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# Climatic niche overlap models reveal niche partitioning among black widow spiders and potential ecological impacts of invasive brown widows in North America

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## Abstract

The introduction of new species can have unpredictable effects on native communities. Understanding the potential for competitive interactions between widow spiders (Theridiidae: *Latrodectus*), and how they may have shaped species' geographic distributions, is critical for predicting the impacts of biological invasions in 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 distributions that are at least partly sympatric. 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, and competition for climatic resources (space) could result in ecological impacts to native widows. Here we aim to model niche differentiation and niche dynamics between native widows, that have coevolved over time, and between native and brown widows to assess the potential for ecological impact. We investigated the potential for climatic niche partitioning to shape sympatric geographic distributions of native widows compared to each other and to *L. geometricus*. We aggregated photographed occurrences from social media communities and online repositories to quantify climatic niche overlap for all four species on a continental scale, to assess niche dynamics 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, except for the two eastern widows, which showed strong overlap and niche equivalency. Conversely, we found greater niche overlap between *L. geometricus* and native widows, possibly because it is too soon to see the effect of competition on species' geographic distributions, or because differences in diet or partitioning of urban versus nonurban microhabitats promote coexistence.

## Highlights

- We estimate climatic niche overlap between widow spiders in North America, assess potential competition between native and invasive species, and evaluate the historical niche dynamics among native widows
- Occurrence data used for modeling climatic niches include 25 occurrences of *L. geometricus* from community submissions on social media
- Invasive *L. geometricus* and native widows have strongly overlapping climatic niches compared to native species among each other.
- This study shows niche differentiation between morphologically cryptic *L. hesperus* and *L. mactans*, and potential for negative competitive interactions between invasive and native species, given strong climatic and geographic niche overlap.

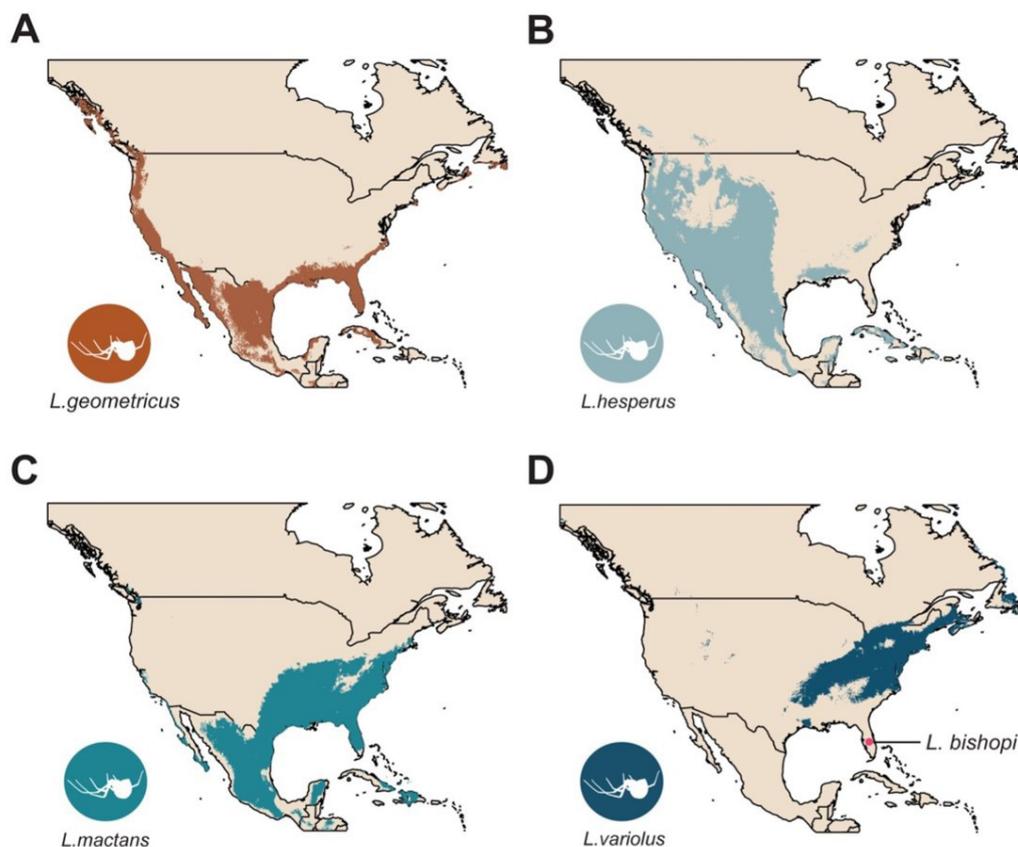
**Keywords:** coevolution, competition, environmental niche overlap, invasive species, niche divergence, niche overlap, social media, spiders

## Introduction

Widow spiders (*Latrodectus*) are a relatively well-studied genus because of their complex sexual behaviors and medical significance. Despite several species living in partial sympatry, little is known about how interactions among species structure species' ranges and facilitate coexistence (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), and their affinity for disturbed habitats, combined with repeated human-mediated introductions of *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.

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 webs in areas with strong 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 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). *L. mactans* 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 feed on introduced fire ants (*Solenopsis invicta*) (Nyffeler et al. 1988). The natural habitat of *L. variolus* is in xeric to mesic deciduous forests. This species shows a preference for building webs at tall heights in trees (Wang et al. 2018). Its range extends from northern Florida to southeast Canada and as far west as central Oklahoma. Unlike its large-range native relatives, *L. bishopi* is endemic to sand pine scrub habitats in Florida and has a specialized diet, feeding on endemic beetles (Carrel 2001, Carrel and Deyrup 2014). These distinct feeding habitats, combined with varying degrees of sympatry among species, suggest complex roles of both climatic and microhabitat partitioning in facilitating species' coexistence.



**Figure 1.** Distribution maps of A) *Latrodectus geometricus*, B) *L. hesperus*, C) *L. mactans*, D) *L. variolus* and *L. bishopi*. Distributions were estimated based on models from Sadir & Marske (2021) that use the same climatic data as this study.

The niche conservation hypothesis proposes that closely related taxa share more similar niches (Peterson 1999). This hypothesis supposes that speciation occurs in geographic dimensions, and ecological differences evolve later (Peterson 1999, Warren 2008). Although niches of related species may be similar, they are rarely equivalent, and occur on a continuum ranging from identical to more similar than random (Warren et al. 2008). Under niche partitioning, competition drives closely-related species to differentiate how they use resources to limit competition and over time, niches diverge (Graham et al. 2009). Niche partitioning thus allows species to co-occur in the same geographic area by reducing the potential for competitive and antagonistic encounters (Schoener 1974). Previous studies have mapped distributions and observed different habitat preferences of native widows, but the extent to which climatic niche divergence has structured native widows' distributions relative to each other remains uncertain.

How brown widows (*Latrodectus geometricus*) share or partition resources with native species is important for assessing the potential for negative competitive interactions and, ultimately, ecological impacts. Brown widows originated in southern Africa and were introduced to North America in 1935 (Pearson 1936, Garb et al. 2004). They have notably expanded their range since the start of the 21<sup>st</sup> 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). Several factors could potentially give *L. geometricus* competitive advantages over native species. First, life history traits that favor rapid reproduction may give *L. geometricus* a competitive advantage over other widows where they cooccur: 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, the parasitic flies *Pseudogaurax signatus* commonly infest *L. hesperus* egg sacs but not *L. geometricus* (Vetter et al. 2012b). *Latrodectus geometricus* also undergo enemy release from an egg sac parasitoid wasp, *Philolema latroedecti*, in Israel, where field surveys and lab experiments show the parasitoid wasps oviposited longer on native, *L. pallidus*, egg sacs (Mowery et al. 2022). Notably, 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.

We have previously demonstrated that human population density was an important predictor of the North American distribution of brown widows, but not as strong a predictor for native widows (Sadir and Marske 2021), concurring with previous studies that have shown a preference for human-associated habitats in brown widows (Muller 1993, Vetter et al. 2012a 2016). Where diet and habit niche partitioning do not occur, differences in climatic niche may facilitate

geographic partitioning among species. A previous study found that *L. geometricus* favors subtropical climates, and its global climatic niche is best predicted by mean annual temperature and precipitation (Taucare-Rios et al. 2016), which most closely matches the climate *L. mactans* occupies in North America. We also previously found that *L. geometricus* geographically overlaps with *L. hesperus* and *L. mactans* across North America (Sadir and Marske 2021), suggesting the potential for competitive interactions with brown widows to impact native populations in these areas. Although geographic overlap is a useful measurement of co-occurrence, we did not measure climatic niche overlap. 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.

We quantify climatic niche overlap between *L. geometricus*, *L. hesperus*, *L. mactans*, and *L. variolus* in North America to assess the role of climate versus microhabitat niche partitioning in shaping the distributions of North American widows relative to each other, and the potential for negative interactions with brown widows to impact native widow species. To estimate niche divergence, we quantified niche similarity and overlap for each pairwise combination of species in climatic space. Given that brown widows may still be undergoing geographic expansion, with populations only recently detectable in some areas, we leverage a combination of social media, citizen science and museum-based observations of these species to obtain the widest possible distribution of occurrence data.

We hypothesize that native widows will have more strongly partitioned niches—either climate or microhabitat—from each other than they do with *L. geometricus*. Further, we expect to see strong climatic overlap among species with strong partitioning of other aspects of the niche, such as diet or microhabitat, than among those without such partitioning. In contrast, weak climate overlap of species which only partially co-occur, or strong climate overlap among species which do not co-occur, might suggest partitioning of the climatic niche. Finally, if species do not have overlapping climatic niches and do not co-occur, niche differentiation may be due to differences in accessibility to environments rather than climate partitioning. We also hypothesize that niche overlap between the invasive *L. geometricus* and native widows will correspond to the extent of their geographic overlap, as consequences of negative interactions among species have not yet had time to shape species' distributions. Here, the strength of niche overlap suggests greater opportunities for negative interactions to impact native species.

## Materials & Methods

### Data Collection

For this project, we used social media to engage the community to send pictures of *L. geometricus* sightings. Widows are morphologically recognizable and of interest to the public, making them an ideal candidate

for community science. *L. geometricus* has particularly distinguishing features like an orange hourglass marking on their ventral abdomen and a distinctive “spiky” egg sac (Muller 1993). Over a period of two months, we contacted members from Facebook groups (“Spider/Bug Questions with TheBugGirl” and “Spider and Insect Enthusiast”) and Reddit (“r/whatsthisbug” and “r/spiderbro”) and requested submission of photographs of brown widow sightings with locality information. Because widows are venomous, we asked participants to take precautions when photographing specimens. At the end of two months, we retained 25 submissions with sufficient locality data that could be positively identified. Community submissions were regionally biased because most participants in the Facebook groups we contacted are from southern California (Figure 2).

We supplemented these submitted occurrences with 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 (geo-locate.org). We visually verified occurrences that were far outside of previously established ranges (Wang et al. 2018, Schraft et al. 2021) and eliminated points that could not be confirmed. 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*;

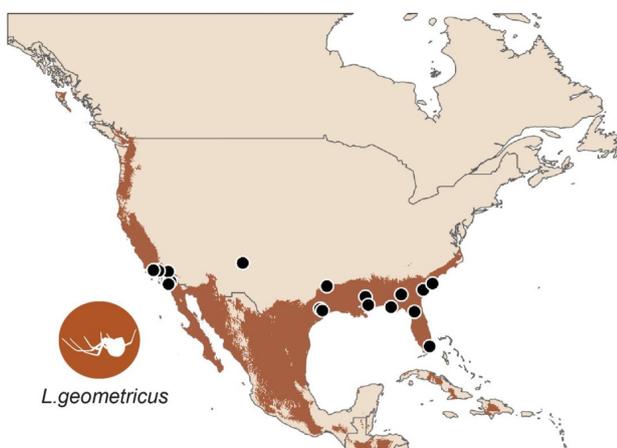
*L. geometricus*/*L. mactans*; *L. geometricus*/*L. variolus*; *L. hesperus*/*L. mactans*; *L. hesperus*/*L. variolus*; *L. mactans*/*L. variolus*. Data, from 19 CHELSA Bioclim variables (Karger et al. 2017), were first obtained from Paleoclim.org (Brown et al. 2018), where they have been rescaled to 2.5 arc-min resolution. 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) within R version 4.0.4. Boosted regression trees is a machine learning 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).

### 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 (Broennimann et al. 2007).

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 Components Analysis (PCA) space, where each cell represents a unique set of environments accessible to each species. Quantifying niche overlap in environmental space (hereafter E-space) rather than geographic space minimizes biases introduced by spatial resolution and corrects occurrence density based on availability of particular environmental conditions within the study region, without assuming equal distribution of habitats (Broennimann et al. 2012). Next, we estimated the niche of each species by projecting occurrence points into E-space and smoothing the response using density kernel smoothing, where more densely populated environments reflect more suitable habitats. The environmental background and estimated niche of both species were 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). 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. Environments that are accessible to one species, but not the other,



**Figure 2.** Confirmed occurrences of *Latrodectus geometricus* collected from community submissions using social media, overlaid on the geographic range of the species modeled in Sadir and Marske (2021).

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

Species Comparison	Selected Variables
<i>L. geometricus</i> / <i>L. hesperus</i>	Mean diurnal range (Bio2), minimum temperature of coldest month (Bio6), precipitation of warmest quarter (Bio18), mean temperature of the coldest quarter (Bio11)
<i>L. geometricus</i> / <i>L. mactans</i>	Annual mean temperature (Bio1), mean diurnal range (Bio2), minimum temperature of coldest month (Bio6), precipitation of warmest quarter (Bio18)
<i>L. geometricus</i> / <i>L. variolus</i>	Minimum temperature of coldest month (Bio6), mean temperature of warmest quarter (Bio10), mean temperature of the coldest quarter (Bio11), precipitation of the driest month (Bio14), precipitation seasonality (Bio15), precipitation of warmest quarter (Bio18)
<i>L. hesperus</i> / <i>L. mactans</i>	Annual mean temperature (Bio1), mean diurnal range (Bio2), precipitation of warmest quarter (Bio18)
<i>L. hesperus</i> / <i>L. variolus</i>	Mean diurnal range (Bio2), mean temperature of warmest quarter (Bio10), precipitation seasonality (Bio15), precipitation of warmest quarter (Bio18)
<i>L. mactans</i> / <i>L. variolus</i>	Annual mean temperature (Bio1), minimum temperature of coldest month (Bio6), precipitation of the driest month (Bio14), precipitation seasonality (Bio15)

are non-analogous E-space. 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. For both tests, niche similarity (the degree of niche overlap) was measured using Schoener's D similarity index (Schoener 1968), which ranges from 0 (no overlap) to 1 (complete overlap).

Niches may be similar without being equivalent (i.e., no statistical difference in the E-space they contain). For each test (NOT and NDT), we also 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 the 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, which 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 each comparison) 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 the other species (Species 2) and the randomly sampled niche of 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).

#### 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 (Brown and Carnaval 2019). 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 (Brown and Carnaval 2019). 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 (Brown and Carnaval 2019).

## Results

Consistent with our predictions for the invasive brown widow, we found that *L. geometricus* had greater niche overlap with native species than the native species did with each other, apart from *L. mactans* and *L. variolus* (Table 2). Niche overlap, measured using the 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*, and *L. hesperus*/*L. variolus*, showed low overlap (0.005, 0.047, and 0.004, respectively). We also ran two tests on each pairwise comparison: Niche Overlap Test (NOT) and the Niche Divergence Test (NDT). For each test, we measured niche equivalency (equivalency statistic) and the power of those equivalency models (background statistic) to evaluate the statistical significance of niche similarity. The NOT measures similarity between the niches and the NDT evaluates the likelihood of the result being a signal of true niche divergence, or simply due to differences in access to environments. 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).

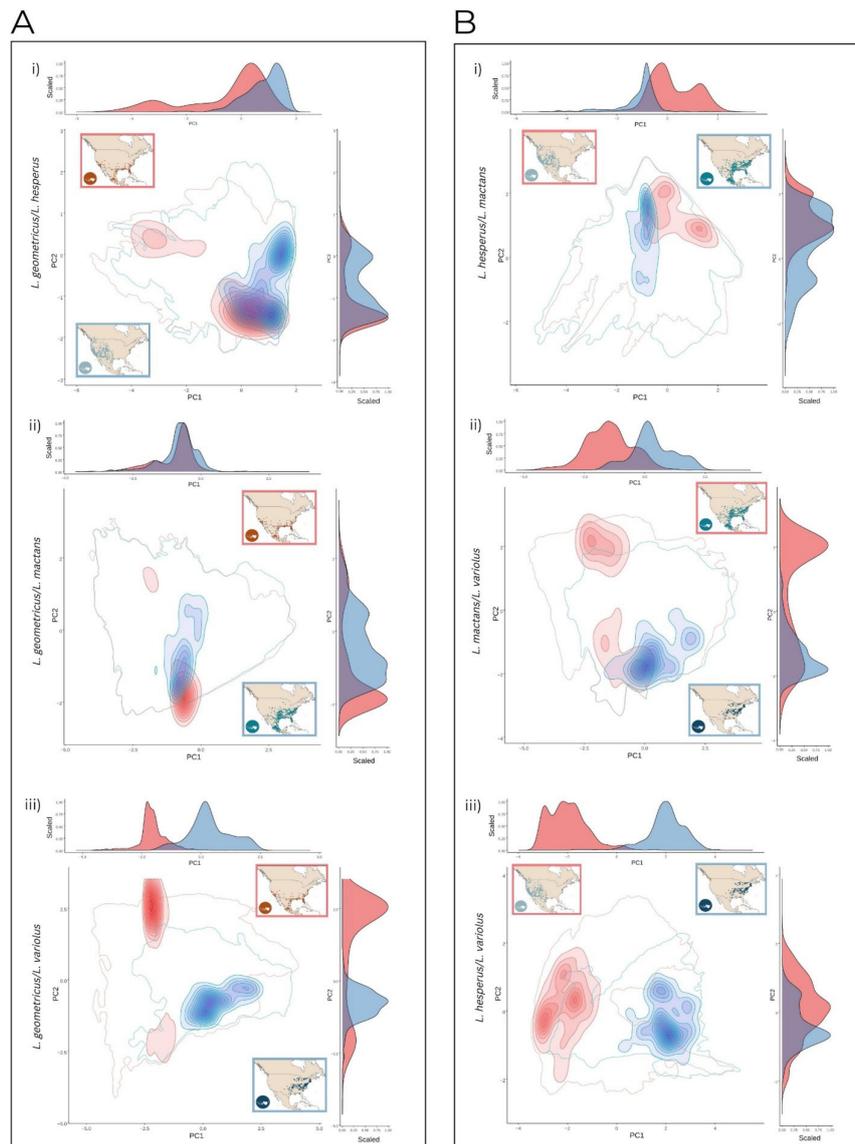
Overlap maps represent species' niches as kernel density isopleths, where the densest centroids characterize the most suitable environments for survival. Among the native species, niches of *L. hesperus* and *L. variolus* do not appear to overlap at all, and only the margin of *L. mactans*' niche overlaps with that of *L. hesperus* (Figure 3). 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 3). Native species generally share less analogous E-space and less overlap than they do with *L. geometricus*.

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 3). 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. Most of the niche of *L. geometricus* lies within the niche of *L. hesperus* (Figure 3). 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 3).

Niche truncation was generally high across all species, except for *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

**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 of *Latrodectus* species within the Niche Overlap Test and the Niche Differentiation Test. \* 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)	<i>L. geometricus</i> / <i>L. hesperus</i>	0.232	0.242	0.002*	0.429	0.353
	<i>L. geometricus</i> / <i>L. mactans</i>	0.467	0.42	0.002*	0.046*	0.234
	<i>L. geometricus</i> / <i>L. variolus</i>	0.005	0.08	0.002*	0.769	0.289
	<i>L. hesperus</i> / <i>L. mactans</i>	0.047	0.047	0.002*	0.601	0.625
	<i>L. hesperus</i> / <i>L. variolus</i>	0.004	0.035	0.002*	0.86	0.186
	<i>L. mactans</i> / <i>L. variolus</i>	0.207	0.274	1	0.505	0.297
Niche Divergence Test (NDT)	<i>L. geometricus</i> / <i>L. hesperus</i>	0.191	0.201	0.002*	0.473	0.461
	<i>L. geometricus</i> / <i>L. mactans</i>	0.467	0.482	0.002*	0.026*	0.17
	<i>L. geometricus</i> / <i>L. variolus</i>	0.005	0.082	0.002*	0.689	0.23
	<i>L. hesperus</i> / <i>L. mactans</i>	0.047	0.048	0.002*	0.593	0.537
	<i>L. hesperus</i> / <i>L. variolus</i>	0.004	0.035	0.002*	0.984	0.214
	<i>L. mactans</i> / <i>L. variolus</i>	0.207	0.274	1	0.509	0.349



**Figure 3.** Niche overlap plots between invasive and native species (A) and among native species of *Latrodectus* (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.

*Latrodectus geometricus* was 0.32, which is between moderate and high.

Variable selection, using bootstrap regression trees, shows similar climatic variables shared between invasive/native and native/native interactions (Table 1). *Latrodectus hesperus* shows the greatest difference in variable selection between invasive and native niche models. The most common variable, present in 5/6 comparisons, was precipitation of the warmest quarter (Bio18). Also common, present in 4/6 comparisons, were mean diurnal range (Bio2) and minimum temperature of the coldest month (Bio6).

## Discussion

North American widow spiders present an interesting 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 the invasive *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* has greater niche overlap with native species than most native species do with each other, apart from *L. variolus*.

Over time, repeated competitive interactions can structure species' geographic distributions (Bull 1991, Kirkpatrick and Barton 1997). However, co-occurrence can be facilitated by partitioning of microhabitats or resources (Schoener 1974), reducing the opportunity for competitive interactions among sympatric populations. The most closely related widows in this study, *L. hesperus* and *L. mactans*, have expansive geographic overlap, suggesting they co-occur across much of their ranges. 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. One cause for this pattern may be niche partitioning over time allowing these species to co-exist. The models also showed the realized niche of both species is not an accurate representation of their fundamental niche, suggesting these species may be blocking each other from continuing to expand their range into potentially suitable environments, so the estimated niche is not in equilibrium. We found *L. variolus* and *L. mactans*, the two eastern widows, have significantly overlapping climatic niches as well as overlapping geographic ranges. It is also possible that co-occurrence is facilitated by some factor other than climate, such as differences in diet or microhabitats. *Latrodectus variolus* also prefers building webs at taller heights, which may mediate competitive interactions in sympatric populations (Lamoral 1968, Wang et al. 2018). *L. variolus* and *L. hesperus*, which are located in eastern and western North America, respectively, do not have overlapping niches and co-occur to only a limited extent around eastern Oklahoma and Texas, which suggests niche differentiation may be due to differences in accessible environments. The division between their geographic ranges also reflects a biogeographic precipitation barrier that divides the east and west of North America. This is also reflected in their overlap plots that show little analogous E-space (Figure 3).

Unlike native species, for which histories of biotic interactions have potentially shaped their climatic niches and geographic distributions, *L. geometricus* are rapidly expanding their range and may present a risk to native widows with which they experience niche overlap. *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 those of *L. mactans* and *L. hesperus*, two species that share significant parts of its current distribution (Sadir & Marske 2021). Interestingly, the

most important variables for predicting niche overlap between species were similar between invasive/native and native/native species interactions (Table 1). However, for *L. hesperus*, minimum temperature of the coldest month (Bio6) and mean precipitation of the coldest quarter (Bio11) were two variables that were predictive of niche overlap with *L. geometricus*, but not predictive for overlap with native congeners. The novelty of competing for climatic space that was previously unchallenged, is a potential risk for *L. hesperus*.

Relatively recent range expansion of *L. geometricus* may explain its co-occurrence with native widows despite niche overlap. If competition is occurring among these large-ranged species, its impacts at large spatial scales may not yet be obvious based on contemporary distributions despite potential impacts occurring at more localized scales (Vilà et al. 2011). In Colombia, *L. geometricus* displaced populations of *L. curacaviensis* in the Tatacoa desert (Rueda 2018). In California, urban populations of *L. hesperus* are decreasing in population size, possibly as a result of competition with a growing population of *L. geometricus* (Vetter et al. 2012a). During encounters on webs, *L. hesperus* displays signaling behaviors to ward off intruders and avoid energetically costly and potentially dangerous aggressive interactions, which are ignored by *L. geometricus*, resulting in violent escalations (Jones et al. 2020). However, during encounters under lab conditions, *L. geometricus* never successfully usurped *L. hesperus* webs (Jones et al. 2020). Given the chance of negative encounters, there is possible risk of ecological impact in the long-term, depending on synergistic factors like colonization/propagule pressure, biotic resistance, or enemy release (Ricciardi et al. 2013). However, *L. geometricus*' preference for urban habitats may limit potential impact on non-urban widow populations: differences in diet or microhabitats, such as an apparent preference for human-made structures as web-building sites (Vetter et al. 2016), might allow *L. geometricus* to co-occur with *L. hesperus* and *L. mactans* despite climatic niche overlap. Our previous work has also shown that *L. geometricus* prefers urban environments over non-urban environments, in contrast to their native congeners (Sadir and Marske 2021). Given the dietary plasticity *L. mactans* displays in urban and agricultural populations, where it feeds 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.

Niche dynamics of invasive species in their introduced range are rarely in equilibrium and can be unpredictable as they shift, underfill, 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 compared to most spider genera, this is the first study to our knowledge to evaluate potential competitive interactions between congeners on a continental scale. We found that niche dynamics and impacts of invasion on species' 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 the ecological impacts of *L. geometricus* invasion.

Biological invasions are a threat to biodiversity and local economies (Diagne et al. 2021), and early response is crucial for management efforts (Reaser et al. 2020). Traditional data from repositories are highly valuable because they are curated, verified, and more robustly sampled. However, in the case of recent introductions of recognizable species, like the brown widow, community scientists can deliver reliable data at speeds that are previously unmatched. In a two-month period requesting community submissions on social media, we received energetic engagement and retained dozens of photographically confirmed occurrence points, across eight states. Using these data, we were able to discern how climatic niche partitioning may shape the geographic extent of sympatry among widows in North America. In addition to being useful for communicating risk, social media can be leveraged as a tool for expanding surveillance efforts of species that can be identified by photograph. Information collected by the public can be used to augment assessments of species' potential impacts on ecological communities.

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## Data Availability Statement

The original data presented in the study are the same as Sadir and Marske (2021), R scripts used for

analyses are included at <https://github.com/ecosadir/brownwidow>, and further inquiries can be directed to the corresponding author/s.

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