.2).

These results are supported by the projections of the American model to each native region (Fig 5). The suitability values assigned by the American Model to the South African

occurrences were higher than those assigned to the Mediterranean occurrences ($t = -3.38$, $gI = 31.26$, $p=0.002$, Fig. 3. B), with an average suitability value of $0.06 (\pm 0.09, SD)$ for the South African occurrences and $0.002 (\pm 0.011, SD)$ for the Mediterranean occurrences. When the suitability values were binarized, more occurrences were consistently omitted by the American model in the Mediterranean region in comparison to the South African occurrences, regardless of the threshold used (Table 3, Fig. 6, Fig. Suppl. Mat. Fig. S.3).

Both models shared a low to moderate portion of their predicted suitable areas that *C. citricola* occupies in America, as indicated by Schoener's D index value of 0.24, and 0.50 for the Hellinger's I index. According to the Schoener's index value, the predictions of the American model and the South African model shared a low portion of their predictions ($D=0.33$), but according to the Hellinger's index, they shared a high portion of their predictions ($I=0.64$). The Mediterranean model shared a moderate to high proportion to the American model's predictions, with a D index value of 0.42 and a I index of 0.65.

In contrast, the environmental PCA analyses, showed more evident differences between both native regions when compared to the American prediction. The environmental characteristics of the geographic distribution occupied by *C. citricola* in South Africa had a greater overlap (stability 58%) with its distribution in America, than the Mediterranean distribution (stability 20%) (Fig 7). This also indicates that this spider has occupied new environmental combinations (expansion) in America in relation to the conditions existing on the native regions, at least 42% based on the South African model, and 80% concerning the Mediterranean Model.

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

Region	South Africa	Mediterranean	America
Data partition method	Blocks	Checkerboard 2	Checkerboard 2
Feature Class[†]	H	LQH	LQHP
Regularization multiplier	3.5	1.5	5
OR_{MTP} (var) *	0.06 (0.01)	0.01 (0.00)	0.01 (0.00)
AUC_{TEST} (var)**	0.82 (0.13)	0.97 (0.00)	0.93 (0.00)
OR₁₀ (var)***	0.22 (0.07)	0.11 (0.00)	0.10 (0.00)
Parameters	14	40	24

[†]Feature classes: H= hinge, LQH= Linear-Quadratic-Hinge, LQHP=Linear-Quadratic-Hinge-Product.

* OR_{MTP}: Minimum training presence omission rate.

** AUC_{TEST}: Area Under the Curve.

*** OR₁₀ : 10% Training omission rate.

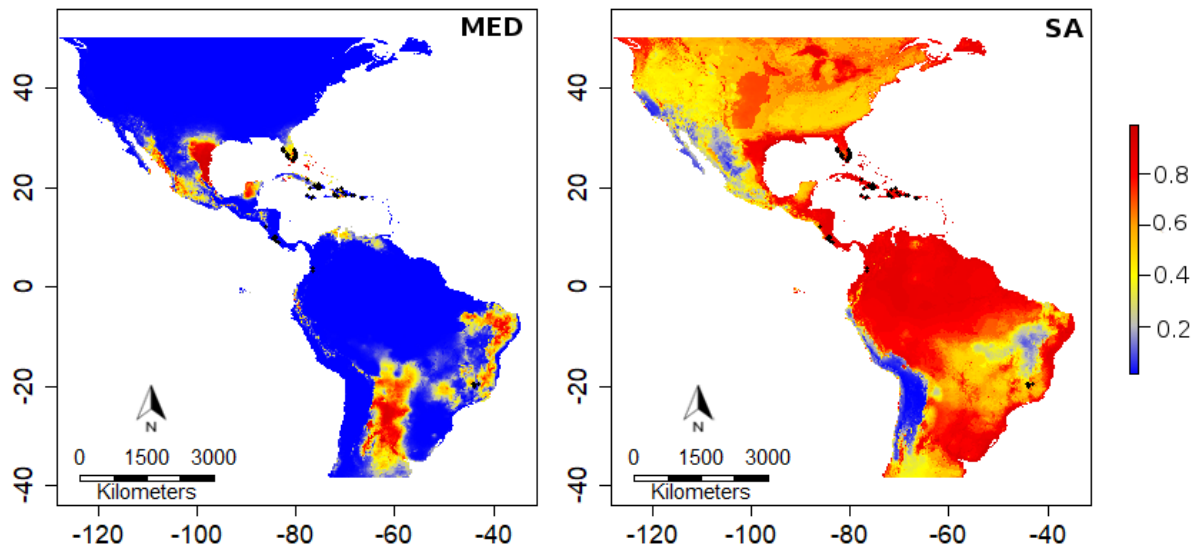


Figure 2. Predictions of the distribution of *Cyrtophora citricola* in America projected from the two native models. MED- depicts the predictions made by the Mediterranean model; and SA- depicts or shows the prediction made by the South African model.

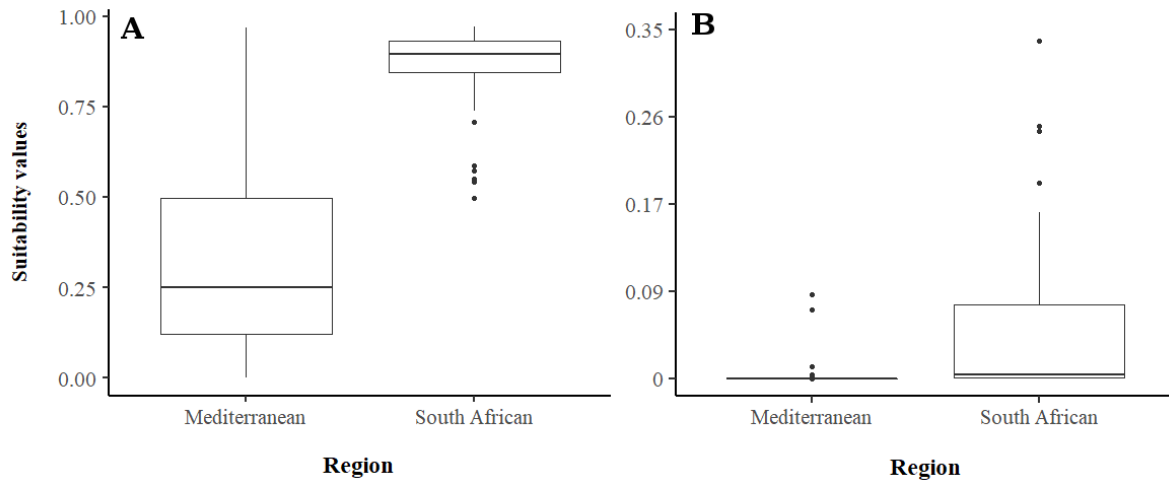


Figure 3. A. Suitability values obtained by the South African model and the Mediterranean model for the 122 occurrences of *Cyrtophora citricola* in America. **B.** Suitability values assigned by the American Model for 32 occurrences in the South African region and 108 Mediterranean occurrences.

Table 2. Threshold values and number of American occurrences omitted (absences) by the binarization of the two native models using three different methods to calculate threshold values.

	South African Model		Mediterranean Model	
	Threshold	Absences	Threshold	Absences
MTP	0.1611	1	0.0278	21
P10	0.1867	1	0.1892	53
MSS	0.3464	1	0.0655	26

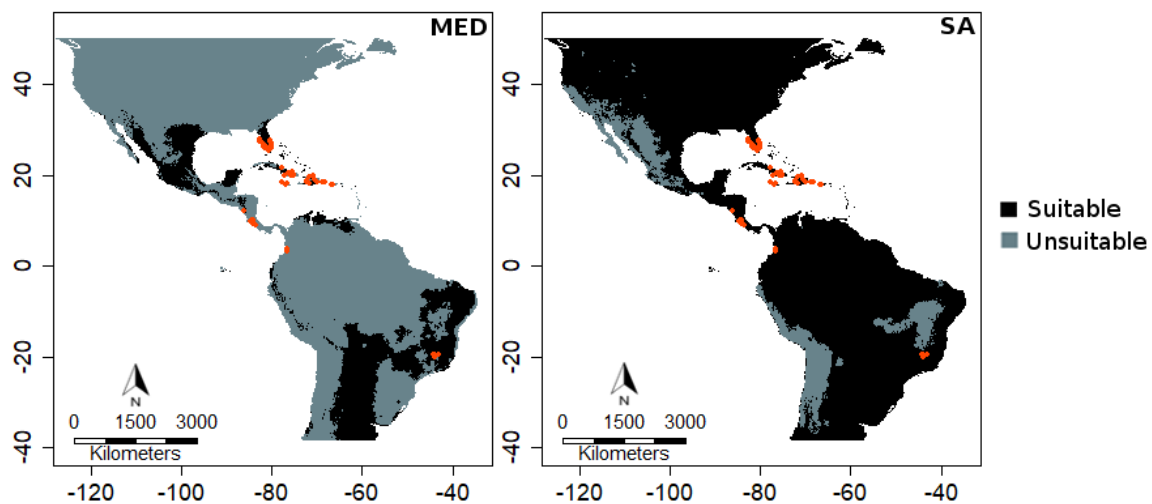


Figure 4. Binarized predictions of suitable and unsuitable sites for the establishment of *Cyrtophora citricola* in America, according to two Niche Models based on two possible origin regions: the Mediterranean region (ME) and South Africa (SA), using the Maximum training sensitivity plus specificity logistic threshold (MSS).

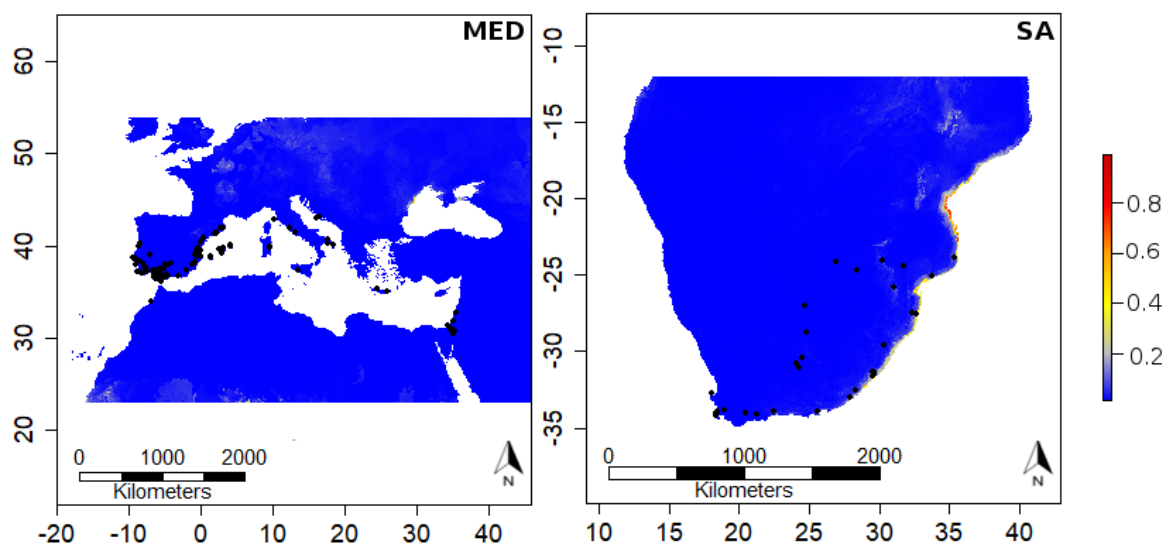


Figure 5. Projection of the American model of the distribution of *Cyrtophora citricola* on the two native regions analyzed. MED-Projection on the Mediterranean. SA-Projection on the South African region.

Table 3. Threshold values and number of occurrences omitted (absences) by the binarization of the projection of the invaded model in each region using three different methods to calculate threshold values.

	Threshold	South Africa	Mediterranean
Occurrences	-	32	108
MTP	0.0033	47% (15)	96% (104)
P10	0.0483	66% (21)	98% (106)
MSS	0.1652	84% (27)	100% (108)

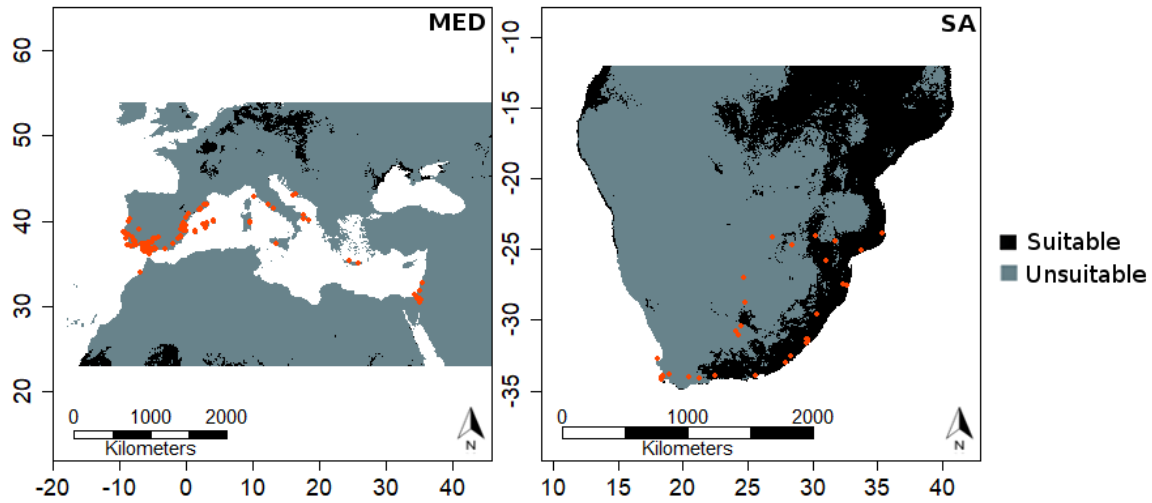


Figure 6. Binarized predictions of suitable and unsuitable sites for the establishment of *Cyrtophora citricola* in the two native regions, using information of the American invaded model. The predictions for the Mediterranean (ME) and South African (SA) regions, are showed using the Minimum training presence threshold (MTP).

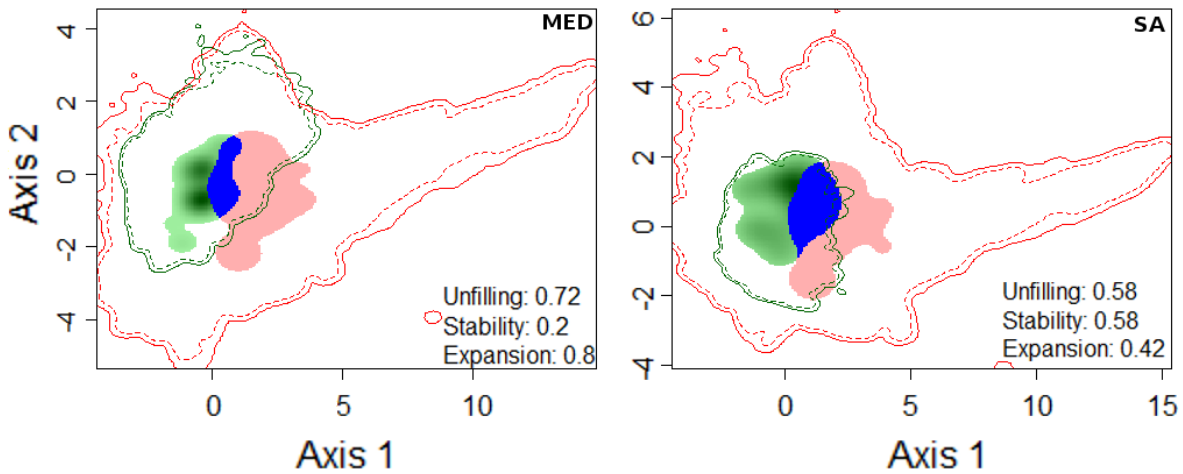


Figure 7. Environmental PCA comparing the American continent conditions with two possible native regions of *Cyrtophora citricola*: the Mediterranean (MED) and South Africa (SA). The red line represents the environmental conditions available in America, the green line shows the conditions available in each native site. The pink area represents the environmental conditions where the species has exclusively established in America, the green area the conditions where the species has exclusively established in each native site, and the blue area shows the environmental conditions where the species has established in both invaded and native region.

DISCUSSION

Our results consistently support that the invasive populations of *C. citricola* in America inhabit environments with more similar conditions to those of the South African region than to those of the Mediterranean region. This is supported by the South African model, which assigns higher suitability values and has fewer omissions – when binarized to presence-absence – than the Mediterranean model. In addition, when projecting the American model onto the native regions, this model was better fitted on the South African region. The PCA also showed that the environmental conditions occupied by *C. citricola* in America are more similar to those in South African region than to those occupied in the Mediterranean region.

Both the Mediterranean and the South African models indicate that this spider has expanded its distribution in America into a new set of environmental conditions during the last two decades, and that some of these conditions are not present in any of the native regions analyzed (Fig.7). This is evident, as well, from the low suitability values obtained for the native occurrences when the invaded model was projected in both native regions (Fig. 3). There are two possible processes that could explain these results. First, *C. citricola* in America may not be facing the same environmental and biological constraints as in the native regions (Blanke 1972; Brown et al., 1996). Considering that ENM's are based on the species' realized niche (Araujo & Guisan, 2006; Broennimann et al., 2007; Guisan & Thuiller, 2005), it is possible that *C. citricola* could be exploiting resources and tolerating conditions different from those defined by its realized niche, but that are still within the species physiological tolerance thresholds (fundamental niche) (Broennimann et al., 2007). Therefore, this species has been able to expand

its distribution into sites with different characteristics than the original region. Second *C. citricola* may have rapidly adapted to this new set of environmental conditions (Yoshida, Goka, Ishihama, Ishihara, & Kudo, 2007). However, these two possibilities remain to be examined in further detail, as there are no studies regarding these issues on this species.

Some environmental variables are expected to have a larger effect in determining *C. citricola*'s distribution. In the South African model the Minimum Annual Temperature has a large effect on the distribution of this species and could explain why this model predicts that the areas far north of the continent are suitable for this species, where low temperatures are dominant. However, it has been reported that populations of *C. citricola* in Spain are not tolerant to temperatures below zero (Blanke, 1972). Therefore, it is possible that populations around the Mediterranean are not adapted to tolerate cold conditions, while those from South Africa are capable of surviving colder temperatures, and are establishing in colder sites, as the South African model predicts.

However, the records in America show that this species is establishing in warm areas in America. Edwards (2006) reports this species in Florida in 2006 and its distribution has remained with little change – as there have been no reports of expansion towards the colder regions- since then; whereas populations in Cuba (Martín-Castejón & Sánchez-Ruiz, 2010) and Costa Rica (LS and GB unpubl. data) have rapidly and consistently expanded in the last few years. This is inconsistent with the predictions made by the South African Model, therefore it is important to consider that even when niche modeling techniques provide a very useful tool to study invasions, predictions should be taken with caution since they are subject to each species specific traits

(Araujo & Guisan, 2006; Elith, Kearney, & Phillips, 2010; Elith & Leathwick, 2009).

The predictions obtained with these techniques are based on relatively static climatic conditions – exemplified by the environmental trait means collected in a determined time period – and, for this reason, applying these techniques to range-shifting species (to which the occurrence records might not reflect a stable population (Elith et al., 2010; Elith & Leathwick, 2009)) proves to be a challenge in terms of the precision of the predictions obtained (Elith et al., 2010; Guisan & Zimmermann, 2000). However, this also provides the opportunity to evaluate the adaptability, and the effect of microclimate and other environmental conditions (Cavieres, Badano, Sierra-Almeida, & Molina-Montenegro, 2007; Lounibos et al., 2010) on invader species occupying new areas. For instance, populations of *C. citricola* in America with only 20 years since its introduction may not be stable yet, and many records might not reflect suitable sites for the species establishment. However, in Costa Rica, as well as updated invasive status in Cuba (Martín-Castejón & Sánchez-Ruiz, 2010) show that the species continue expanding its distribution into areas within the invaded region, suggesting a large capability of this species to adapt to new environmental conditions, and to use efficiently particular microclimates in America..

The success a species has in occupying a new geographic area relies, in part, on the environmental features of the recipient area and species-specific life history traits, such as dispersal capability, demographic structure (e.g., sex proportion), and adaptability to different environmental conditions and to novel biotic interactions (e.g., a new set of predators and parasites) (Brown et al., 1996; Guisan & Zimmermann, 2000). After arrival, the environmental

conditions could play a fundamental role on the species establishment (Nuñez & Medley, 2011; Peterson, 2003; van Wilgen & Richardson, 2012). Therefore, species arriving to places that have similar conditions to those of the native area are more likely to succeed in their establishment than species arriving to sites with a different combination of environmental conditions (Peterson, 2003). Given that *C. citricola* is a recent invasion, that our results show higher similarity with the South African region conditions and that it has been previously suggested that populations in America are genetically similar to those in South Africa, we consider that it is more likely that the species arrived from this region rather than from the Mediterranean region.

Similar to other invasive species, *C. citricola* has several traits that facilitates its expansion. *C. citricola* is a generalist predator that is not limited by a specific diet (Chauhan et al., 2009), it has a high reproductive rate since one female can produce several eggs sacs during a single reproductive season (Chauhan et al., 2009; Leborgne, Cantarella, & Pasquet, 1998), and it has a dispersal method (balloning) that allows a rapid expansion into new areas (Teruel et al., 2014). The species is also highly tolerant of disturbed environments, favoring its establishment in open areas around cities (Nedvěd et al., 2011; Sánchez-Ruiz & Teruel, 2006; Teruel et al., 2014). Another factor that could play an important role in the successful range expansion of *C. citricola* in its invaded distribution, and the potential exclusion of native species found in the same habitat (LS and GB unpubl. data).

Considering this expansion, it is important to assess the possible impacts *C. citricola* might have in the invaded region. This can be aided by the analyses provided in this study (Peterson, 2003). The establishment of individuals has been reported in a broad diversity of

plants, including some of economical importance such as various *Citrus* species (Edwards, 2006). In addition, it has also been reported that dense colonies of *C. citricola* are capable of drying the plants in which they establish, causing leaf loss, terminal twig die back or even killing the whole plant (Barba-Díaz et al., 2014; Edwards, 2006). However, it has also been suggested that webs could act as biological pest control agents that protect plants from plagues (Chauhan et al., 2009; Edwards, 2006). Also, it has been noted that colonies of *C. citricola* are usually established in plants and structures present in open areas (Sánchez-Ruiz & Teruel, 2006), however, colonization of places with dense vegetation is not likely (LS and GB, unpubl. data). With our analyses, we are able to determine which regions within the continent will more likely be suitable for the establishment of this species (Fig. 2). In general, *C. citricola* will possibly establish and expand in warm areas in the neotropical region, but we consider that plantations, cities and roadside areas will more likely be the sites where *C. citricola* could establish, as it has been previously observed and reported in both its native and invaded range (Edwards, 2006; Lubin, 1980; Sánchez-Ruiz & Teruel, 2006; Teruel et al., 2014; Viquez, 2007). However, there is no recorded information of the detailed impacts this species may have in crop fields in the invaded region, so more detailed studies of its negative, or even positive, impacts remain to be done in order to correctly assess its risks.

Our results give some insight of the possible arriving sites of *C. citricola* to America. Sánchez-Ruiz and Teruel (2006) suggest that this species colonized America through at least four different sites: Florida's Peninsula, the Greater Antilles, the West coast of South America (Colombia), and East coast of South America (around Espiritu Santo, Brazil). The South African

model does not exclude any of these arriving sites, but the Mediterranean model excludes all the sites suggested. Therefore, we consider it is possible that the species might have arrived through different sites to the continent, through trade vessels traveling between the continents. It is also important to note that it is possible that *C. citricola* migrated to America from a different population than the ones considered here. However, our findings are supported by preliminary molecular analyses, which evidence a possible South African origin of the populations of *C. citricola* in the American continent as well.

The analyses conducted in this investigation provides greater support to the hypothesis that the populations of *C. citricola* in America are more closely related to the South African populations, than to the Mediterranean populations. This is congruent with preliminary molecular data which shows a stronger molecular affinity between American and South African populations. Our results provide evidence of the expansion *C. citricola* into a new set of environmental conditions during its invasion to America, as result of either plasticity allowing quickly adaptation (Yoshida et al., 2007) or the absence of biological or physical constraints present in its native range (Broennimann et al., 2007; Roy, Lawson Handley, Schönrogge, Poland, & Purse, 2011). Further studies focusing on physiological tests, adaptation strategies, and biological constraints for the species in both native and invasive populations may help to understand better the processes driving rapid expansion that this species has shown particularly in the tropical areas of the invaded region.

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SUPPLEMENTARY MATERIAL

Table S.1. Parameters and evaluation metrics related to the South African Model done with the data partitioning method Checkerboard 2.

Parameter	Value
Data partitioning method	Checkerboard 2
FC	LQ
β	1.5
OR _{MTP} (var)	0.05 (0.01)
AUC _{TEST} (var)	0.87(0.02)
OR ₁₀ (var)	0.22 (0.03)
Number of parameters	14

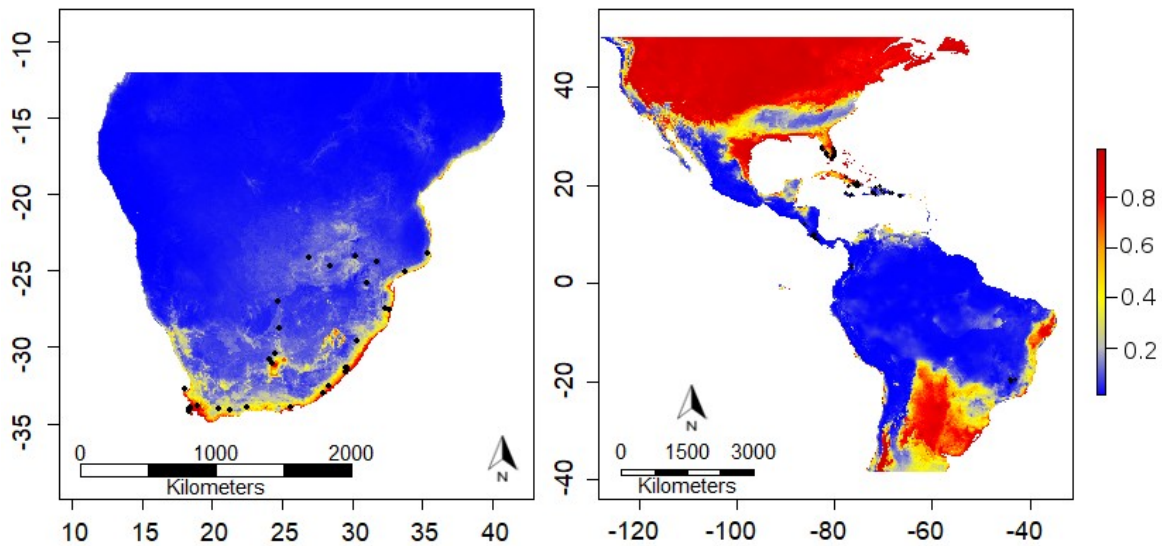


Figure S.1. Predicted environmental suitability for *Cyrtophora citricola* according to the South African model created by using the Checkerboard 2 partitioning method. On the left, the prediction in South Africa is depicted; on the right the prediction in America is shown.

Table S.2. Occurrences of *Cyrtophora citricola* compiled from different sources.

Latitude	Longitude	Country	Col/Obs date	Source	Region
17.8833028	-66.5285806	Puerto Rico		2010 de Armas, 2010	Invaded
25.4702722	-80.3795389	Florida, USA		2006 Edwards, 2006	Invaded
25.4811278	-80.5421194	Florida, USA		2006 Edwards, 2006	Invaded
25.5519583	-80.3315306	Florida, USA		2006 Edwards, 2006	Invaded
25.5170417	-80.5427	Florida, USA		2007 Edwards, 2006	Invaded
25.4875306	-80.3802306	Florida, USA		2006 Edwards, 2006	Invaded
25.5832972	-80.4783083	Florida, USA		2006 Edwards, 2006	Invaded
25.4894361	-80.3635917	Florida, USA		2006 Edwards, 2006	Invaded
25.5977917	-80.3771389	Florida, USA		2006 Edwards, 2006	Invaded
25.6327083	-80.4470444	Florida, USA		2006 Edwards, 2006	Invaded
25.6377778	-80.4798167	Florida, USA		2006 Edwards, 2006	Invaded
3.81132222	-76.626375	Colombia		1997 Levi 1997	Invaded
18.0391972	-71.7414056	Republica Dominicana		2001 Alayón 2001 en Sanchez-Ruiz y Teruel	Invaded
18.5937083	-72.3070583	Haiti		2005 Starr 2005, en Sanchez-ruiz y Teruel	Invaded
18.9882222	-70.604925	Republica Dominicana		2006 Sánchez-Ruiz y Teruel, 2006	Invaded
19.9977444	-75.6851778	Cuba		2006 Sánchez-Ruiz y Teruel, 2006	Invaded
20.0479861	-75.815325	Cuba		2006 Sánchez-Ruiz y Teruel, 2006	Invaded
19.9106056	-77.3243528	Cuba		2006 Sánchez-Ruiz y Teruel, 2006	Invaded
20.1439278	-75.2173667	Cuba		2006 Sánchez-Ruiz y Teruel, 2006	Invaded
20.1402444	-75.247825	Cuba		2006 Sánchez-Ruiz y Teruel, 2006	Invaded
20.1359583	-75.277875	Cuba		2006 Sánchez-Ruiz y Teruel, 2006	Invaded
20.12775	-75.3075528	Cuba		2006 Sánchez-Ruiz y Teruel, 2006	Invaded
20.1263639	-75.3325611	Cuba		2006 Sánchez-Ruiz y Teruel, 2006	Invaded
20.1348333	-75.342825	Cuba		2006 Sánchez-Ruiz y Teruel, 2006	Invaded
20.1324889	-75.4523389	Cuba		2006 Sánchez-Ruiz y Teruel, 2006	Invaded
20.1421611	-75.4767972	Cuba		2006 Sánchez-Ruiz y Teruel, 2006	Invaded
20.1506806	-75.5031028	Cuba		2006 Sánchez-Ruiz y Teruel, 2006	Invaded
20.1593167	-75.5294111	Cuba		2006 Sánchez-Ruiz y Teruel, 2006	Invaded
20.1566778	-75.5560528	Cuba		2006 Sánchez-Ruiz y Teruel, 2006	Invaded
20.1626028	-75.5831778	Cuba		2006 Sánchez-Ruiz y Teruel, 2006	Invaded
20.1753389	-75.6107417	Cuba		2006 Sánchez-Ruiz y Teruel, 2006	Invaded
20.1759083	-75.6368583	Cuba		2006 Sánchez-Ruiz y Teruel, 2006	Invaded
20.1683556	-75.6474861	Cuba		2006 Sánchez-Ruiz y Teruel, 2006	Invaded
20.0090528	-75.769125	Cuba		2006 Sánchez-Ruiz y Teruel, 2006	Invaded
19.9167056	-77.3095139	Cuba		2006 Sánchez-Ruiz y Teruel, 2006	Invaded
19.914275	-77.2813889	Cuba		2006 Sánchez-Ruiz y Teruel, 2006	Invaded
19.9113694	-77.2529028	Cuba		2006 Sánchez-Ruiz y Teruel, 2006	Invaded
19.9106417	-77.22405	Cuba		2006 Sánchez-Ruiz y Teruel, 2006	Invaded
19.9222417	-77.1958583	Cuba		2006 Sánchez-Ruiz y Teruel, 2006	Invaded
20.2973139	-76.2505389	Cuba		2006 Sánchez-Ruiz y Teruel, 2006	Invaded
20.3003139	-76.2719972	Cuba		2006 Sánchez-Ruiz y Teruel, 2006	Invaded
20.3035028	-76.2869194	Cuba		2006 Sánchez-Ruiz y Teruel, 2006	Invaded
20.3068278	-76.3018333	Cuba		2006 Sánchez-Ruiz y Teruel, 2006	Invaded
20.30955	-76.3165056	Cuba		2006 Sánchez-Ruiz y Teruel, 2006	Invaded
20.3092278	-76.3311083	Cuba		2006 Sánchez-Ruiz y Teruel, 2006	Invaded
20.0434944	-75.8172667	Cuba		2006 Sánchez-Ruiz y Teruel, 2006	Invaded
20.0258472	-75.8189444	Cuba		2006 Sánchez-Ruiz y Teruel, 2006	Invaded

Table S.2. Continued.

Latitude	Longitude	Country	Col/Obs date	Source	Region
20.0140444	-75.7697056	Cuba		2006 Sánchez-Ruiz y Teruel, 2006	Invaded
20.0146472	-75.7818806	Cuba		2006 Sánchez-Ruiz y Teruel, 2006	Invaded
20.0177528	-75.7942556	Cuba		2006 Sánchez-Ruiz y Teruel, 2006	Invaded
19.9605472	-75.7053389	Cuba		2006 Sánchez-Ruiz y Teruel, 2006	Invaded
19.8898833	-75.5146361	Cuba		2006 Sánchez-Ruiz y Teruel, 2006	Invaded
19.9235361	-75.6417028	Cuba		2006 Sánchez-Ruiz y Teruel, 2006	Invaded
20.1652556	-75.6873278	Cuba		2006 Sánchez-Ruiz y Teruel, 2006	Invaded
20.6982667	-75.4768222	Cuba		2006 Sánchez-Ruiz y Teruel, 2006	Invaded
20.1159028	-75.4484583	Cuba		2006 Sánchez-Ruiz y Teruel, 2006	Invaded
20.1236861	-75.4377944	Cuba		2006 Sánchez-Ruiz y Teruel, 2006	Invaded
20.1317667	-75.4278111	Cuba		2006 Sánchez-Ruiz y Teruel, 2006	Invaded
20.1290611	-75.4125778	Cuba		2006 Sánchez-Ruiz y Teruel, 2006	Invaded
20.1319611	-75.3875111	Cuba		2006 Sánchez-Ruiz y Teruel, 2006	Invaded
20.1373917	-75.3600944	Cuba		2006 Sánchez-Ruiz y Teruel, 2006	Invaded
20.1578444	-75.2126056	Cuba		2006 Sánchez-Ruiz y Teruel, 2006	Invaded
-19.8666667	-43.9666667	Brasil		2004 Soares y De Maria 2004	Invaded
-19.5	-43.1166667	Brasil		2004 Soares y De Maria 2004	Invaded
-19.5	-43.1166667	Brasil		2004 Soares y De Maria 2004	Invaded
10.0056944	-84.1580278	Costa Rica	2007-03-12T01:00Z	Viquez 2007	Invaded
10.01385	-84.1472611	Costa Rica	2008-03-12T01:00Z	Viquez 2007	Invaded
9.98193056	-84.1420306	Costa Rica	2009-03-12T01:00Z	Viquez 2007	Invaded
9.99887778	-84.161975	Costa Rica	2010-03-12T01:00Z	Viquez 2007	Invaded
9.80087778	-84.6060194	Costa Rica	2011-03-12T01:00Z	Viquez 2007	Invaded
10.0058194	-84.2941389	Costa Rica	2012-03-12T01:00Z	Viquez 2007	Invaded
9.94412222	-84.0457361	Costa Rica	2014-2015	Personal observation L.S y GB	Invaded
9.93938333	-84.0447556	Costa Rica	2014-2015	Personal observation L.S y GB	Invaded
9.93703611	-84.0494639	Costa Rica	2014-2015	Personal observation L.S y GB	Invaded
9.93940278	-84.0099611	Costa Rica	2014-2015	Personal observation L.S y GB	Invaded
9.91101944	-84.5235944	Costa Rica	2014-2015	Personal observation L.S y GB	Invaded
10.0736778	-84.3120278	Costa Rica	2014-2015	Personal observation L.S y GB	Invaded
9.92737778	-84.0906556	Costa Rica	2014-2015	Personal observation L.S y GB	Invaded
9.97936389	-84.0906556	Costa Rica	2014-2015	Personal observation L.S y GB	Invaded
9.95613611	-84.0356083	Costa Rica	2014-2015	Personal observation L.S y GB	Invaded
8.96336944	-83.4563528	Costa Rica	2014-2015	Personal observation L.S y GB	Invaded
9.52052222	-84.3241028	Costa Rica	2014-2015	Personal observation L.S y GB	Invaded
9.36043333	-84.0053889	Costa Rica	2014-2015	Personal observation L.S y GB	Invaded
9.36956111	-83.9817917	Costa Rica	2014-2015	Personal observation L.S y GB	Invaded
30.7036111	35.2713889	Israel		2008 Johannesen et al.,2012	Mediterranean
30.5663889	35.195	Israel		2008 Johannesen et al.,2012	Mediterranean
30.3786111	35.155	Israel		2008 Johannesen et al.,2012	Mediterranean
30.95	35.1213889	Israel		2008 Johannesen et al.,2012	Mediterranean
31.325	34.4033333	Israel		2008 Johannesen et al.,2012	Mediterranean
31.0477778	34.7305556	Israel		2008 Johannesen et al.,2012	Mediterranean
32.7027778	35.5872222	Israel		2008 Johannesen et al.,2012	Mediterranean

Table S.3. Contribution (permutation importance) of the environmental variables to each of the Niche Models analyzed for *Cyrtophora citricola*.

Model	South African	Mediterranean	American
Bio1: Annual Mean Temperature	0.00	0.01	0.00
Bio2: Mean Diurnal Range	1.43	0.00	2.65
Bio3: Isothermality	8.61	1.16	0.00
Bio4: Temperature Seasonality	0.00	10.97	0.87
Bio5: Max Temperature of Warmest Month	0.00	0.00	0.00
Bio6: Min Temperature of Coldest Month	0.00	0.00	2.91
Bio7: Temperature Annual Range	0.79	0.00	6.56
Bio8: Mean Temperature of Wettest Quarter	0.00	0.26	19.90
Bio9: Mean Temperature of Driest Quarter	0.00	0.11	18.17
Bio10: Mean Temperature of Warmest Quarter	1.45	0.00	0.00
Bio11: Mean Temperature of Coldest Quarter	0.00	30.31	0.13
Bio12: Annual Precipitation	2.19	5.51	0.00
Bio13: Precipitation of Wettest Month	0.59	31.49	5.70
Bio14: Precipitation of Driest Month	0.00	2.85	4.18
Bio15: Precipitation Seasonality	0.00	0.52	0.00
Bio16: Precipitation of Wettest Quarter	0.00	0.07	0.00
Bio17: Precipitation of Driest Quarter	80.24	7.52	0.00
Bio18: Precipitation of Warmest Quarter	0.00	2.26	0.21
Bio19: Precipitation of Coldest Quarter	0.00	5.91	6.49
AAP: Average Annual Precipitation	0.00	0.10	0.00
MAT: Minimum Annual Temperature	4.44	0.28	0.01
MWS: Maximum annual Wind Speed	0.27	0.66	32.23

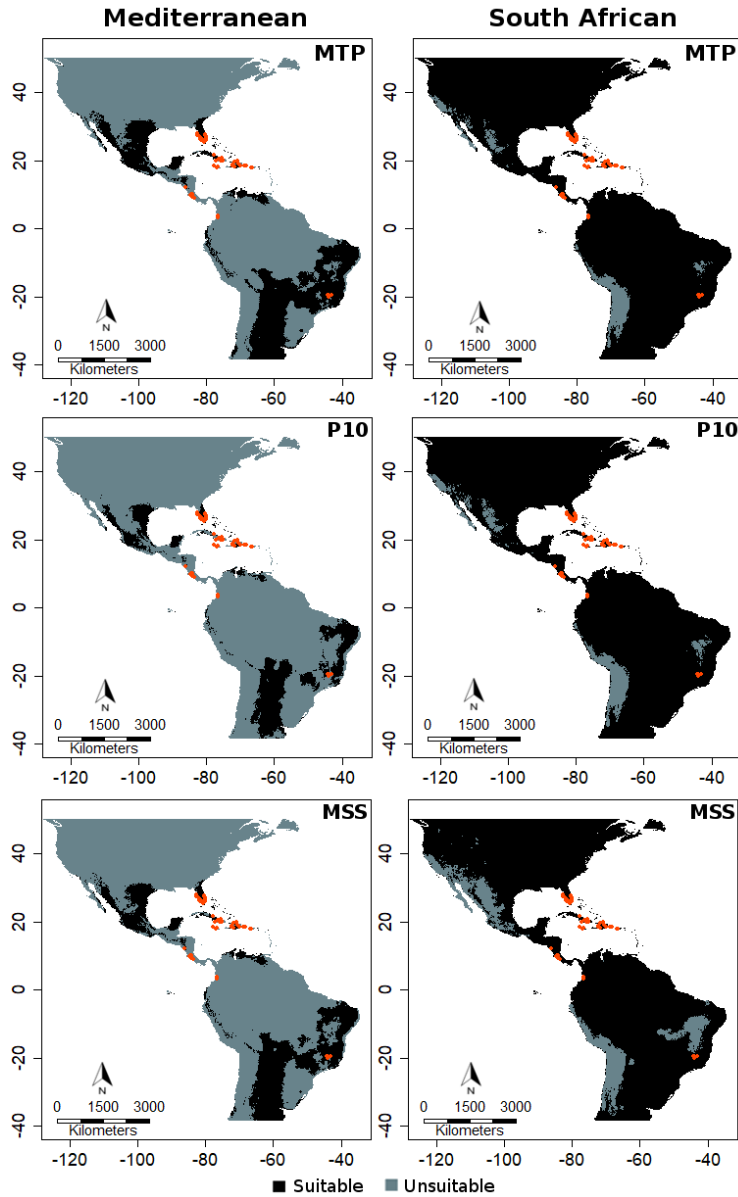


Figure S.2. Binarized predictions of suitable and unsuitable sites for the establishment of *Cyrtophora citricola* based on predictions constructed in two possible origin regions of the invasion (Mediterranean and South African) projected in America. Three different thresholds were used to define the binarization: Minimum Training Present (MTP), 10th Percentile (P10) and Maximum training sensitivity plus specificity logistic threshold value (MSS).

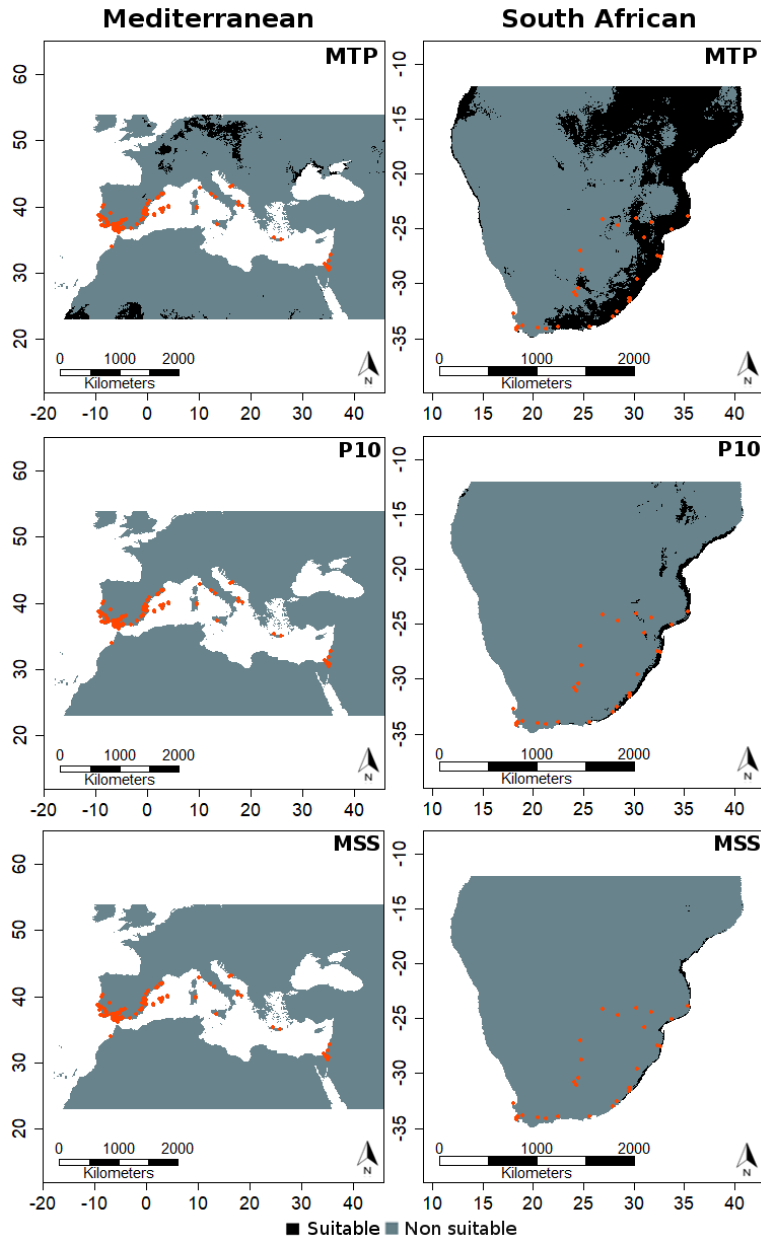


Figure S.3. Binarized predictions of suitable and unsuitable sites for the establishment of *Cyrtophora citricola* based on predictions made by the in American model and projected to the two possible origin regions of the invasion (Mediterranean and South African). Three different thresholds were used to define the binarization: Minimum Training Present (MTP), 10th Percentile (P10) and Maximum training sensitivity plus specificity logistic threshold value (MSS).

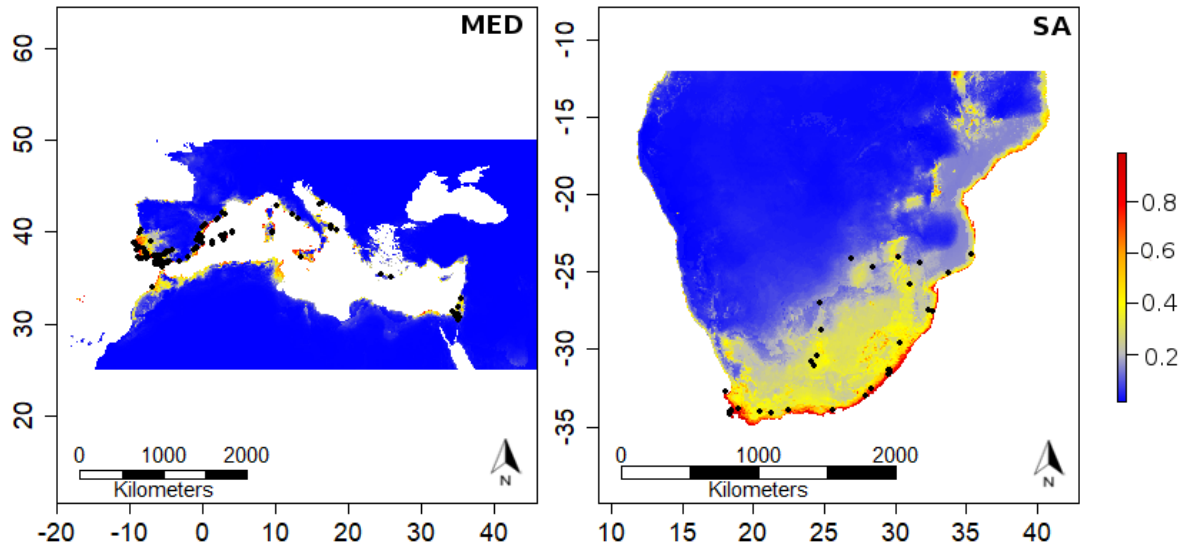


Figure S.4. Predicted environmental suitability for *Cyrtophora citricola* in both its proposed native regions according to each native model selected. On the left, the prediction in South Africa is depicted; on the right the prediction in the Mediterranean is shown.