



# Urban Environments Aid Invasion of Brown Widows (*Theridiidae: Latrodectus geometricus*) in North America, Constraining Regions of Overlap and Mitigating Potential Impact on Native Widows

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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 the geographic ranges 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.

**Keywords:** species distribution models, anthropogenic activity, urbanization, biological invasion, spiders, North America, microhabitat selection

## 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; Pyšek et al., 2020). 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

the ecological niche 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; Bowler et al., 2020). 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 as prey themselves. 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, United States, 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, promoting 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). 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 geographic extent 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,b;

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 human-made structures. They are widely feared by the public, in part due to the media sharing false and sensationalistic information about widow spiders, as was noted for the Mediterranean black widow, *L. tenebrosus* (Mammola et al., 2019). 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 remain poorly understood.

*Latrodectus geometricus* is native to southern Africa and have drastically expanded its 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 expanding their range throughout southeastern United States beginning in the late 1990s, with confirmed occurrence records now reaching as far north as Connecticut (Vincent et al., 2008; Vetter et al., 2012). By 2008, several populations had also 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., 2012) 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 geographic extent of any given species shows limitation to urban centers in the anthropogenic model, then its range is assumed to be 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. For invasive species, time of residence has a positive correlation with range size (Wilson et al., 2007; Williamson et al., 2009; Schmidt et al., 2017). Because brown widows have been established for a longer period in the southeastern extent of the continent, they have had time to grow viable populations and locally expand their range, so we expect more extensive ranges for them in these regions. We therefore hypothesize that *L. geometricus* will have the strongest overlap with *L. mactans*.

## MATERIALS AND METHODS

### 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. 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

**TABLE 1** | Counts for total occurrence points collected, systematically subsampled points, and pseudo-absences retained for model evaluation for each species.

Species	Total occurrences	Subsampled occurrences	Pseudo-absences
<i>L. geometricus</i>	1,140	604	3,020
<i>L. hesperus</i>	2,485	1,153	5,765
<i>L. mactans</i>	2,436	1,106	5,530
<i>L. variolus</i>	342	238	1,190

The number of pseudo-absences was standardized to five times the amount of subsampled occurrences for each species.

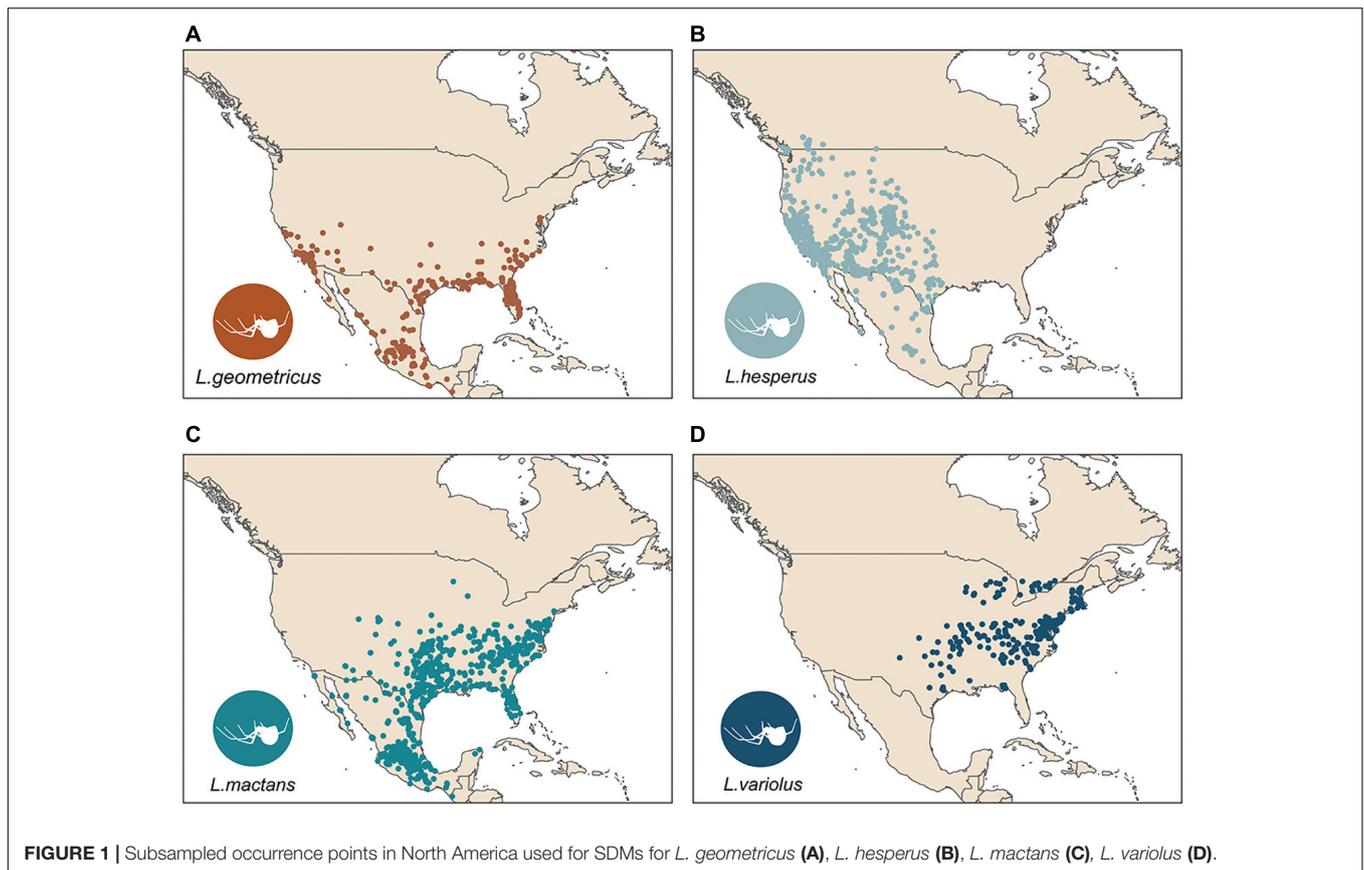
Questions with TheBugGirl" and "Spider and Insect Enthusiast") and Reddit ("r/whatsthisbug" and "r/spiderbro"). We included all occurrences with sufficient collection data that we were able to positively identify based on the photograph. The rest of our samples were generously provided by contacts at extension offices in Oklahoma and Texas, and opportunistic field collections in Oklahoma, Florida, and Arizona. Museum records with adequate locality information but no coordinates were georeferenced using the GEOLocate Web Application.

Clustered occurrences were systematically subsampled to a single point per cell on a 10 × 10 km 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 and Table 1).

### Environmental Variables

We obtained CHELSA Bioclim variables, averaged from 1973 to 2013, from Paleoclim.org (Karger et al., 2017; Brown et al., 2018), 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 (Center for International Earth Science Information Network - CIESIN - Columbia University, 2016). 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.

## Species Distribution Modeling

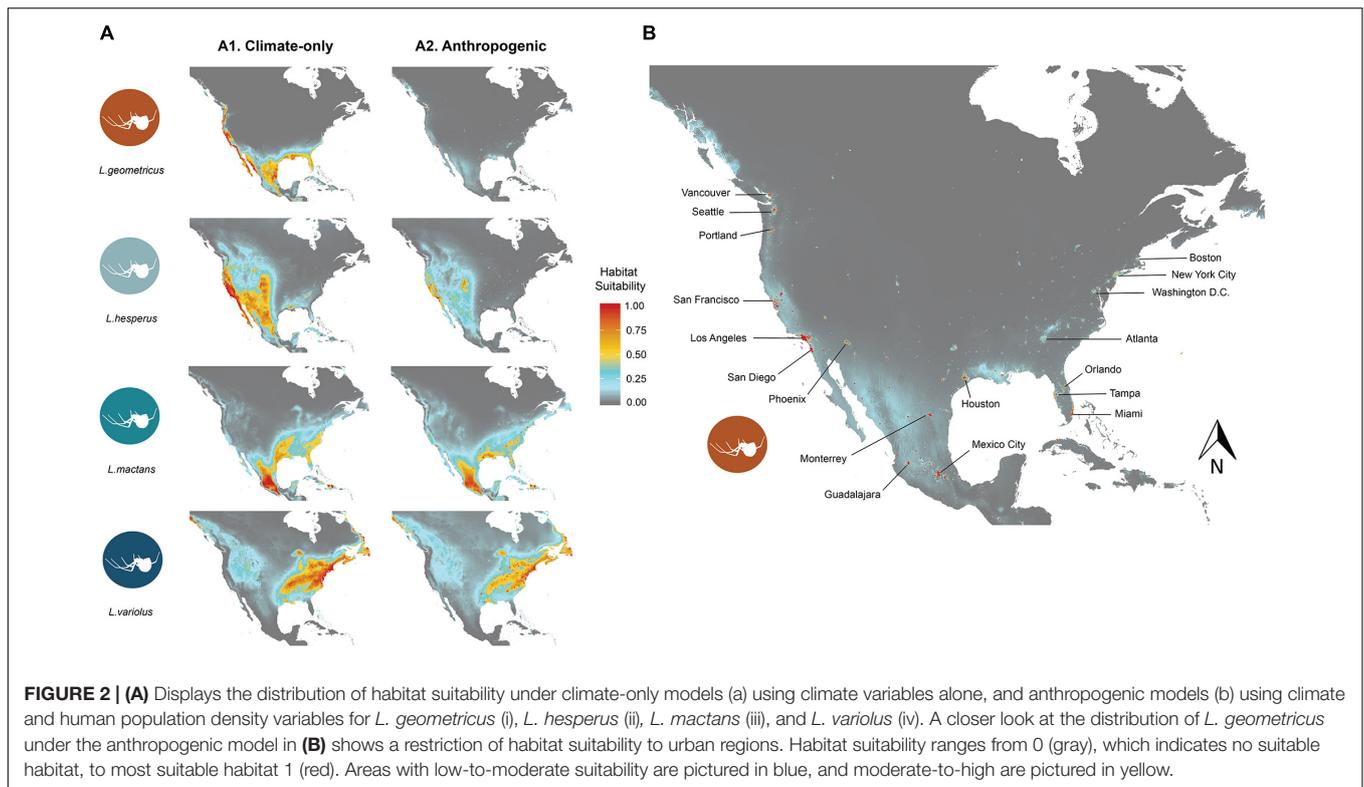
SDMs are quantitative tools that combine species occurrence data with relevant environmental variables to predict species habitat suitability across geographic space (Elith and Leathwick, 2009; Merow et al., 2013). To assess the importance of urbanization on geographic range of native and invasive widows, we ran two models to compare per species: first using climatic variables alone, and then using climatic and human population density variables.

We modeled our species distributions using Maxent 3.4.1. There are many software that extrapolate SDMs, but we chose Maxent because 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., 2019). 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. We partitioned training data using 10-fold cross-validation and ran models across multiple user-tuned parameters. We tuned our parameters by running multiple models across every combination of three feature classes, which determine the

potential shape of the response curves (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. 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). Furthermore, we used multiple performance metrics to evaluate our best-fit models: AUC, AIC, AICc, and Boyce Index (BI). BI was calculated using “ecospat” package on R, and values range from  $-1$  to  $1$ . Positive BI values suggest predictions are consistent with the distribution presence data, values close to zero suggest results are no different from a random model, and negative values suggests no predicted occurrence in areas with actual presences (Boyce et al., 2002; Hirzel et al., 2006). Habitat suitability scores for range maps were rescaled to a clog-log scale of  $0-1$ , 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  $\text{km}^2$ , 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. 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.

To ensure reproducibility (Zurell et al., 2020) we have included a standardized ODMAP report of SDM parameters and assumptions in **Supplementary Material**.

## 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. Overlap analyses use projections of two species' niches, in the case of geographic overlap using SDM outputs, to count the number of shared cells, resulting in a niche similarity measurement. Geographic overlap analyses were performed using "ENMTools" package (Warren

et al., 2021) to obtain two overlap metrics: Schoener's D and similarity index I, proposed by Warren et al. (2008). 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**).

## RESULTS

Overall, we found that *L. geometricus* show strongest constraint to urban environments, consistent with our hypothesis of

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

Model	Species	Model parameters		Model performance			
		Feature class (FC)	Regularization multiplier (RM)	AUC	diffAUC	AICc	BI
Climate-only	<i>L. geometricus</i>	LQ	1	0.89	0.007	13751.72	0.88
	<i>L. hesperus</i>	LQ	1	0.79	0.013	28205.34	0.95
	<i>L. mactans</i>	LQP	1	0.85	0.001	26530.06	0.96
	<i>L. variolus</i>	LQ	1	0.77	0.007	5927.48	0.96
Anthropogenic	<i>L. geometricus</i>	LQ	1	0.94	0.005	12105.32	0.94
	<i>L. hesperus</i>	LQ	1	0.85	0.012	26543.02	0.98
	<i>L. mactans</i>	LQ	1	0.87	0.008	25937.034	0.97
	<i>L. variolus</i>	LQP	1.5	0.80	0.021	5830.46	0.99

**TABLE 3** | Percent permutation importance of climatic and anthropogenic predictors used in the anthropogenic model for each species.

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
<i>L. geometricus</i>	12.77	5.89	19.25	1.02	6.14	0	10.63	44.3
<i>L. hesperus</i>	8	13.93	16.43	30.44	8.67	3.76	0.48	18.29
<i>L. mactans</i>	6.34	0.27	15.51	6.27	40.74	12.14	14.91	3.82
<i>L. variolus</i>	7.73	3.08	53.95	4.96	5.64	1.3	5.67	17.68

Results for the climate-only model can be found in **Supplementary Table 3**. 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.

synanthropic invasion. Unexpectedly, *L. hesperus* show moderate constraint to urban habitats, suggesting 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.

## Species Distribution Models

### 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 to excellent performance (0.70 > AUC < 0.90; 0.85 > BI) (Araújo et al., 2005).

### 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 in the anthropogenic model. Areas of habitat suitability for *L. mactans* and *L. variolus*

**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
<i>L. hesperus</i>	0.416	0.702
<i>L. mactans</i>	0.567	0.842
<i>L. variolus</i>	0.226	0.506

remained like their projected ranges in the climate-only models (Figure 2).

All selected models had fair to excellent performance ( $0.70 > \text{AUC} < 0.90$ ;  $0.85 > \text{BI}$ ) (Araújo et al., 2005). The estimated optimal anthropogenic model parameters and performance metrics for each species are shown in Table 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% 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).

## 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 and Supplementary Figure 1). Ranges of both *L. hesperus* and *L. geometricus* show constraint to urban centers in California, where they strongly overlap (Figure 2 and Supplementary Figure 1). *L. variolus* shows limited overlap with *L. geometricus* in southeastern United States, excluding Florida (Table 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 non-native 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 reduced risk of ecological impact on native widows overall because areas of overlap are more highly 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., 2012). 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., 2012). 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 in southern North America 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, 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 are heritable (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., 2012). 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 toward 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 from photographs and systematically subsampling occurrence data on a 10 × 10 km grid to reduce spatial bias around more populated areas. We note 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 and are a growing threat to local economies (Diagne et al., 2021). 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 methods 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.

## DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/**Supplementary Material**, further inquiries can be directed to the corresponding author/s.

## AUTHOR CONTRIBUTIONS

MS collected data and ran analyses. MS led the writing with input and revisions by KM. Both authors conceived the study.

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## SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fevo.2021.757902/full#supplementary-material>

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