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MODELING ECOLOGICAL IMPACTS AND ROLE OF URBANIZATION ON INVASION SUCCESS OF BROWN WIDOWS (LATRODECTUS GEOMETRICUS) IN NORTH AMERICA

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MODELING ECOLOGICAL IMPACTS AND ROLE OF URBANIZATION ON INVASION SUCCESS OF BROWN WIDOWS (LATRODECTUS GEOMETRICUS) IN NORTH AMERICA

A THESIS APPROVED FOR THE

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ABSTRACT

The Anthropocene is characterized by human influence on the environment, including aiding movement of non-native species to new regions. The impacts of invasive species on native communities are complex, especially for generalist predators like the brown widow spider (*L. geometricus*). Brown widows are native to southern Africa but have hitchhiked their way across the world, with help the help of humans, and are now established on every continent other than Antarctica. Following introduction, the role humans play in aiding invasion success remains poorly understood. In my thesis, I explore the role of urbanization in aiding the invasion of the rapidly-expanding invasive brown widow spider (*Latrodectus geometricus*) in North America, and assess potential ecological impacts of invasion on native widows (*L. hesperus, L. mactans, L. variolus*) on a continental scale. The first chapter of my thesis describes the geographic ranges of all four widow species under two models: a climatic model that uses climate variables alone to extrapolate the niche of each species in geographic space, and an anthropogenic model that includes human population density, as a proxy for urbanization, in addition to climate. I also quantified geographic overlap of *L. geometricus* with each native species to gauge the geographic extent of potential ecological impacts and identify species likely to be impacted. We found that native widow ranges were strongly limited by climate, whereas brown widows were more strongly limited by urbanization. Urban environments aid in invasion success by weakening the significance of climate on the realized niche of *L. geometricus* and facilitating establishment. Constraint to urban environments mitigates the magnitude of ecological impact by limiting the geographic extent of impact to cities. As *L. geometricus* expand their range, it is unclear how they share resources with their relatives and competition for climatic resources puts native species at risk of ecological impact. Thus, for the second chapter of my thesis, I use climatic niche overlap models to study how climatic niche partitioning sympatric geographic distributions of native widows compared to *L. geometricus.* We found that native species generally show weak niche overlap and have more strongly partitioned niches, with the exception of *L. mactans* and *L. variolus* which showed strong overlap and niche equivalency. We also found *L. geometricus'* strongly overlap with native widows. This overlap may suggest that although brown widows are competing with native widows for climatic resources, differences in diet or urban microhabitats promote coexistence, or it is also likely that it is too soon to see the effect of competition preventing co-occurrence at large spatial scales.

The results of both studies paint a picture of a biological invasion at a large spatial scale that provides valuable insights on the niche dynamics of brown widow invasion in the context of the native communities they invade.

Chapter 1: Urban environments aid invasion of brown widows (Theridiidae: *Latrodectus geometricus*) in North America, constraining regions of overlap and mitigating potential impact on native widows

Abstract

Urbanization is a major cause of biotic homogenization and habitat fragmentation for native communities. However, the role of urbanization on the success of biological invasions on a continental scale has yet to be explored. Urbanization may facilitate the establishment success of invasive species by minimizing niche differentiation between native and invaded ranges. In such cases, we might expect anthropogenic variables to have stronger influence on the geographic distribution of invasive compared to native populations. In this study, we use ecological niche modeling to define the distribution of non-native brown widow spider (*Latrodectus geometricus*) and three native black widows (*L. hespersus, L. mactans, L. variolus*) in North America and gauge the importance of urbanization on niche dynamics of widows at a continental scale. We also quantify the geographic overlap of *L. geometricus* with each native widow to assess potential species and regions at risk of ecological impact. Consistent with our hypothesis, we find that the distribution of *L. geometricus* is strongly constrained to urban environments, while native widow distributions are more strongly driven by climatic factors. These results show that urbanization plays a significant role in facilitating the success of invasion, weakening the significance of climate on the realized niche in its invaded range.

1| Introduction

The Anthropocene is characterized by human impacts driving shifts in ecological processes, with biological invasions ranking as one of the major threats to biodiversity (Sala et al., 2000; Simberloff et al., 2013; Pievani, 2014; Russell and Kueffer, 2019). Global trade is responsible for the movement of species from their native range into novel habitats, leaving native communities vulnerable to ecological impacts (Hastings et al. 2004, Olden 2006, von der Lippe and Kowarik 2008, Aronson et al. 2014). Geographic distributions of invasive species can be used to characterize ecological niche dynamics and predict the risks of future invasions across

spatial scales (Graham et al., 2004; Broennimann et al., 2007; Warren et al., 2014; Atwater, 2018). The ecological niche is generally a set of biotic and abiotic conditions that allow a species to maintain a viable population within some environmental or geographic limit (Peterson, 2011). A fundamental assumption in predictive modeling of ecological niches is that these sets of conditions are conserved over space and time (Pearman et al., 2008). Recent studies have found that invasive species are likely to conserve their climatic niche (i.e. climatic requirements for survival) during invasion (Petitpierre et al., 2012; Liu et al., 2020). However, previous studies have described the possibility of climatic niches shifting when exposed to novel conditions, reducing the predictability of invasion risk (Broennimann et al., 2007; Pearman et al., 2008). A key, and likely confounding, aspect that is lacking in our understanding of biological invasions is the influence of human disturbance on the establishment and spread of species in their introduced range. Recent surges in availability of large-scale datasets of anthropogenic disturbance provide the opportunity to study the role of humans in aiding this process (Balk et al., 2018). Insights from such studies could have widespread implications for predicting invasion risks and impacts, especially of invasive synanthropic species that live in close association with humans.

Generalist arthropod predators have rapid and complex interactions with native communities when introduced into novel environments relative to specialist counterparts (Snyder and Evans, 2006; Crowder and Snyder, 2010). They link trophic levels by feeding on herbivores, detritivores, other predators, plant products, and by serving as prey for other predators. Previous studies have shown harmful, beneficial, and mixed impacts of these predators within the same native communities. For example, the introduction of Chinese mantids (*Tenodera sinensis*) in Delaware induced fleeing responses in other predators, leading to the displacement of native wolf spiders from the community, which should have directly benefited grazing insects by removing a prominent predator and therefore promoted over-grazing of the plant community (Moran et al., 1996). However, mantids consume more than the predators they displaced, significantly reducing biomass of herbivores and indirectly increasing biomass of plants and altering top-down control (Moran et al., 1996). In addition to displacing species and altering top-down control, introduced arthropod predators can also affect communities by introducing new pathogens, disrupting mating systems, inducing behavioral responses in native species, and further cascading impacts (Snyder and Evans, 2006). Given the complex and potentially adverse

effects of invasive arthropod predators, there is a pressing need for approaches to monitor impacts of ongoing invasions. Studying the niche dynamics of invasions at large spatial scales provides an opportunity to understand these processes that could have crucial implications for predicting invasion risk and, ultimately, protecting native communities.

Widow spiders of the genus *Latrodectus* (Araneae: Theridiidae) have historically been studied for their cannibalistic sexual behavior, but they are also vital native predators of many arthropods in their natural ecosystems, including the invasive and venomous fire ant, *Solenopsis invicta* (Nyffeler et al., 1988; Andrade, 1996; Segoli et al., 2006, 2008a, 2008b; Vetter and Isbister, 2008; Vassilevski et al., 2009; Yan and Wang, 2015). They are regarded as pests due to their potent venom and because several species are considered synanthropic, constructing webs on man-made structures. Synanthropic widow species are commonly transported and introduced to novel regions, but brown widows (*L. geometricus*) have had the clearest success in range expansion and establishment globally (Garb et al., 2004). The mechanisms responsible for their success at establishing a cosmopolitan distribution remains poorly understood.

Latrodectus geometricus are native to southern Africa and have drastically expanded their range, colonizing every continent other than Antarctica (Garb et al., 2004). Their spread in North America has been documented for decades, beginning with the first record in Florida in 1935 (Pearson, 1936; Brown et al., 2008), although they were not commonly found in the state until the 1960s, when they became abundant in coastal cities (Levi, 1959; McCrone and Stone, 1965; Vincent et al., 2008). Their presence was restricted to peninsular Florida for decades before notable range expansion beginning in the late 1990s throughout southeastern United States, with confirmed occurrence records now reaching as far north as Connecticut (Vincent et al., 2008; Vetter et al., 2012a). By 2008, several populations were established in southern California, with museum specimens verifying their first record in the state in 2003. As a relatively well-documented introduced species in North America that relies on human development for shelter and dispersal, *L. geometricus* serve as a model for understanding the ecological impact of invasive generalist predators on native communities and the role of urbanization on their establishment and spread.

North America is also home to four native widow species: western (*L. hesperus*), southern (*L. mactans*), northern (*L. variolus*), and red (*L. bishopi*) widows. Black and brown widows are large-range, generalist predators, and generally prefer low, dark corners of low-traffic areas of residences to build their distinctive tangle-web shelters (Vetter et al., 2016). *Latrodectus geometricus* almost exclusively reside in the presence of humans, including in their native range, whereas black widows opportunistically use urban structures for shelter while maintaining populations in their native habitats (Lamoral, 1968; Johnson et al., 2012; Schraft et al., 2021). Previous experimental studies have demonstrated that *L. geometricus* show significant preference for establishing tangle-web refugia on rough surfaces and tight spaces with acute, 30˚ angles that are more frequently observed in urban architecture than in nature (Gutiérrez-Fonseca and Ortiz-Rivas, 2014; Vetter et al., 2016). Unlike their relatives, red widows (*L. bishopi*) do not live with humans at all, and are endemic to sand pine scrub habitats in Florida where they build retreats almost exclusively on saw palmetto (*Serenoa repens*) (Carrel, 2001; Carrel and Deyrup, 2014). Native black widows are potentially at risk of ecological impact from *L. geometricus* invasion because similarities in niche requirements increases the chance of competitive biotic encounters. For example, urban populations of *L. hesperus* in southern Californian (Vetter et al., 2012a) and *L. mactans* in Jamaica (Baerg, 1954) show evidence of displacement, but little is known about the magnitude or extent of future impact as *L. geometricus* expand their geographic range.

Here we use species distribution models (SDMs) to extrapolate the geographic range of invasive *L. geometricus* and native black widows with similar range size (*L. hesperus*, *L. mactans*, and *L. variolus*) to compare the impact of urbanization on their distributions on a continental scale. To test this, we compared the species' distributions using a climatic SDM model, which includes climate variables alone, and an anthropogenic model, which incorporates human population density as an urban variable, in addition to climate. If the niche dynamics of any given species shows range constriction to urban centers in the anthropogenic model, then their range is limited by human activity. We refer to this as the "synanthropic invasion hypothesis". This hypothesis predicts two fundamental patterns, first that *L. geometricus'* geographic range will be strongly limited by human population density, and second that black widow distributions to be more strongly influenced by climate variables and will therefore show weak constraint to urban centers

under the anthropogenic model. We propose three possible mechanisms to explain this pattern: urban heat island effect, homogenization of landscapes, and microhabitat selection. We expect urban microhabitat preferences provide a sheltering effect for *L. geometricus*, thereby reducing the significance of climate on their geographic distribution compared to native species, and facilitating their ability to establish and expand in novel environments. We also quantify the extent of geographic overlap of *L. geometricus* with each native widow to identify potential species and regions at risk of ecological impact. We hypothesize that, because they have been established for longest in the southern extent of North America, *L. geometricus* will have the strongest overlap with *L. mactans*.

2 | Methods

2.1 Occurrence Data

We compiled a dataset of 6,703 georeferenced occurrences for all four species (Table 1). We collected presence-only data from GBIF (Global Biodiversity Information Facility, GBIF.org 2020), which compiles occurrence records from museum collections and online community science repositories: iNaturalist and BugGuide. Data quality from these repositories have been criticized for misleading identifications of species (Beck et al., 2013; Ferro and Flick, 2015). To moderate this concern, occurrences from these sources that were far outside of previously established ranges (Wang et al., 2018; Schraft et al., 2021) were visually verified by one of the authors (MS) on the original online post and eliminated were if they could not be confirmed. We also compiled data directly from community submissions from Facebook groups ("Spider/Bug Questions with TheBugGirl" and "Spider and Insect Enthusiast") and Reddit ("r/whatsthisbug" and "r/spriderbro"). We included all occurrences with sufficient collection data that we were able to positively identify based on the photograph. The rest of our samples were generously provided by contacts at extension offices in Oklahoma and Texas, and opportunistic field collections by colleagues at the University of Oklahoma, University of Florida, and the University of Arizona. Museum records with adequate locality information but no coordinates were georeferenced using the GEOLocate Web Application.

Clustered occurrences were then systematically subsampled to a single point per cell on a 10x10km grid to reduce the effects of sampling bias on model performance (Fourcade et al., 2014). Following systematic subsampling, we retained 3,101 total points for climatic model evaluations (Figure 1, Table 1).

2.2 Environmental Variables

We obtained CHELSA Bioclim variables, averaged from 1973 to 2013, from Paleoclim.org (Brown et al. 2018, Karger et al. 2017), where they had been rescaled to 2.5 arc-min resolution. We initially selected the most biologically significant variables *a priori* based on previous niche studies on spiders (Saupe et al., 2011; Taucare-Ríos et al., 2016; Wang et al., 2018). To minimize variable collinearity, we ran a principal component analysis (PCA) to reduce the pool of factors. Our final selection of bioclimatic variables include: isothermality (Bio3), temperature seasonality (Bio4), maximum temperature of warmest month (Bio5), minimum temperature of coldest month (Bio6), annual precipitation (Bio12), precipitation of the warmest quarter (Bio16), and precipitation of the coldest quarter (Bio17).

To assess the importance of humans on the distribution of widows, we further included human population density variables as proxies for urbanization. Using combined census and satellite-derived rasters of human demographics is a consistent way to estimate urbanization across space and time (Balk et al., 2018). We downloaded human population density data for the years 2000 and 2020 at 2.5 arc-min resolution from the NASA GPW v4, Gridded Population of the World, dataset built using remote-sensing data in conjunction with census data from the U.S. Bureau of the Census and other global intelligence agencies (CIESIN 2017). We used the 2020 NASA population density raster as a contemporary urban factor and created a raster for the change in human population between 2000 and 2020 to include population growth as a factor in widow range limitations.

2.3 Species Distribution Modelling

Species distribution models (SDMs) are quantitative tools that combine species occurrence data with relevant environmental variables to predict species habitat suitability across geographic space (Elith and Leathwick, 2009; Merow et al., 2013). To assess the importance

of urbanization on geographic range of native and invasive widows, we ran two models to compare per species: first using climatic variables alone, second using both climatic and anthropogenic human population density variables.

We modeled our species distributions using Maxent 3.4.1, as its prediction accuracy has been shown to outperform other methods given presence-only data, even in the case of invasion modeling (Elith et al. 2006, 2011, Mothes et al. 2018). Maxent is a machine-learning method that estimates species ranges by finding the probability distribution of maximum entropy (Elith et al., 2006). We performed all analyses in R version 3.6.1, using the package "ENMeval" (Muscarella et al. 2014) to run and evaluate Maxent models across a range of custom, user-defined feature classes and regularization multipliers, and selected four evaluation metrics (AUCtest, AUCdiff, AICc, deltaAIC) for assessing model fit and performance (Merow et al., 2013; Muscarella et al., 2014).

We partitioned training data using 10-fold cross-validation and ran models across three feature classes (L— linear, LQ— linear-quadratic, and LQP— linear-quadratic-product), and a series of regularization multipliers (1, 1.5, 2, 2.5, 3) to smooth the model response and avoid overfitting of testing data (Elith et al., 2011; Muscarella et al., 2014). Of the resulting 15 model outputs, we first selected the best-fit model, indicated by a deltaAIC score of 0. We used area under the receiver operating curve (AUC) as our primary performance metric. Use of AUC has been criticized as a means of comparing model performance, however in this study we are only using this metric to evaluate whether selected best-fit models performed above an acceptable (0.7) threshold (Lobo et al., 2008; Fourcade et al., 2014). Habitat suitability scores for range maps were rescaled to a clog-log scale of 0 to 1, where 0 denotes unsuitable habitat and 1 indicates the complete habitat suitability.

We calculated the difference in area between climate and anthropogenic models for each species as a measure of magnitude of range restriction to urban regions. This metric was measured by first quantifying the area, in km^2, of moderate-to-high habitat suitability (suitability threshold set to >0.5) in both models. Next, we calculated the percent change in area between the climate-only and anthropogenic models of each species.

We evaluated the importance of each variable using jackknife analyses to generate permutation importance measurements for each variable. Permutation importance is calculated by randomly arranging values of an environmental variable among points used in the training model, reevaluating the model, and measuring difference in AUC between the training and random model. A greater decrease in AUC suggests a greater impact on model performance. Preliminary analyses showed minimal permutation importance of change in population density between 2000 and 2020 (Supplementary Table 1), so we did not include this variable in our models.

2.4 Geographic Overlap Analysis

To identify the geographic extent of ecological impact of *L. geometricus* on native widows, we quantified geographic overlap of *L. geometricus* with each native widow species using their projected distributions under the anthropogenic model. Here, areas of geographic overlap indicate regions of more probable co-occurrence, and thus a heightened opportunity for antagonistic encounters and competition. Geographic overlap analyses were performed using "ENMTools" package (Warren and Dinnage 2020) to obtain overlap metrics: Schoener's "D" and similarity index "I", proposed by Warren et al. (2008). Overlap analyses using SDM outputs quantify the relative suitability at each shared cell, which is biased toward more common habitat types and violates the assumption that suitable habitats of each species are equally represented in geographic space (Brown and Carnaval, 2019). Schoener's D remains the most commonly used metric of geographic overlap and has been demonstrated to be a reliable measure of niche similarity in environmental space (Brown and Carnaval, 2019). Though results for these metrics rarely differ qualitatively, ecological implications of Schoener's D, which is traditionally used to measure niche similarity of microhabitats and diet, can be misleading with SDMs (Warren et al., 2008). Because we are concerned with the geographic extent of overlap, rather than similarities in niche requirements, we also include Warren's I, which does not assign biological meaning to the probability of distributions and is specific to geographic space (Warren et al., 2008). Warren's I is a variation of the Hellinger (H) metric, which measures distance between two geographic extents, and is calculated as one minus H (Warren et al., 2008). Schoener's D, on the other hand, is

calculated by subtracting the total variation distance between two niches by one (Schoener 1968). Both metrics range from 0 (no overlap) to 1 (complete overlap).

To narrow down regions of potential impact, as well as regions safe from impact, we also overlaid maps for each species with *L. geometricus* and regions of overlap with moderate-to-high (threshold set to >0.5) habitat suitability (Supplementary Figure 1).

3 | Results

Overall, we found that *L. geometricus* show strongest constraint to urban environments, consistent with our hypothesis of synanthropic invasion. Unexpectedly, *L. hesperus* show a similar pattern of constraint to a lesser degree, which suggests they have the strongest synanthropic association to humans of the native species. We also found strong geographic overlap between these two species, which in conjunction with shared preferences for urban environments, leaves *L. hesperus* at greatest risk of ecological impact by *L. geometricus* invasion.

3.1 Species Distribution Models

3.1.1 Climate-Only Model

While habitat suitability varies across the study region for each species, all species ranges are characterized by large extents of high habitat suitability (>0.75) that correspond to expected distributions (Figure 2). Areas of high habitat suitability for *L. geometricus* primarily occur along coastlines, especially along the west coast (Figure 2). *L. hesperus* has high habitat suitability along the west coast and expanding west to Oklahoma and as far north as southern Alberta (Figure 2). *L. mactans* optimal habitat are in southcentral Mexico and reaching east to Florida, but they are restricted to the southern regions of North America (Figure 2). The northeast has the most suitable habitat for *L. variolus* (Figure 2). Models showed low suitable habitat in the Rockies for *L. variolus*.

As expected, because of its large range but smaller sample size in this study, *L. variolus* had the lowest performing model (0.77 AUC). To ensure accurate evaluation, we also report the difference in training and test AUC (AUCdiff), as well as the corrected Akaike

information criteria (AICc). These performance metrics also indicated good model performance across species (Table 2). We selected best-fit models with performance metrics deltaAIC of 0 (Muscarella et al., 2014). The estimated optimal climate-only model feature class and regularization multiplier for each species are shown in Table 2. All selected models had fair (0.70>AUC<80) to excellent (AUC>0.90) performance (Araújo et al., 2005).

3.1.2 Anthropogenic Model

Climate + anthropogenic SDMs (hereafter, anthropogenic models) showed significantly less highly suitable areas (habitat suitability >0.5) for *L. geometricus* (94%) and *L. hesperus* (87%) than those calibrated with climate only. For *L. mactans* and *L. variolus*, adding human population density resulted in much less change, with *L. mactans* and *L. variolus* showing only a 21% and 19% reduction in range size, respectively. Areas of high habitat suitability for *L. geometricus* are highly restricted to regions with high human population density, corresponding to major urban centers: Los Angeles, San Francisco, Sacramento, San Diego, Miami-Dade, Tampa, Orlando, Mexico City, Guadalajara, and Monterey, with intervening non-urban areas showing a reduction in suitability relative to the climate-only models (Figure 2). *Latrodectus hesperus* had the greatest reduction of suitable area of the native species. Similar to *L. geometricus*, their range contracted toward urban centers. Areas of habitat suitability for *L. mactans* and *L. variolus* remained similar to their projected ranges in the climate-only models (Figure 2).

All selected models had fair (0.70>AUC<80) to excellent (AUC>0.90) performance (Araújo et al., 2005). The estimated optimal anthropogenic model parameters and performance metrics for each species are shown in Table 2.

3.2 Variable Importance

Jackknife analyses of permutation importance show that, consistent with our hypotheses, human population density is the most important variable in defining the range of the invasive widow, while native species distributions are primarily predicted by climatic variables. Human population density explained over 40% of the distribution of *L. geometricus*, but less

than 20% of for *L. hesperus* and *L. variolus*, and less than 5% for *L. mactans* (Table 3). The highest contributing climatic variables for each native species in the anthropogenic model were: isothermality (30.4%) for *L. hesperus*, temperature seasonality (40.7%) for *L. mactans*, and precipitation of the driest quarter (54.0%) for *L. variolus* (Table 3).

3.3 Geographic Overlap

Using both I and D metrics, our results show strongest pairwise comparison of range overlap in the anthropogenic model to be between *L. geometricus* and *L. mactans,* whose ranges overlap throughout the gulf coast and Mexico (Supplementary Figure 1). Although they can both be found throughout these regions, *L. geometricus* have a patchy distribution restricted to cities, while *L. mactans* that have a more continuous range widely distributed outside of regions of high human population density (Figure 2, Supplementary Figure 1). Ranges of both *L. hesperus* and *L. geometricus* show constraint to urban centers in California, where they strongly overlap (Figure 2, Supplementary Figure 1). *L. variolus* shows limited overlap with *L. geometricus* in southeastern United States, excluding Florida (Table 4).

4 | Discussion

Widow spiders in North America provide unique insights for addressing the role of humans on invasion success of an invasive generalist predator with close relatives throughout its introduced range. Invasion success for species with close associations to people is aided by repeated introductions from global trade routes lessening dispersal limitations and increasing propagule pressure in urban ports of entry. Still, humans can also aid in establishment success by sheltering species from climatic conditions that might lie beyond their climatic niche. In this study, we considered the role of urban environments, in addition to climate, in shaping the distribution of nonnative compared to native widows and compared geographic overlap of *L. geometricus* with each black widow species to assess potential areas and species at risk of ecological impact. Consistent with our "synanthropic invasion hypothesis", we found that the geographic distribution of *L. geometricus* is patchy and more strongly constrained to urban environments, while native widows have more continuous distributions that are limited by climatic factors.

Using geographic overlap as a proxy for negative interactions between species, these findings suggest minimal risk of ecological impact on native widows overall, with areas of overlap constrained to urban environments. This leaves populations of black widows in their native habitats outside of urban areas at low risk of co-occurrence. Therefore, we also considered areas where they do not overlap as regions of sanctuary from impact in our risk assessment. We expected that there would be the strongest overlap with *L. mactans* because of the longer establishment period of *L. geometricus* within their range in southern North America beginning in the 1940s. Overlap maps, in conjunction with D and I metrics, confirmed geographic overlap of *L. geometricus* was strongest with *L. mactans*. However, their range also has large, continuously distributed areas of highly suitable habitat outside of major urban centers to maintain viable populations, buffering the risk of impact.

Unexpectedly, we found that *L. hesperus* showed strong overlap as well (Table 4). In addition, their patchy distribution in the Anthropogenic model suggests they find urban habitats highly suitable (Figure 2). This increases the possibility of co-occurrence with *L. geometricus* given reduced areas in their native habitat for maintaining viable populations safe from antagonistic encounters. Empirical studies demonstrating impact are lacking, however *L. geometricus* were found to significantly outnumber and produce more egg sacs than *L. hesperus* at sampled sites in urban Southern California, showing evidence for risk of displacement (Vetter et al., 2012a). Furthermore, *L. geometricus* may also experience competitive release within their shared range with *L. hesperus*. While they are impacted by parasitoid wasps of *L. mactans* in their southern range, they are not fed upon by *Pseudogaurax signatus*, a fly that commonly infests *L. hesperus* egg sacs (Vetter et al., 2012a). Because of the apparent constraint to urban environments, the strong signal of overlap, and higher potential for competitive release, *L. hesperus* are at greatest risk of ecological impact from the invasion of *L. geometricus* in North America. Still, range restriction of *L. geometricus* to urban habitats suggests impact on native species is likely to be reserved to urban populations

The strength of human population density as a predictor of *L. geometricus* presence in their invaded range indicates urbanization is a potential driver for invasion success of the species. Although the mechanism remains unclear, we identified three possible mechanisms that are not mutually exclusive: the urban heat island effect, which reflects locally favorable climatic

conditions in urban areas; homogenization of landscapes, which decreases biotic resistance; and microhabitat selection, which limits species to specific local conditions for shelter and may advantage some species over others. Urban heat islands are cities that have more elevated temperatures than surrounding areas (Oke, 1982; Kim, 1992), potentially allowing species to inhabit regions that are colder than predicted by their climatic niche, sheltered by the warming effects of urban heat (Murakami et al., 2007; Sołtysiak, 2020). Although urban heat island effect may influence establishment success of *L. geometricus,* particularly in Denver, New York City, and up to Boston, it does not explain why they are not occupying non-urban areas that fall within their climatic needs.

The two remaining mechanisms both relate to habitat. The second potential mechanism explaining this restricted range pattern may be that urbanization homogenizes landscapes, thereby decreasing biotic resistance and making these environments more easily invadable by introduced species (McKinney, 2006; La Sorte et al., 2007; Shochat et al., 2010; Aronson et al., 2014). Availability of similar habitats globally enables range expansion by facilitating establishment once the species is introduced to a novel region. Under this mechanism, *L. geometricus* would be restricted to urban areas because they fail to establish outside of urban areas where biotic resistance is higher. Within these homogenized landscapes, micro-habitat selection is a likely mechanism that addresses range-restriction for these spiders via positive selection of urban habitats. One of the many ways spiders use silk is to create complex web structures that are used as temporary or permanent shelters. The characteristic tangle-web of female widow spiders is used for both shelter and prey capture. As generalist predators that feed on a variety of invertebrates and occasional small vertebrates, their webs are structured with different silk lines used to capture both aerial and ground-dwelling prey. Web-building is energetically costly, especially for widow spiders that build semi-permanent webs. Preferences for web-site features thus have a strong effect on widow spider fitness and have been found to be inherited (Salomon et al., 2010; Gutiérrez-Fonseca and Ortiz-Rivas, 2014). Selection of web-site microhabitats is therefore likely an important predictor of their niche that would restrict habitat suitability to regions that support conditions suitable for shelter. An experimental study found that *L. geometricus* prefer web-sites with deep cavities and 30˚ or 90˚ angles, a prominent feature of urban architecture, because these angles fit the conical retreats of *L. geometricus* web

structures (Vetter et al., 2016). Unlike black widows, they also prefer web-sites that have been previously occupied by conspecifics (Vetter et al., 2016). In the field, brown widows are often found under objects with minimal but strong material cover that contain 30˚/90 angles, such as between fencing, in gaps of objects like trash bin handles, and under tables and chairs with solid tops (Vetter et al., 2012a). In their native range, *L. geometricus* are also highly synanthropic. There, they are distinguished from another widow species native to South Africa, *L. indistinctus,* by their predilection for residing on garden furniture over grass and shrubbery in veld habitats (Muller, 1993). Synanthropic adaptation such as this in their native range shows a tendency for using human-made objects for web-site construction that could predispose the species to fare well under urban conditions in an introduced environment (Simberloff et al., 2012). Microhabitat selection also shapes the restricted range of some conspecifics, including the red widow, which builds its webs exclusively on the endemic saw palmetto (*S. repens*) of the Florida sand pine scrubs (Carrel, 2001; Carrel and Deyrup, 2014). Given strong enough preferences, web-site selection may be an important range-limiting factor for some spiders, including *L geometricus*. Although the actual mechanisms behind this pattern were not uncovered in this study, invasion success of *L. geometricus* appears to be facilitated by urbanization, minimizing the importance of the climatic niche on survival and facilitating spread and establishment of the species in North America.

Widow spiders are one of the most distinguishable spiders, yet, like many other invertebrates, sampling efforts from online data repositories present a challenge in ensuring representation. Most occurrence data for this study were acquired from GBIF, an online database that compiles museum and community science data acquired iNaturalist and BugGuide. Though these data repositories are the best we have for large-scale studies of many invertebrates, and are valuable for the breadth of area sampled, they are still limited by species misidentifications, and sampling that is unstandardized and geographically biased towards sites that are more accessible to people (e.g. roads, trails, backyards). Sampling efforts made by natural history collections tend to be biased to the geographic scope of individual collections, so we incorporated specimens from multiple museum collections to improve accuracy of our models (Ferro and Flick, 2015). Community science efforts are especially controversial for acquiring quality data due to the lack of representativeness across species distributions and misidentifications of species (Ferro and

Flick, 2015; Zhang and Zhu, 2018). To moderate this concern, we performed data quality checks by manually verifying identifications based off photographs and systematically subsampled occurrence data on a 10x10km grid to reduce spatial bias around more populated areas. It should be noted that although community sampling efforts are patchy and ad hoc, they show a relatively robust sampling across the entire distribution of each species because widows are widespread, abundant spiders of particular interest to the community due to their venomous bite.

With rates of urbanization and trade of goods increasing globally, introduction and establishment of invasive species are becoming a greater risk to biodiversity. Descriptions of the distributions of invasive species have historically focused on the climatic niche to predict geographic ranges (Fourcade et al., 2017). This is in part due to limited availability of biotic and non-climatic abiotic data at appropriate resolutions for continental and global-scale modeling. In recent years, advances in technologies in remote sensing and statistical methodologies have led to an increase in available human activity data. In this study, we observed drastic differences in the implications of invasion risk when incorporating anthropogenic predictors. When modeling using climatic variables alone, signals for invasion risk are much stronger, but insights on *L. geometricus'* urban range restriction reveal minimal impact as long as native habitats remain intact. Looking forward, anthropogenic activity data provide an opportunity to estimate disturbance and expand beyond climatic predictors for modeling distributions, proving to be an invaluable tool for predictive modeling of invasive spread to forecast regions and species at risk of impact.

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7| Tables and Figures

Table 1. Counts for total occurrence points collected, systematically subsampled points, and pseudo-absences retained for model evaluation for each species. The number of pseudo-absences was standardized to five times the amount of subsampled occurrences for each species.

Species	Total Occurrences	Subsampled Occurrences	Pseudo-Absences
L. geometricus	1140	604	3020
L. hesperus	2485	1153	5765
L. mactans	2436	1106	5530
L. variolus	342	238	1190

Table 2. Optimal model parameters (feature class, regularization multiplier) and performance metrics (AUC, diffAUC, AICc) for climate-only and anthropogenic models.

Model	Species	Model Parameters		Model Performance		
		Feature Class (FC)	Regularization Multiplier (RM)	AUC	diffAUC	AICc
Climate-Only	*L. geometricus*	LQ	1	0.89	0.007	13751.72
	L. hesperus	LQ	1	0.79	0.013	28205.34
	L. mactans	LQP	1	0.85	0.001	26530.06
	L. variolus	LQ	1	0.77	0.007	5927.48
Anthropogenic	*L. geometricus*	LQ	1	0.94	0.005	12105.32
	L. hesperus	LQ	1	0.85	0.012	26543.02
	L. mactans	LQ	1	0.87	0.008	25937.034
	L. variolus	LQP	1.5	0.80	0.021	5830.46

Table 3. Percent permutation importance of climatic and anthropogenic predictors used in the anthropogenic model for each species. Climatic variables include: annual precipitation, precipitation of the wettest and driest quarters, isothermality, temperature seasonality, maximum and minimum temperatures of the hottest and coldest month, respectively. The anthropogenic variable is human population density.

Species	**Permutation Importance (%)**							
	Annual Precipitation	Precipitation of the Wettest Quarter	Precipitation of the Driest Quarter	Isothermality	Temperature Seasonality	Max Temperature	Min Temperature	Human Population Density
L. geometricus	12.77	5.89	19.25	1.02	6.14	0	10.63	44.3
L. hesperus	8	13.93	16.43	30.44	8.67	3.76	0.48	18.29
L. mactans	6.34	0.27	15.51	6.27	40.74	12.14	14.91	3.82
L. variolus	7.73	3.08	53.95	4.96	5.64	1.3	5.67	17.68

Table 4. Similarity indices, Schoener's D and Warren's I, ranging from 0 (no overlap) to 1 (complete overlap) of species geographic overlap with *L. geometricus*.

Species	**Similarity Indices**	
	Schoener's D	**Warren's I**
L. hesperus	0.416	0.702
L. mactans	0.567	0.842
L. variolus	0.226	0.506

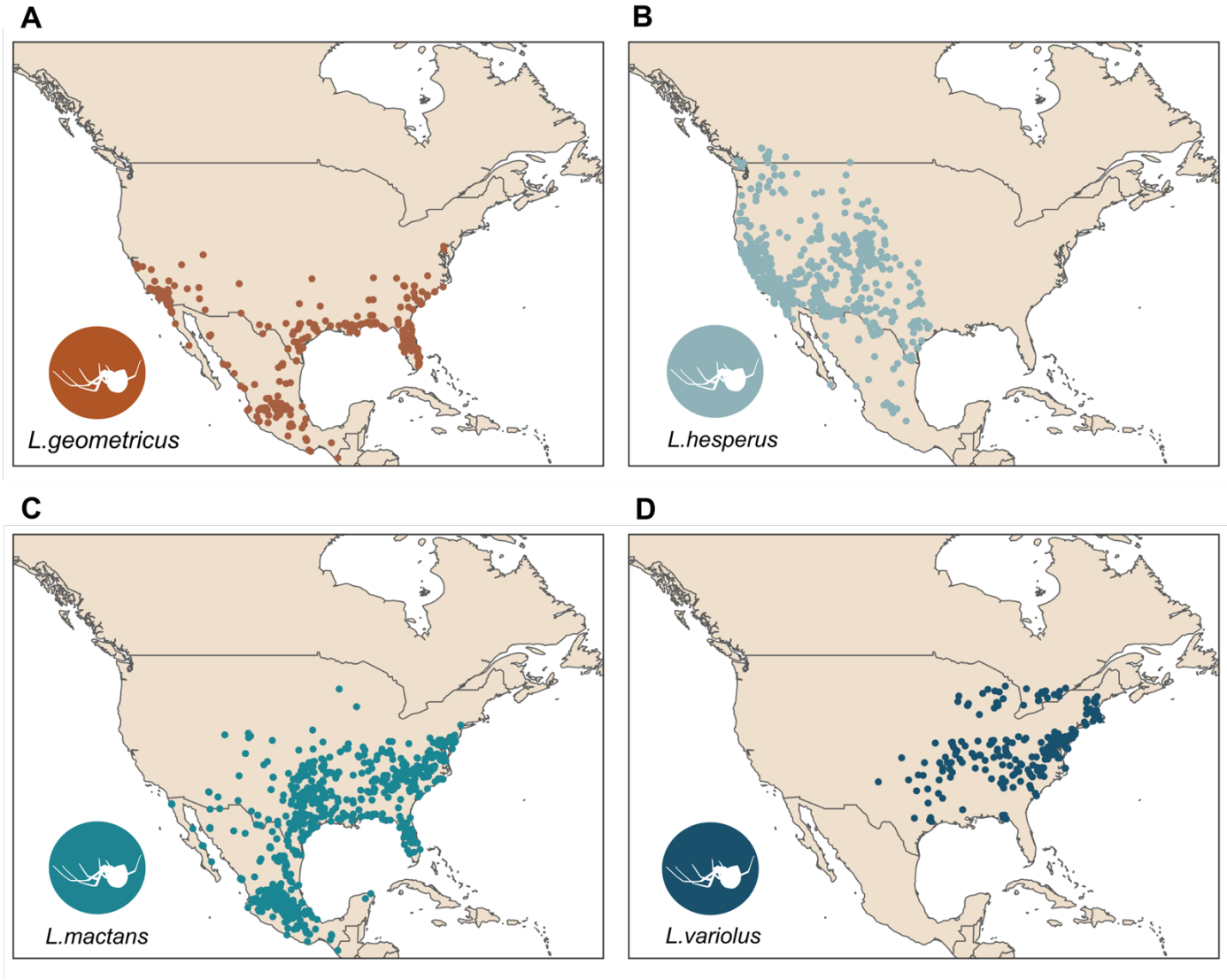


Figure 1. Subsampled occurrence points in North America used for SDMs for A) *L. geometricus,* B) *L. hesperus,* C) *L. mactans,* D) *L. variolus*.

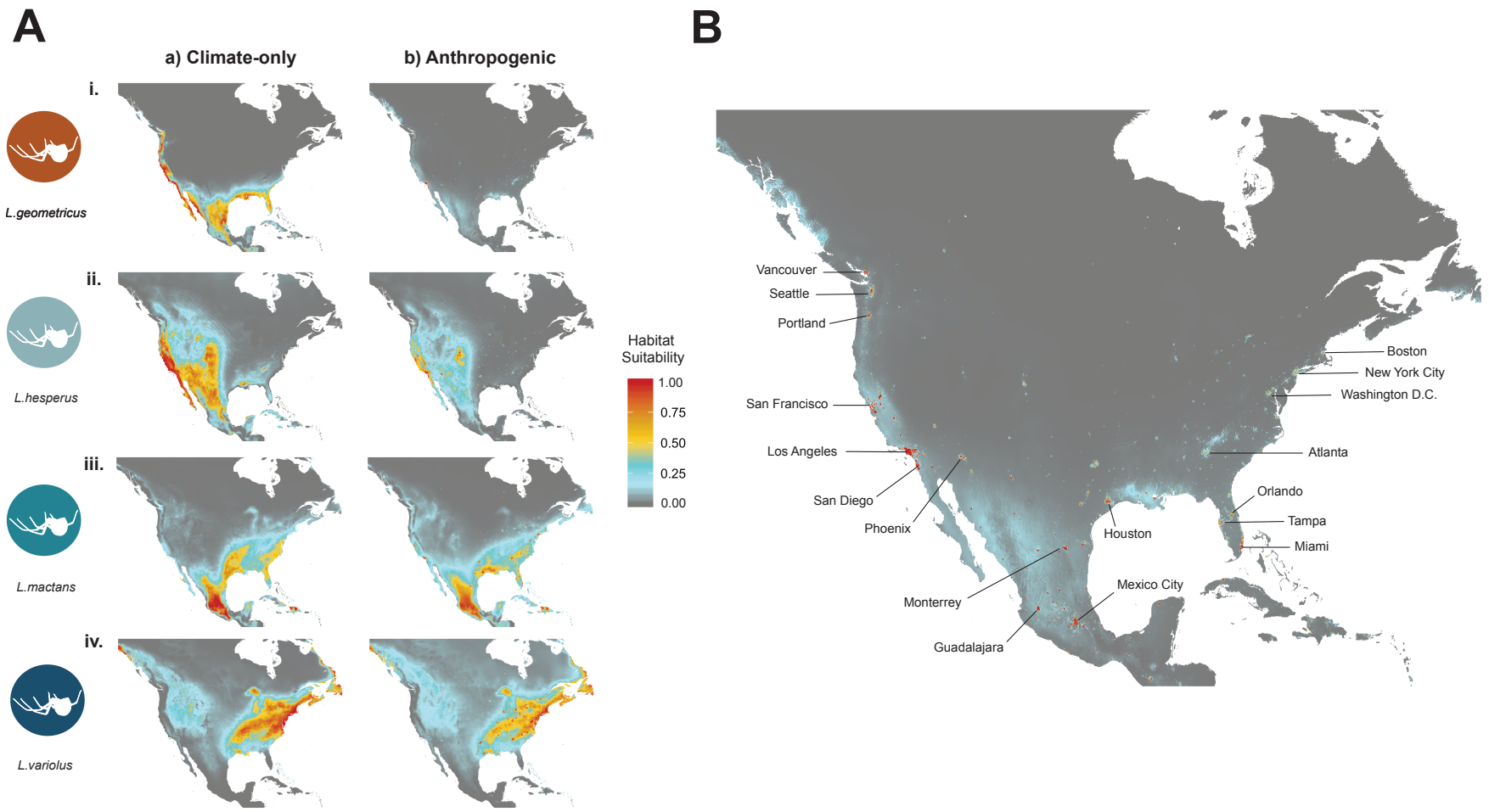


Figure 2. Panel A displays the distribution of habitat suitability under (a) climate-only models using climate variables alone, and (b) anthropogenic models using climate and human population density variables for *L. geometricus* (i), *L. hesperus* (ii*), L. mactans* (iii), and *L. variolus* (iv). A closer look at the distribution of *L. geometricus* under the anthropogenic model in panel B shows a restriction of habitat suitability to urban regions. Habitat suitability ranges from 0 (gray), which indicates no suitable habitat, to most suitable habitat 1 (red). Areas with low-to-moderate suitability are pictured in blue, and moderate-to-high are pictured in yellow.

Supplementary Tables and Figures

Supplementary Table 1. Optimal model parameters, performance metrics, and permutation importance of variables under the Anthropogenic Change model. Variables include: annual precipitation, precipitation of the wettest quarter, precipitation of driest quarter, isothermality, temperature seasonality, maximum temperature of the warmest month, minimum temperature of the coldest month, human population density 2020, and human population density from 2000-2020. The variable for Human Population Density from 2000-2020 signifies the change in population between 2000 and 2020. Results show that change in human population between 2000 and 2020 does not significantly contribute to distribution models for any widows in this study.

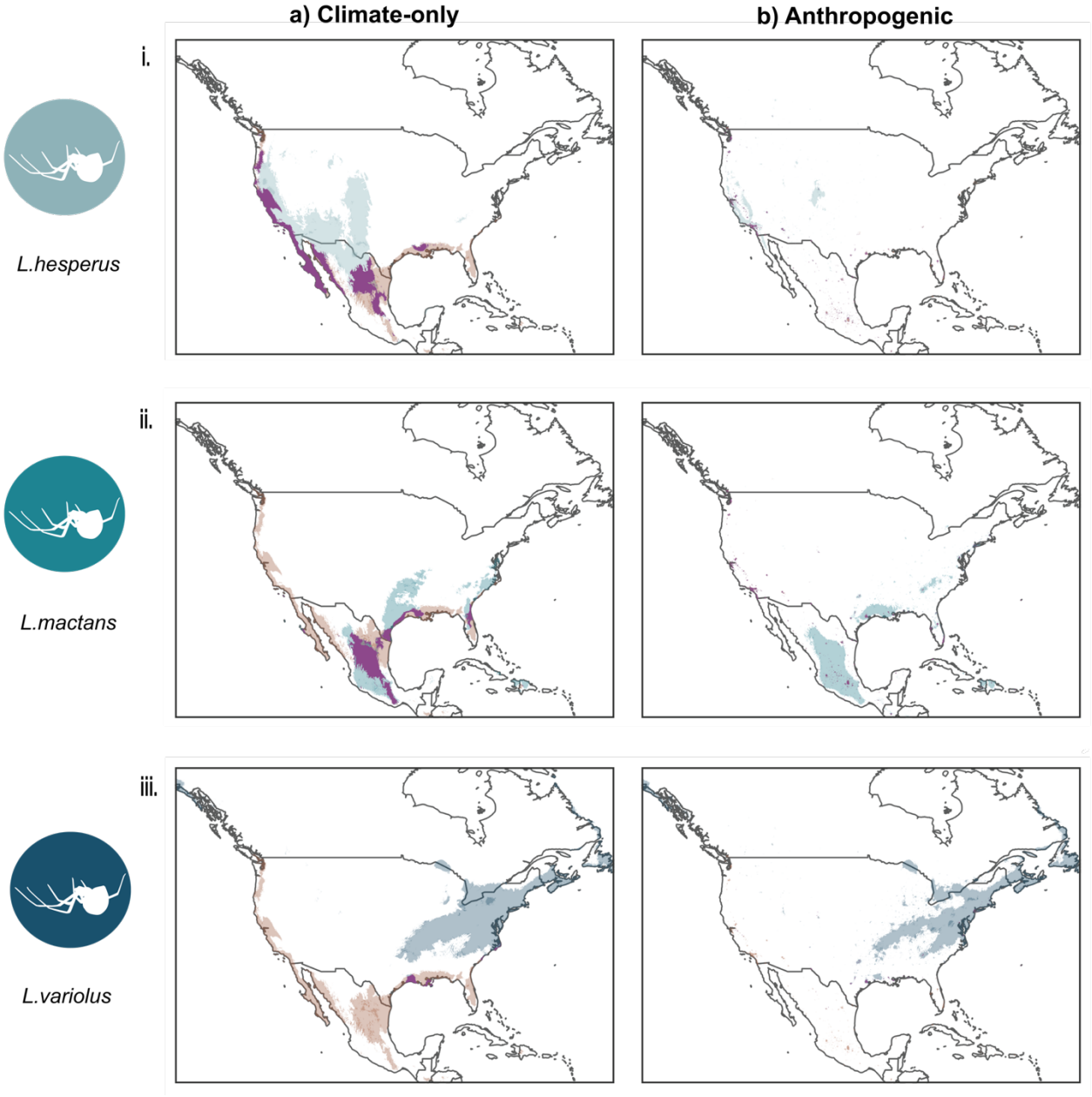
		Model Parameters		Model Performance			Permutation Importance								
Model	Species	Feature Class	RM	AUC	diffAUC	AICc	Annual Precip	Precip Wettest Quarter	Precip Driest Quarter	Isothermality	Temp Seasonality	Max Temp	Min Temp	Human Population Density 2020	Human Pop. Density from 2000-2020
Anthropogenic Change 2000-2020	*L. geometricus*	LQ	1	0.94891	0.00628	12135.5	0.3	2.1	0.5	6.9	24.5	0.6	11.7	53.6	0.2
	L.hesperus	LQ	1	0.84075	0.00691	27123.5	3.2	10.6	10.3	33.9	13.7	9.2	4.9	14.2	0
	L. mactans	LQ	1	0.86991	0.00556	26100.9	6.7	0	13.3	9.9	40.2	11.9	14.8	2.9	0.2
	L.variolus	LQ	1	0.80180	0.01826	5788.2	12.5	10.2	55.1	2.4	0	2.5	2.9	14.1	0.5

Supplementary Table 2. Area of geographic extent (km2) under Climate-only and Anthropogenic models, percent change in suitable area between Climate-only and Anthropogenic models (positive value indicates decrease and negative value indicates increase in suitable area), and area (km2) of geographic overlap between *L. geometricus* and native widows across three thresholds of habitat suitability. High habitat suitability is characterized by values >0.75, moderate-to-high suitability is indicated by values >0.5, and low-to-high suitability is >0.25.

Species	Habitat Suitability	Climate-Only Area (km2)	Anthropogenic Area (km2)	Area Diff (%)	Anthropogenic Overlap (km2)	Climate-Only Overlap (km2)
L. geometricus	High (>0.75)	412860	48535	88	-	-
	Moderate-high (>0.5)	1396979	70739	95	-	-
	Low-high (>0.25)	2419130	119937	95	-	-
L. hesperus	High (>0.75)	86397	698896	88	30888	1487974.656
	Moderate-high (>0.5)	301009	2484307	88	47787	710168.75
	Low-high (>0.25)	2038206	4568353	55	81156	202911.4687
L. mactans	High (>0.75)	405652	387983	4	39145	1511547.125
	Moderate-high (>0.5)	1304850	1030108	21	65306	433545.1875
	Low-high (>0.25)	3488982	3676535	-5	112515	11807.625
L. variolus	High (>0.75)	924674	359213	61	3701	186611.8125
	Moderate-high (>0.5)	2348498	1902354	19	11915	36898.82812
	Low-high (>0.25)	4878089	4785275	2	47958	641.71875

Supplementary Table 3. Percent permutation importance of environmental predictors used in the Climate-only model for each species. Variables include: annual precipitation, precipitation of the wettest quarter, precipitation of driest quarter, isothermality, temperature seasonality, maximum temperature of the warmest month, and minimum temperature of the coldest month.

		Permutation Importance						
Model	Species	Annual Precip	Precip Wettest Quarter	Precip Driest Quarter	Isothermality	Temp Seasonality	Max Temp	Min Temp
Climate-Only	*L. geometricus*	15.3731	14.965	22.6473	0	8.0421	4.2506	34.7219
	L.hesperus	10.6763	17.0089	22.5123	31.1552	10.1228	6.074	2.4505
	L. mactans	12.136	5.0334	14.338	6.244	37.358	12.2965	12.5942
	L.variolus	6.1205	0.9395	28.1324	15.3881	19.1078	13.0878	17.2239



Supplementary Figure 1. This figure shows the geographic overlap of brown widows with i) *L. hesperus*, ii) *L. mactans*, and iii) *L. variolus* under a) Climate-only and b) Anthropogenic models. Habitat suitability >0.5 of each native widow is displayed in blue and *L. geometricus* in brown. Areas of overlap between *L. geometricus* and each native widow is presented in purple

Chapter 2: Climatic niche overlap models reveal historical competitive interactions structure native black widow niches and potential ecological impacts of brown widows (*L. geometricus*) in North America

Abstract

Understanding competitive interactions between widow spiders (Theridiidae: *Latrodectus*) and how they shape geographic distributions is invaluable to deciphering the relationships of this historically cryptic group. North America is home to three native widows (*L. hesperus, L. mactans, L. variolus*) and one invasive widow *(L. geometricus)* with sympatric distributions. Native species have coevolved to avoid competitive and antagonistic encounters with congeners by partitioning their niches, allowing them to co-occur in the same geographic areas. Given the relative novelty of *L. geometricus* in native communities as they expand their range, it is unclear if and how they share resources with their congeners. Competition for climatic resources (space) could result in ecological impacts, so we aimed to study climatic niche partitioning and how it shapes sympatric geographic distributions of native widows compared to *L. geometricus.* We quantified climatic niche overlap for all four species on a continental scale and evaluated niche partitioning among native species and between invasive and native species. We found that native species had distributions that were more strongly partitioned, showing weaker niche overlap, with the exception of *L. mactans* and *L. variolus* which showed strong overlap and niche equivalency. Conversely, we found greater niche overlap between *L. geometricus* and native widows, possibly because they do not compete, or it is too soon to see the effect of competition preventing co-occurrence, or because differences in diet or urban microhabitats promote coexistence.

1 | Introduction

Widow spiders (*Latrodectus*) are a relatively well-studied genus because of their complex sexual behaviors and medical significance, however little is known about competitive interactions between sympatric species (Schraft et al., 2021). This genus has cryptic morphological traits and behaviors that have made disentangling their evolutionary history and niche dynamics particularly difficult (Garb et al., 2004). These species' affinity for disturbed habitats and repeated human-mediated introductions of several *Latrodectus* species to novel regions have also led to invasions across the globe (Schraft et al., 2021). For invasive species that expand their range rapidly, resource competition and its ecological

impact are especially difficult to quantify. One way this competition can be evaluated is by comparing the ecological niche of invasive and native species on a continental scale.

There are many biotic and abiotic factors that define a species' ecological niche at any given time or space. Hutchinson's niche concept describes the niche as an abstracted multi-dimensional hypervolume, where each dimension (axis) represents an abiotic or biotic variable, and where each point represents a unique set of environmental conditions which sustains a species infinitely (Hutchinson, 1957; Colwell and Rangel, 2009; Pironon et al., 2018). This niche concept contrives the distinction between the abstracted fundamental niche, which defines the entire space a species can theoretically occupy without barriers to movement, and the realized niche, a subset of the fundamental niche that describes the conditions currently occupied by species given biogeographic barriers and biotic interactions that limit their range. By attributing niches to species rather than tying them only to the environment, Hutchinson's abstraction of the niche allows us to use geographic coordinates and the corresponding values of *n* environmental variables to estimate the environmental space (i.e. E-space) a species occupies as a representation of their niche for comparative studies (Colwell and Rangel, 2009; Holt, 2009; Pironon et al., 2018).

North American widow communities are comprised of four native species, *L. hesperus, L. mactans, L. variolus*, and *L. bishopi,* and one invasive species, *L. geometricus,* where they co-occur in parts of their geographic ranges (Figure 1). *Latrodectus hesperus* is found from Mexico to southwest Canada, dominating the western half of the continent in relation to its relatives. In their natural habitat, they are found under logs and shrub vegetation, using crevices in the wood as retreats, and show a preference for building their webs in areas with stronger chemical residues of potential ground-dwelling prey (Salomon et al., 2010; Johnson et al., 2012). They are abundant in urban and agricultural habitats, but spiders from these populations have smaller body sizes and reduced fecundity compared to populations in their natural habitats (Johnson et al., 2012). The smallest of the North American widows, *L. mactans*, is found throughout Mexico and expanding east to Florida and just south of the Great Lakes (Schraft et al., 2021). They shelter under logs, in burrows, and construct retreats using silk to adhere tall grasses close to the ground (Lamoral, 1968). They are commonly found in urban and agro-ecosystems, where they primarily feed on fire ants *(Solenopsis invicta)* (Nyffeler et al., 1988). The natural habitat of *L. variolus* is in xeric to mesic deciduous forests and they show preference for building webs at tall heights in trees (Wang et al., 2018). Their range extends from northern Florida to southeast Canada and as far west as central Oklahoma. Unlike their large-range native relatives, *L. bishopi* are endemic to sand pine scrub habitats

in Florida and have a more specialized diet, feeding on endemic beetles (Carrel, 2001; Carrel and Deyrup, 2014). Over time, native species' niches diverge to avoid competitive interactions so that they now occupy different geographic regions or partition their occupied niches in regions where they co-occur to avoid antagonistic encounters (Schoener, 1974).

The niche conservation hypothesis proposes that closely related taxa share more similar niches (Peterson, 1999). This hypothesis suggests that speciation occurs in geographic dimensions, and ecological differences evolve later (Peterson, 1999; Warren, 2008). Although related niches may be similar, they are rarely equivalent and occur on a continuum ranging from identical to niches that are more similar than random (Warren et al., 2008). This suggests that differential selection is important in species differentiation (Graham et al., 2004). The way species share and partition resources largely depends on histories of competitive encounters that can cause closely related species' niches to diverge. Under niche partitioning, competition drives species to differentiate how they use resources to limit competition and over time, niches diverge. Niche partitioning also allows species to co-occur in the same geographic area by reducing competitive and antagonistic encounters that would otherwise occur if they shared the same requirements for survival (Schoener, 1974). Previous studies have mapped distributions and observed some habitat preferences of native widows, but competitive interactions that structure their climatic niches are uncertain.

Since 1993, the IUCN Invasive Species Specialty Group has recognized approximately 8,331 invasive species that have been moved from the native range into novel habitats (ISSGS, 2011), where they can cause rapid and complex ecological impacts on native communities (Snyder and Evans, 2006; Ricciardi et al., 2013). Brown widows (*L. geometricus*) originate from southern Africa and were introduced to North America in 1935 (Pearson, 1936; Garb et al., 2004). They notably expanded their range since the start of the 21st century and can now be found across the southern extent of the continent (Pearson, 1936; Brown et al., 2008; Vincent et al., 2008; Vetter et al., 2012a). Lack of structuring effects that isolate species after multiple generations of competitive interactions, allow invasive species to geographically overlap with native species. Consequently how they share or partition resources is important for assessing competitive interactions and, ultimately, ecological impacts. There are several factors could potentially give *L. geometricus* competitive advantages over native species. First, life history traits that favor rapid reproduction can overcome the effects of drift by increasing population size. In urban populations of southern California, *L. geometricus* produce significantly more egg sacs than *L. hesperus* (Vetter et al., 2012b). Second, invasive species experience enemy release when they initially invade

novel environments, which gives them the competitive advantage of escaping encounters with predators (Callaway et al., 2004). For example, parasitic flies, *Pseudogaurax signatus*, commonly infest *L. hesperus* egg sacs but not *L. geometricus* (Vetter et al., 2012b). However, the effects of enemy release decrease over time (Diez et al., 2010), so although it is a useful mechanism for growing an establishing population, eventually it may not offer any competitive advantage. Finally, partitioning of diet or microhabitats may minimize ecological impact by allowing coexistence of species under the same climatic conditions. Discerning co-occurrence and climatic niche overlap patterns at a continental scale can clarify patterns of niche divergence between *Latrodectus* spiders and the impacts of invasion on native species.

Here we estimate and plot pairwise comparisons of species' climatic niches in environmental space to quantity the amount of niche overlap between *L. geometricus*, *L. hesperus*, *L. mactans*, and *L. variolus* in North America. Climatic niches are based on geographic localities, but are estimated in environmental space, where overlap is not limited by availability of the environments in geographic space. Therefore, it is possible that species have overlapping climatic needs but movement to the geographic locations that meet those needs may be limited by biogeographic barriers or competition. We aim to compare how invasive species partition resources with native species compared to longer-established native species with each other. We hypothesize that native widows will have more strongly partitioned niches because they have coevolved over time. If climate is a limiting factor of co-occurrence, we expect one of two patterns: species will have strong climatic overlap but will not co-occur, in which case they are competing for those environments; or they will co-occur with weak climatic overlap, in which case they are partitioning suitable climates to avoid antagonistic encounters. If some factor other than climate, like diet, is limiting co-occurrence, species will have strong climatic overlap and co-occur, allowing them to co-exist in similar climates without competitive interactions. If species do not have overlapping climatic niches and do not co-occur, niche partitioning may be due to differences in accessibility to environments rather than resource competition. We also hypothesize, as an invasive species, *L. geometricus* will have strong climatic niche overlap with species they co-occur with because they have not had time to coevolve and partition climate resources, which opens opportunities for competitive interactions.

2 | Methods

2.1 Data Collection

Locality data for all four species within North America are the same 3,101 localities as in Sadir & Marske (2021). Briefly, we gathered occurrence data from GBIF (Global Biodiversity Information Facility, GBIF.org 2020), which compiles occurrence records from museum collections and online community science repositories: iNaturalist and BugGuide. Museum records with adequate locality information but no coordinates were georeferenced using the GEOLocate Web Application. We visually verified occurrences that were far outside of previously established ranges (Wang et al., 2018; Schraft et al., 2021) from the original online post and eliminated points that could not be confirmed. Additionally, we gathered community submissions from Facebook groups ("Spider/Bug Questions with TheBugGirl" and "Spider and Insect Enthusiast") and Reddit ("r/whatsthisbug" and "r/spiderbro"). We included all submissions with sufficient collection data that we were able to positively identify based on the photograph. Additional data were generously provided by contacts at extension offices in Oklahoma and Texas, and opportunistic field collections by colleagues at the University of Oklahoma, University of Florida, and the University of Arizona. We compiled a dataset of 6,703 georeferenced occurrences for all four species. After systematic subsampling on a 10x10km grid, as in Sadir & Marske (2021), we retained 3,101 total points for niche overlap models.

For each pairwise comparison, we collected climate data and selected the most relevant variables for six pairwise comparisons: *L. geometricus/L. hesperus; L. geometricus/L. mactans; L. geometricus/L. variolus; L. hesperus/L. mactans; L. hesperus/L. variolus; L. mactans/L. variolus*. Climate data (19 CHELSA Bioclim variables) were first obtained from Paleoclim.org, where they have been rescaled to 2.5 arc-min resolution (Brown et al., 2018; Karger et al., 2017). To find the most relevant variables for each pairwise comparison, we ran generalized boosted regression tree models using the 'humboldt.top.env' function from the 'humboldt' package (Brown and Carnaval, 2019) on R version 4.0.4. Boosted regression trees is a machine leaning technique that determines the top influence factor of variables (Elith et al., 2008). We retained variables that had an influence factor greater than 10% for overlap models (Table 1).

2.2 Climatic Niche Overlap Analyses

We quantified niche similarity by estimating how much two species' niches overlap and evaluated niche divergence in the six pairwise comparisons, following methods proposed by Brown and Carnaval (2019). This method is especially advantageous for studying invasive species because realized niches within the introduced range are typically unstable and do not fairly represent their fundamental niche.

To compare climatic niche overlap among species, we first estimated the environmental background that represents the environments (climates) that are accessible to each species. To do this, we first drew a minimal convex polygon (MCP) around each species' occurrences and added a 500km buffer. The environments in the MCP were then plotted on a gridded, two-dimensional Principal Component Analysis (PCA) space, where each cell represents a unique set of environments accessible to each species. Quantifying niche overlap in E-space rather than geographic space minimizes biases introduced by spatial resolution and corrects occurrence density based on availability of particular sets of environmental conditions without assuming equal distribution of habitats across the study region (Broennimann et al., 2012). Next, we estimated the niche of each species by projecting occurrence points in E-space and smoothing the response using density kernel smoothing, where more densely populated environments reflect more suitable habitats they inhabit. The environmental background and estimated niche of both species are then plotted in the same space to measure the amount of overlap between them.

We performed two tests to quantify niche overlap and evaluate niche divergence, Niche Overlap Test (NOT) and the Niche Divergence Test (NDT). For both tests, niche similarity (the degree of niche overlap) is measured using Schoener's D similarity index (Schoener, 1968), which ranges from 0 (no overlap) to 1 (complete overlap). The NOT estimates the similarity between the realized niches of two species and the NDT evaluates whether differences between the two niches are likely the result of true niche divergence or differentiation in access to environments due to biogeographic barriers. Accessible environments that are shared by both species are termed analogous E-space. Both species can theoretically occupy analogous E-space, so it represents the environments they might have to compete for. Environments that are accessible to one species, but not the other, are non-analogous E-space. These are the environments that are safe from encounters with the other species. The difference between the two tests is the extent of E-space in which niche similarity is measured. The NOT measures the amount of niche overlap in total E-space (both analogous and non-analogous), while the NDT measures niche overlap only in analogous E-space. By limiting the testing region to areas where species have access to the same environments, we can determine whether the differences in two species occupied niches is due to true niche divergence or confounding factors such as dispersal limitation.

Although niches may be similar, they may not necessarily be equivalent, in which case there would be no statistical difference between them. For each test (NOT and NDT), we measured niche equivalency (equivalency statistic) and the power of those equivalency models (background statistic) to evaluate the

statistical significance of niche similarity. To test for equivalency, we repeated niche similarity measurements 500 times. Next, we randomly sampled points by reshuffling occurrence points across the total extent of E-space (analogous and non-analogous) 500 times to derive a null distribution. The distribution of the niche similarity was then assessed against the corresponding null distribution. We then assessed the power of the model to accurately detect a significant equivalence statistic using the background statistic. The background statistic calculates whether climatic niches are more different than would be expected given the differences in their corresponding E-space. Essentially, it determines whether the difference in species' niches is simply the result of underlying differences in the environments they have access to. To do this, we compared niche similarity measurements of observed niches against a null distribution. To build the null distribution, we first randomly shifted the spatial distribution of one species (species 1) in geographic space, to estimate random E-space within the geographic limits of species 1. We then estimated niche similarity of the observed niche of one species (species 2) and the randomly sampled niche of the other species (species 1). We repeated this 500 times to create a null distribution of E-space within the study region of species 1 that is accessible to species 2. Non-significant background tests for significant equivalency tests are still considered to provide evidence of true niche divergence (Brown and Carnaval, 2019).

2.3 Potential Niche Truncation

To further test the robustness of our overlap models, we used the Potential Niche Truncation Index (PNTI) to quantify the potential for a species' realized niche to be truncated, or cut-off, by the available E-space. This test describes how accurately the contemporary realized niche represents the fundamental niche of the species by quantifying how much of the species' estimated niche falls outside the margin of the study region's E-space, a particular concern for invasive species. Low niche truncation indicates that a species occupies all the environments that are accessible to them, and that the estimated niche is an accurate representation of the fundamental niche. High niche truncation suggests that the species' realized niche poorly reflects the fundamental niche. This can either be because the locality data selected for the models do not completely reflect the range of environments accessible to the species, or because the species' niche is not in equilibrium. The niche truncation index thus gives us confidence in our estimates of niche overlap. If PNTI is low, we can be confident that the estimated realized niche is a suitable approximation of the fundamental niche. If PNTI is high, we have lower confidence that the estimated realized niche is an accurate representation of the fundamental niche. If PNTI is less than 0.15, risk that the realized niche does not accurately reflect the fundamental niche of the species is low.

Risk is moderate if it is equal to 0.15-0.3, and high if it is >0.3. PNTI was evaluated three times (once for each pairwise comparison) and averaged to calculate mean PNTI for each species.

3 | Results

Consistent with our predictions for the invasive brown widow, we found that *L. geometricus* had greater niche overlap with native species than native species did with each other, apart from *L. mactans* and *L. variolus* (Table 2). Niche overlap, measured using similarity index D, was greatest between *L. geometricus* and *L. mactans* (0.47), followed by *L. geometricus* and *L. hesperus* (0.232). Unexpectedly, *L. variolus* and *L. mactans* had high niche overlap (0.207). All other pairwise comparisons, *L. geometricus/L. variolus, L. hesperus/L. mactans, L. hesperus/ L. variolus,* showed low overlap (0.005, 0.047, 0.004, respectively). Niche equivalency was significant (p-value < 0.05) for all NOTs, apart from *L. mactans/L. variolus.* Niche equivalency statistics for NDTs other than *L. mactans/L. variolus* were also significant. Background statistics for NOTs and NDTs were all non-significant other than *L. geometricus/L. mactans* (Table 2).

Overlap maps represent species' niches as kernel density isopleths, where the densest centroids characterize most suitable environments for survival. Overlap maps of *L. geometricus* and *L. mactans* show that the niche of *L. mactans* occupies a wider breadth of environments but both species have one main centroid (Figure 2). The centroid of *L. mactans* primarily overlaps on less dense kernels of *L. geometricus* so the most suitable habitats of both species do not actually overlap. The majority of the niche of *L. geometricus* lies within the niche of *L. hesperus* (Figure 2). However, *L. hesperus* also has another centroid that is completely unoccupied by *L. geometricus*. *Latrodectus geometricus* and *L. variolus* do not have overlapping niches (Figure 2). Native species generally share less analogous E-space and less overlap than they do with *L. geometricus*. Niches of *L. hesperus* and *L. variolus* do not appear to overlap at all, and only the margin of *L. mactans*' niche overlaps with that of *L. hesperus* (Figure 2). The niches of *L. mactans* and *L. variolus* overlap around the centroid of *L. variolus*' niche; however, habitats with the greatest density of occurrence for *L. mactans* lie in non-analogous space (Figure 2).

Niche truncation was generally high across all species, with the exception of *L. variolus*. The mean PNTI of *L. variolus* was low (PNTI = 0.16). Unexpectedly, *L. mactans* and *L. hesperus* had the highest mean PNTI (0.463 and 0.45, respectively). Mean PNTI for *Latrodectus geometricus* was 0.32, which is between moderate and high.

4 | Discussion

North American widow spiders present an interesting study system to compare how congeneric niche partitioning shapes geographic distributions among native species and between native and invasive species. *L. hesperus, L. mactans,* and *L. variolus* are native and have partially sympatric distributions with no obvious biogeographic barriers separating them, while *L. geometricus* has a large distribution that geographically overlaps with all three native widows. We studied the role of niche partitioning in shaping the geographic distributions of four widow species by quantifying climatic niche overlap on a continental scale. Consistent with our hypothesis, we found that *L. geometricus* have greater niche overlap with native species than native species do with each other, apart from *L. variolus*.

Over time, repeated immigrations and competitive interactions structure geographic distributions. Related species with strong niche overlap inhibit coexistence through niche preemption, in which case priority effects determine which species has access to resources for survival (Fukami, 2015). Under niche partitioning, co-occurrence is facilitated by niche partitioning (Schoener, 1974), so sympatric populations likely do not encounter many competitive interactions because their niches have diverged. The most closely related widows in this study, *L. hesperus* and *L. mactans,* reflect the strongest signal for historical niche partitioning. Both species have expansive geographic ranges that overlap in Mexico and central USA but climatic niche overlap for the pair is weak, suggesting niche differentiation over time. It may also be that species block each other from continuing to expand their range, so the estimated niche is not in equilibrium. Niche overlap comparisons of *L. variolus* were particularly illuminating considering they are largely understudied compared to their native relatives (Schraft et al., 2021). Consistent with our hypothesis, *L. variolus* and *L. hesperus* do not have overlapping niches and limitedly co-occur around eastern Oklahoma and Texas, which suggests niche partitioning may be due to differences in accessible environments. This is also reflected in their overlap plots that show little analogous E-space (Figure 2). Unexpectedly, we found *L. variolus* and *L. mactans* have significantly overlapping and equivalent climatic niches. Because they share similar climatic needs but occupy different geographic regions, it is possible that niche preemption has historically structured their geographic distributions, and co-occurrence in eastern USA may be due to stochastic effects at their range margins due to small population sizes and genetic drift. It is also possible that co-occurrence is facilitated by some factor other than climate, such as differences in diet or microhabitats. *Latrodectus variolus* prefer building webs at taller heights which may mediate competitive interactions in sympatric populations (Lamoral, 1968; Wang et al., 2018).

Unlike native species with long histories of competitive interactions that shape their climatic niches and geographic distributions, *L. geometricus* are rapidly expanding their range and present a risk to the stability of the historically partitioned niches of native widows. *Latrodectus geometricus* are found widely throughout the southern extent of North America, but their range has not expanded sufficiently northward to be a risk to the northern widow, *L. variolus*. We found that these two species do not overlap climatically either, making the risk of ecological impact on *L. variolus* minimal. On the other hand, we found that *L. geometricus'* climatic niche strongly overlaps with *L. mactans* and *L. hesperus,* two species with whom they share significant parts of their distribution (Sadir & Marske, 2021). Relatively recent range expansion of *L. geometricus* may be the mechanism behind co-occurrence patterns. As large-range species, the impact of competitive interactions at large spatial scales may not be obvious based on contemporary distributions because impacts of competition are still occurring at more localized scales (Vila et al 2011). Studies have described potential competition and displacement of urban widow communities as a result of their invasion at local scales (Bianchi, 1945; Vetter et al., 2012a, 2012b). In this case, there is possible risk of ecological impact in the long-term depending on synergistic factors like colonization/propagule pressure, biotic resistance, enemy release, and more (Ricciardi et al., 2013). However, *L. geometricus'* preference for urban habitats limits potential impact on non-urban widow populations (Sadir and Marske, 2021). Differences in diet or microhabitats might also allow *L. geometricus* to co-occur with *L. hesperus* and *L. mactans* despite climatic niche overlap. Given the dietary plasticity *L. mactans* display in urban and agricultural populations, where they feed on invasive fire ants (Nyffeler et al., 1988), this species may also be less impacted by *L. geometricus* than predicted by geographic and niche overlap. Unlike black widows, *L. geometricus* prefer deep cavities and 30˚ or 90˚ angles to build their web structures (Vetter et al., 2016), which may also reduce the probability of competitive interactions.

Niche dynamics of invasive species in their introduced range are rarely in equilibrium and can be unpredictable as they shift, underfill, and/or expand, making them difficult to model with certainty (Broennimann et al., 2007; Pearman et al., 2008; Strubbe et al., 2013; Guisan et al., 2014; Atwater, 2018). We estimated how well the contemporary realized niche, based on locality data, reflects the fundamental niche of each species, using PNTI, to test the predictive power of overlap models. We found that the estimated niche of *L. variolus* likely accurately reflects their fundamental niche, suggesting the robustness of niche comparisons. On the other hand, all three other species' niches poorly reflect their fundamental niche, which can be the result of insufficient locality data to accurately estimate the niche. However, it may also be an accurate reflection of a niche out of equilibrium, which is

a common state for invasive species that are moved by humans and by species in their native range facing changing climates (Elith et al., 2010). Either way, it indicates lower model predictive power, so results for these species should be taken with caution.

Although widow spiders are well-studied, this is the first study to our knowledge to evaluate potential competitive interactions between congeners on a continental scale. We were able to discern how climatic niche partitioning may shape the geographic extent of sympatric distributions of widows in North America. The instability of invasive species' niches made it more difficult to interpret co-occurrence patterns in their introduced range. Niche dynamics and impacts of invasion on co-occurrence may be particularly complex in central USA, where all three native black widows and the brown widow have sympatric distributions. Local and regional studies in that region may be particularly informative for future assessments of ecological impacts of *L. geometricus* invasion.

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7 | Tables and Figures

Table 1. Bioclim variables with influence factors >10% selected for each pairwise comparison using boosted regression trees.

Species Comparison	Selected Variables
L. geometricus/ L. hesperus	Mean diurnal range (Bio 2), minimum temperature of coldest month (Bio 6), precipitation of warmest quarter (Bio18), mean temperature of the coldest quarter (Bio 11)
L. geometricus/ L. mactans	Annual mean temperature (Bio 1), mean diurnal range (Bio 2), minimum temperature of coldest month (Bio6), precipitation of warmest quarter (Bio18)
L. geometricus/ L. variolus	Minimum temperature of coldest month (Bio 6), mean temperature of warmest quarter (Bio 10), mean temperature of the coldest quarter (Bio 11), precipitation of the driest month (Bio 14), precipitation seasonality (Bio15), precipitation of warmest quarter (Bio18)
L. hesperus/ L. mactans	Annual mean temperature (Bio 1), mean diurnal range (Bio 2), precipitation of warmest quarter (Bio18)
L. hesperus/ L. variolus	Mean diurnal range (Bio 2), mean temperature of warmest quarter (Bio 10), precipitation seasonality (Bio15), precipitation of warmest quarter (Bio18)
L. mactans/ L. variolus	Annual mean temperature (Bio 1), minimum temperature of coldest month (Bio 6), precipitation of the driest month (Bio14), precipitation seasonality (Bio 15)

Table 2. Niche similarity indices (D ranges from 0 to 1, where 0 indicates no niche overlap and 1 suggests complete niche overlap), equivalence and background statistics for each pairwise comparison in the NOT and NDT. * indicate significant p-values.

	Species Comparison	Niche Similarity (D)		Equivalency Statistic (P-Value)	Background Statistic (P-Value)	
	-	Total E-space	Analogous E-space	-	Env2 > Env1	Env1 > Env2
Niche Overlap Test (NOT)	*L. geometricus/ L. hesperus*	0.232	0.242	0.002*	0.429	0.353
	L. geometricus/ L. mactans	0.467	0.42	0.002*	0.046*	0.234
	L. geometricus/ L. variolus	0.005	0.08	0.002*	0.769	0.289
	L. hesperus/ L. mactans	0.047	0.047	0.002*	0.601	0.625
	L. hesperus/ L. variolus	0.004	0.035	0.002*	0.86	0.186
	L. mactans/ L. variolus	0.207	0.274	1	0.505	0.297
Niche Divergence Test (NDT)	*L. geometricus/ L. hesperus*	0.191	0.201	0.002*	0.473	0.461
	L. geometricus/ L. mactans	0.467	0.482	0.002*	0.026*	0.17
	L. geometricus/ L. variolus	0.005	0.082	0.002*	0.689	0.23
	L. hesperus/ L. mactans	0.047	0.048	0.002*	0.593	0.537
	L. hesperus/ L. variolus	0.004	0.035	0.002*	0.984	0.214
	L. mactans/ L. variolus	0.207	0.274	1	0.509	0.349

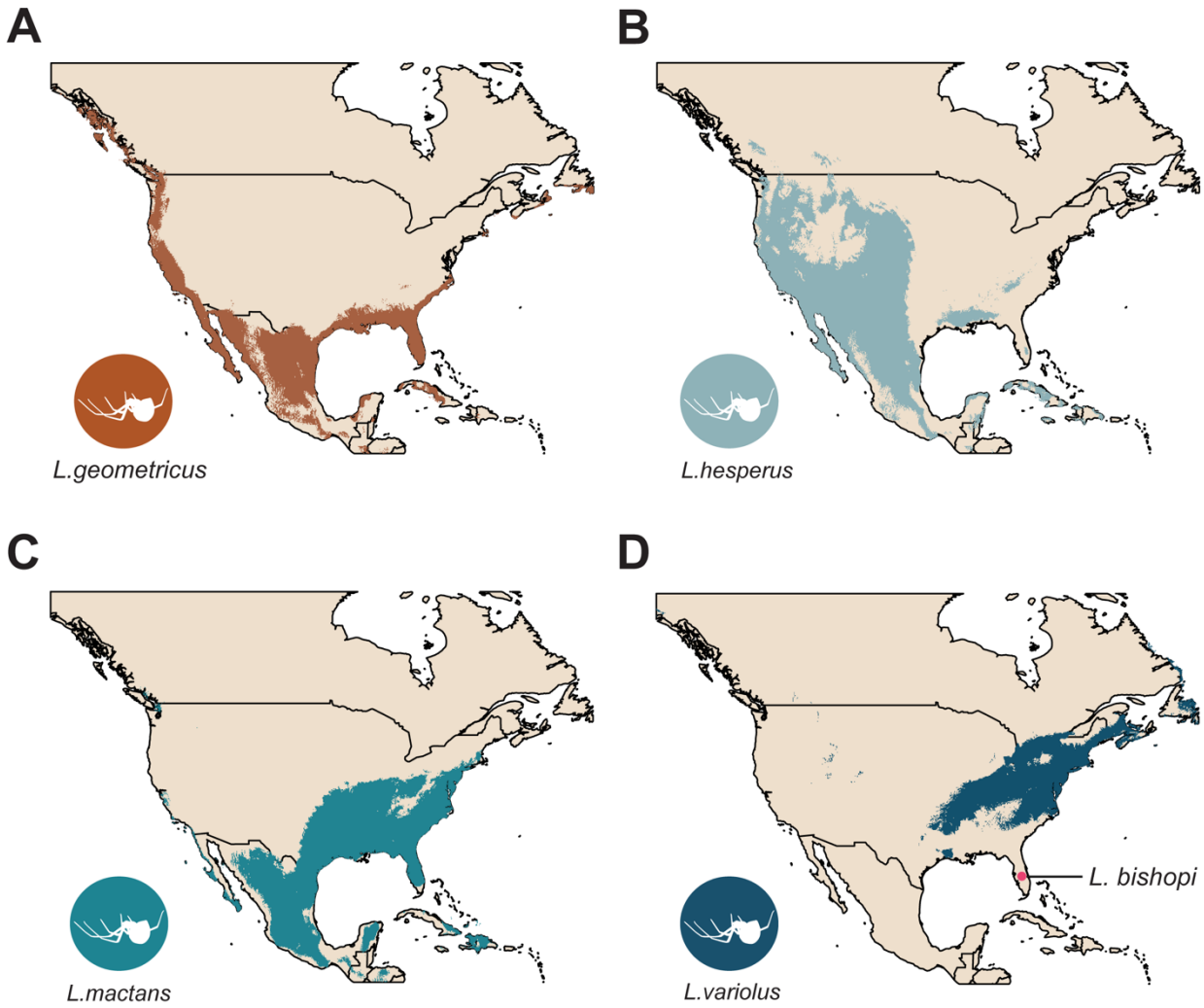


Figure 1. Distribution maps of A) *L. geometricus*, B) *L. hesperus*, C) *L. mactans*, D) *L. variolus* and *L. bishopi*. Distributions were estimated based on Sadir & Marske (2021).

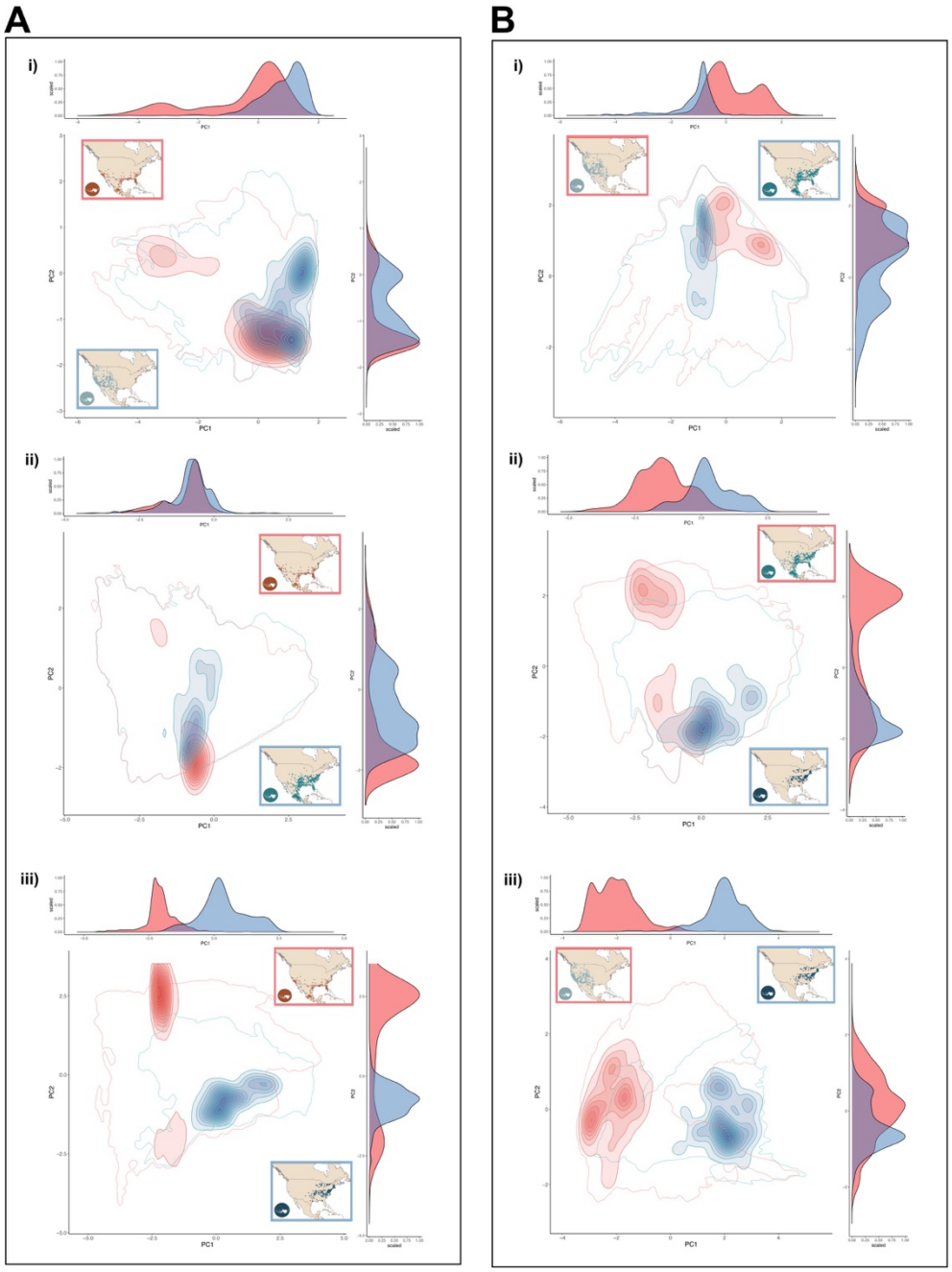


Figure 2. Niche overlap plots between invasive and native species (A) and among native species (B). Filled kernel density isopleths represent the climatic niche of each species, with more dense regions representing highly occupied parts of the niche. Empty, outlined regions represent E-space accessible to each species. For each PC, the density of each species' niche is displayed as a density histogram. Panel A shows overlap between *L. geometricus* and *L. hesperus* (A-i), *L. mactans* (A-ii), and *L. variolus* (A-iii). Panel B shows overlap between *L. hesperus*/*L. mactans* (B-i), *L. mactans*/*L. variolus* (B-ii), and *L. hesperus*/*L. variolus* (B-iii). Each overlap plot includes maps with occurrence points for each species being compared with border colors to indicate corresponding kernel color on overlap plot.