A Decade of Dominance? The Impact of the Presence of *Trichonephila clavata* (Araneae: Araneidae) on Araneid Spider Observations and Community Science Data in the Eastern United States¹

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Abstract Trichonephila clavata L. Koch (Araneae: Araneidae), the Joro° spider, was first observed in Georgia in 2014. This large, colorful spider has received nationwide attention for its potential to disperse through the United States. Community scientists have the potential to contribute important information to spider conservation biologists, and public captivation with this spider might lead to more spider observations by community scientists. The objectives of this study were to determine whether (1) T. clavata was the dominant observed araneid spider, (2) the presence of T. clavata inspired more community scientists to post observations of spiders and other araneids, and (3) the observed araneid communities differed in states where T. clavata was present and absent. Although T. clavata was the most-observed araneid spider in Georgia according to iNaturalist observations, its presence did not lead to more spider and araneid iNaturalist observations in states with T. clavata than those without, but Argiope aurantia Lucas and Trichonephila clavipes L., the other two most-observed spiders, were observed more often in states with T. clavata. Araneid communities recorded to the Global Biodiversity Information Facility did not statistically differ in Georgia, North Carolina, South Carolina, and Tennessee before and after its first observations in those states. Further observations by community scientists will only help professional scientists, and professional scientists are encouraged to communicate with community scientists about the importance of repeated submissions of observations of all spiders.

Key Words citizen science, exotic species, Global Biodiversity Information Facility, Joro° spider, iNaturalist

The first North American reports of *Trichonephila clavata* L. Koch (Araneae: Araneidae), the Joro[°] spider, were in Georgia, USA, in Barrow, Jackson, and Madison counties in 2014 (Hoebeke et al. 2015; E.C.L. unpubl.). *Trichonephila clavata* is native to eastern Asia, found in at least 10 Asian countries (Chuang et al. 2023, Giulian et al. 2024) and was potentially introduced into Georgia in shipping containers. Davis and Frick (2022) gained considerable national attention (e.g., Hataway 2022, Romo 2022) by suggesting that *T. clavata* could survive low temperatures and could possibly establish in North America at latitudes up to 45°N (i.e., the New England area).

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Exotic species are considered one of the most important threats to global biodiversity (Bellard et al. 2016, Simberloff et al. 2013). Although the public might view exotic spiders such as T. clavata primarily as a venomous hazard occupying their outdoor spaces, either leading to or due to numerous articles headlining potential bites (e.g., Frau 2024, Loehrke 2024), there is also the potential for this exotic species to compete with native araneids and other orb-weavers. Previous studies have found interspecific competition among other araneid species causes a decline in survival and population growth (Horton and Wise 1983), but the negative effects of competing species can be diminished by niche partitioning between long-sympatric species (Brown 1981, Richardson and Hanks 2009, Spiller 1986). This niche partitioning might be less likely in the case of exotic and native araneid species because they occupied similar niches previously when their populations were allopatric. Displacement of a native orb-weaving spider by an exotic competitor is perhaps best known in the case of the brown widow, Latrodectus geometricus Koch, which has displaced other Latrodectus spp. in North America (Coticchio et al. 2023, Vetter et al. 2012). Because T. clavata is not aggressive like L. geometricus (Davis and Anerao 2023), any displacement of native araneids is more likely to be due to competition for food and habitat resources.

Trichonephila clavata has now been observed in North America for a decade and captivated arachnid enthusiasts in the eastern United States. It is a large, conspicuously colored green, yellow, red, and black orb-weaver spider that produces golden webs >1 m in diameter (E.C.L. unpubl.). These striking visual features cause *T. clavata* to be frequently observed by curious community scientists, who might be inclined to photograph these spiders to share with friends and family as well as entomologists and arachnologists. Thus, the presence of *T. clavata* might be beneficial for public awareness of spiders. Community scientists who encounter *T. clavata* might be more likely to search for information on this species and, in doing so, collect information on other araneid spiders. Increased public awareness might increase public buy-in of activities that protect native spiders such as habitat protection and counteract the negative spider misinformation that threatens their populations (Mammola et al. 2022). Conversely, the attention *T. clavata* receives might also increase indiscriminate killings by citizens, particularly when citizens read headlines referring to an "invasion" or "infestation."

Entomologists and arachnologists in the eastern United States have fielded numerous questions from the public about *T. clavata* and anecdotal reports of fewer spiders since the introduction of *T. clavata* (E.C.L. unpubl.); however, there are few analyses of how community scientist observations have changed since the introduction of this spider (Deitsch et al. 2024). Herein, community science data were used to determine whether the presence of *T. clavata* influenced observations of resident araneid communities in the eastern United States. Eight states near the locus of entry of *T. clavata* in northern Georgia were selected. The level of state was selected instead of county because sparse records from rural counties made quantitative studies difficult. The first objective was to determine whether the number of *T. clavata*. This objective was met by comparing iNaturalist observations per observer from 2014 to 2023, time interval in states with and without *T. clavata*. The second objective was to determine whether *T. clavata* was the dominant araneid species observed by

community scientists in states with this species and whether its presence affected the relative abundance of potential interspecific competitors. The final objective was to determine whether araneid communities observed by citizen scientists differed before and after colonization by *T. clavata*. This objective was met using a multivariate analysis to statistically compare communities. Community science data, although not systematic (Kosmala et al. 2016, Ward 2014), can contribute to the understanding of *T. clavata*'s impacts on native araneid diversity (Pocock et al. 2024).

Materials and Methods

Data collection. Araneid spider observations from the iNaturalist (www.inaturalist. org) and Global Biodiversity Information Facility (GBIF; www.gBIF.org) databases were downloaded in October 2024. Observations were collected from four states with at least 25 confirmed *T. clavata* iNaturalist records from 2014 to 2023: Georgia, North Carolina, South Carolina, and Tennessee. As of October 2024, iNaturalist observations of *T. clavata* had also been recorded in Maryland, Massachusetts, Oklahoma, Pennsylvania, and West Virgina, but these states were not investigated. Four states with no *T. clavata* records, Alabama, Kentucky, Ohio, and Virginia, were selected for comparisons. Alabama, Kentucky, and Virginia were selected based on their proximity to *T. clavata*'s introduction point in North Georgia (Hoebeke et al. 2015, E.C.L. pers. obs.), whereas Ohio was selected because it was the closest state in the eastern temperate ecoregion with similar human population size to Georgia (World Population Review 2025).

Research-grade, verifiable iNaturalist observations were filtered by state and year. To verify the accuracy of these records, a subsample of \sim 50 *Trichonephila* observations was visually validated by the author. Filtered iNaturalist records were collected to record abundance for five groups: (1) all spiders, (2) all araneids, (3) *T. clavata*, (4) *Trichonephila clavipes* L., and (5) *Argiope aurantia* Lucas. These latter two species were selected as focal established species due to their abundance, similar body sizes, and similar ecological niches (Chuang et al. 2023). Relative abundance of araneids in a given year was calculated by dividing the total number of araneid observations by the total number of spider observations. The relative abundances of spiders identified as *T. clavata*, *T. clavata*, *T. clavata*, *A. aurantia* were similarly calculated, both relative to araneid abundance and all-spider abundance. The number of observers was also recorded for all spiders and araneids to obtain sampling efforts. Sampling efforts were standardized as the observations per observer to account for state population differences.

Relative abundance and sampling efforts. A series of two-way analyses of variance (ANOVAs) were performed to determine whether relative abundances and sampling efforts varied across time and between states with and without *T. clavata*. Year was treated as a fixed factor; year was not treated as a repeated measure because different observers were expected to participate each year. For the second factor, states were combined into two groups based on the presence or absence of *T. clavata* during the study interval. In the first series of ANOVAs, relative abundances of araneids and spiders identified as *T. clavipes* and *A. aurantia* served as dependent variables. For spiders identified as *T. clavipes* and *A. aurantia*, relative abundances among all araneids and all spiders were calculated. In the second series of ANOVAs, sampling effort for spiders (spiders/observer) and araneids (araneids/observer) were compared as the dependent variables. Interaction terms were included in each model;

if significant, the interaction term would indicate annual differences in sampling effort varies between states with and without *T. clavata*. Relative abundances were arcsine transformed to meet the assumptions of parametric statistics. All analyses were performed using the Univariate procedure in SPSS v.29.0 (IBM, Armonk, NY).

Only GBIF records were used for all analyses of the Araneidae communities. These data were filtered to include only the Araneidae for two reasons: (1) *T. clav-ata* belongs to this family and closer relatives are expected to exhibit greater competition (Violle et al. 2011); and (2) araneid spiders, which are larger and have conspicuous webs, are frequently reported by community observers, constituting 24–46% of all iNaturalist spider observations in the states investigated.

Araneid communities. Four measures of diversity, species richness, Shannon index, Simpson index, and Pielou's evenness were estimated using the DIVERSE procedure in PRIMER7 (PRIMER-e, Inc., Albany, Aukland, New Zealand). The Shannon index, which accounts for rare taxa, was expected to reflect changes in abundance of less common taxa, whereas the Simpson index, a measure of dominance (Nagendra 2002), was anticipated to capture the relative prevalence of dominant taxa such as Argiope (the most commonly observed genus) and Trichonephila. Pielou's evenness, a measure of relative abundance of all species in a community, was expected to decrease if one or a few species became disproportionately dominant. Linear regressions were performed to assess trends in each diversity measure over time by using the linear regression procedure in SPSS v.29 (IBM). For states with T. clavata (Georgia, North Carolina, South Carolina, and Tennessee), a series of general linear models (GLMs) were performed to compare the four diversity measures between years with and without T. clavata. The total number of observations each year was included as a covariate to control for sampling effort, which can vary both from year to year and among states. The univariate general linear models procedure in SPSS v.29 was used to perform these analyses.

Community composition was further analyzed using GBIF araneid abundance data, each consisting of nonmetric dimensional scaling (nMDS), analysis of similarity (ANOSIM), and similarity percentage (SIMPER). nMDS, an ordination method, was used to observe community differences based on the abundances of 70+ araneid species. Each point in a two-dimensional nMDS plot represented the observed araneid community in a state during a specific year. ANOSIM accompanied the nMDS as a test of significance, generating R-statistic (0–1) and accompanying *P*-value to identify whether community composition differed based on the presence of *T. clavata* (Clarke and Gorley 2015). If any two communities differed in composition, SIMPER identified the percent of differences attributed to each species in the community. These analyses were performed separately with *T. clavata* numbers included and excluded, with the latter to identify whether the community consisting of all araneids other than *T. clavata* was affected by its presence. nMDS, ANOSIM, and SIMPER analyses were all conducted with PRIMER7.

Results

In total, 179,562 filtered iNaturalist spider observations was recorded in the eight states during the 2014–2023 interval by 71,640 observers, with 61,786 (\sim 34.4%) observations of Araneidae.

The numbers of iNaturalist observations of both all spiders (P < 0.001) and araneids (P < 0.001) increased substantially during the 2014–2023 interval. The rate of increase was slower for araneids ($\beta = 216.5$) than all spiders ($\beta = 656.2$), suggesting that observations of other spider families were contributing to the increase in spider observations. The number of spider and araneid observations, including those identified as *T. clavata*, observed declined substantially in Georgia in 2023, which was not seen in the other seven states. The recorded observations of spiders identified as *T. clavata* (P = 0.007) and *T. clavipes* (P < 0.001, including Alabama) increased, and *A. aurantia* (P < 0.001) observations increased when all eight states were combined during the interval as well. When all eight states were considered, the number of *A. aurantia* observations increased the fastest ($\beta = 52.4$) annually compared with those of the other species.

Relative abundance. Araneids were at least 25% of spider observation in all states in all years except for Alabama in 2019 (24%), and usually much higher. The relative abundance of araneids in spider observations did not differ in states with and without *T. clavata* (F = 1.46; df = 1, 60; P = 0.23), and the interaction term was not significant (F = 1.69; df = 9, 60; P = 0.11). There was no trend in araneid relative abundance of araneids was highest in 2014–2023 interval; however, the relative abundance of araneids was highest in 2014 and lowest in 2022 (Tukey's honestly significant difference test, P = 0.03). The relative abundance of araneids exceeded 50% of all spider observations in 2014 in both Ohio and North Carolina.

Overall, the great majority of observations of spiders identified as *T. clavata* were made in Georgia (87.8%), where *T. clavata* was the dominant spider species (8.7% of all spiders, 36.1% of araneids) over the 10-yr interval (Fig. 1A). The relative abundance of spiders identified as *T. clavata* in both spider and araneid observations increased every year following its first recorded observation in all four states (Fig. 1A). By 2023, spiders identified as *T. clavata* represented >20% of all spider observations in Georgia and >80% of araneid observations.

Trichonephila clavipes was also found in all of the investigated states other than Ohio, and spiders identified as T. clavipes were observed more often than T. clavata in all states other than Georgia. For example, the relative abundance of spiders identified as T. clavipes averaged 40% of all araneids observed in South Carolina. Linear regression showed that relative abundance of spiders identified as T. clavipes among all observed spiders decreased in Georgia during the 10-yr interval ($\beta = 0.007$, P =0.005) as relative abundance of spiders identified as T. clavata among all observed spiders increased in Georgia ($\beta = 0.03$, P < 0.001); the two relative abundances were also negatively correlated according to nonparametric Spearman's correlation coefficients ($\rho = -0.86$, P = 0.001). Relative abundances among araneids of these two species were not correlated ($\rho = -0.5$, P = 0.21). The relative abundance of spiders identified as T. clavipes did not vary by year among all observed spiders (F = 0.15; df = 9, 37; P = 0.99) or among observed araneids (F = 0.41; df = 9, 37; P = 0.93). Relative abundance of spiders identified as T. clavipes among all spiders (F = 0.41; df = 9, 37; P = 0.93) was higher in states with T. clavata present. Neither of the interaction terms were significant for relative abundance (P > 0.8 in both cases).

Argiope aurantia was the most-observed spider in all states except Georgia (9.4% of all spiders, 26.9% of araneids) and the most-observed spider when all eight states were considered (9.3% of all spiders, 26.9% of araneids; Fig. 1B). The

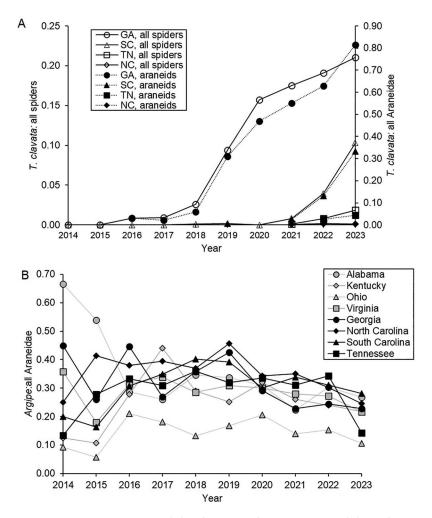


Fig. 1. Relative abundance of (A) *Trichonephila clavata* and (B) *Argiope aurantia* in research-grade iNaturalist observations from 2014 to 2023. In (A), solid lines show trends in relative abundance within all spiders and dashed lines show trends in relative abundance within its family Araneidae. In (B), black symbols and lines represent four states with *T. clavata* and gray symbols and lines represent four states without *T. clavata*.

relative abundance of *A. aurantia* in iNaturalist observations did not increase or decline overall during the 10-yr interval (F = 1.42; df = 9, 60; P = 0.20). The relative abundance of *A. aurantia* among all spiders (F = 7.17; df = 1, 60; P = 0.01) and araneids (F = 5.44; df = 1, 60; P = 0.02; Fig. 1B) was higher in the four states with *T. clavata* observations; however, this is likely due to its low observed relative abundance in Ohio (Fig. 1B).

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Sampling efforts. iNaturalist observers were not enticed to observe more spiders in states in which *T. clavata* was present. The spider sampling effort (spiders/observer) was lower in the four states with *T. clavata* than in the four states without this species (F = 7.001; df = 1, 60; P = 0.010); however, the interaction with year was not significant (F = 0.666; df = 9, 60; P = 0.736). The araneid sampling effort (araneids/observer) did not differ between these two groups of states (F = 1.831; df = 1, 60; P = 0.181), and the interaction with year was not significant (F = 0.556; df = 9, 60; P = 0.827).

Araneid communities. In total, 30,844 GBIF observations of 72 araneid species (including *T. clavata*) from 26 genera was collected from Georgia, North Carolina, South Carolina, and Tennessee. Overall, *A. aurantia* was the most often-observed spider (n = 6,760), followed by *T. clavipes* (n = 3,607), *T. clavata* (n = 3,264), and *Araneus marmoreus* Clerck (n = 2,507). Twenty-two species were observed from the genus *Araneus* alone.

There was no difference in observed araneid communities in the four states with *T. clavata* before and after according to ANOSIM (R = 0.046, P = 0.125). According to the nMDS cluster plot, makeup of all observed araneid communities but one (Tennessee in 2024) was at least 50% similar, and clusters with at least 75% similarity included years both before and after *T. clavata* was present (Fig. 2).

When controlling for the number of observations and including T. clavata presence, only species richness (F = 4.68; df = 1, 37; P = 0.037) differed significantly before and after the establishment of T. clavata. Species richness was higher after the establishment (Table 1), likely because more observations were submitted in more recent years. The covariate of number of observations was significant for species richness (F = 40.60; df = 1, 37; P < 0.001) and Pielou's evenness (F = 10.44; df = 1, 37; P = 100.003), but not for Shannon index (F = 2.12; df = 1, 37; P = 0.15) or Simpson index (F = 1.03; df = 1, 37; P = 0.32). When this nonsignificant covariate was removed from the GLM for the two measures of species diversity, Shannon index was higher after T. clavata establishment (F = 4.93, df = 1, 39; P = 0.03) and Simpson index did not differ (F = 0.57; df = 1, 39; P = 0.45). When number of observations was removed from the GLM, Pielou's evenness was lower once T. clavata was present (F = 45.61, df = 1, 38; P < 0.0001). Diversity indices could not be statistically compared within a state and varied inconsistently before and after T. clavata establishment from state to state (Table 1). Georgia and South Carolina had lower values of Shannon index, Simpson index, and Pielou's evenness than nearby states (Table 1).

Discussion

Trichonephila clavata is a large, striking, and colorful orb-weaver that receives considerable attention from the media and public. There is much potential that community observers might be stimulated to search for and share photographs of this spider. Community scientists searching for *T. clavata* might also locate and observe other araneids, increasing public support for conservation of these spiders (Cardoso et al. 2011). This study provides mixed evidence that community science observations of araneids were influenced by the presence of *T. clavata*. Observations of all spiders, all araneids, the native *A. aurantia*, and the naturalized congener *T. clavipes* all increased during the 10-yr interval in all states studied but

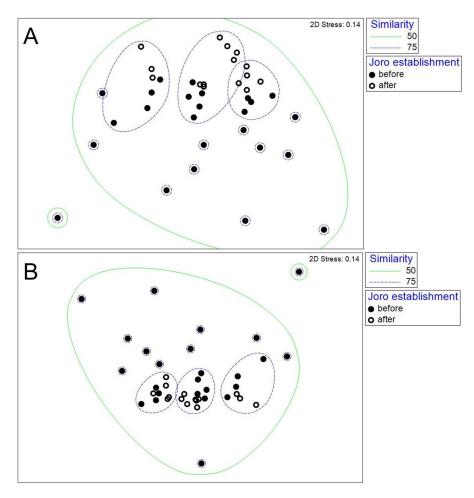


Fig. 2. Nonmetric dimensional scaling scatterplots showing araneid communities in Georgia, North Carolina, South Carolina, and Tennessee as recorded by community scientists 2014–2023. (A) All araneid species, including *T. clavata*. (B) All araneid species other than *T. clavata*.

Georgia; observations in Georgia declined in 2023. Despite this increase, the presence of *T. clavata* did not impact the number of observations or sampling effort. Furthermore, the presence of *T. clavata* did not significantly affect observed araneid species diversity or community makeup. Conversely, the observed relative abundance of spiders identified as *T. clavipes* did decrease annually in Georgia. Moreover, araneid species diversity was lower in Georgia and South Carolina, the states with the most observed *T. clavata*. Last, *T. clavata* was the dominant spider observed in Georgia.

A general trend for increasing spider observations was seen in all states. According to iNaturalist's user data, the number of observations of all taxa increased

Table 1. Combined values for four diversity indices of araneid spider com-
munities in eight eastern U.S. states. Values before and after
Trichonephila clavata observations are shown for Georgia, North
Carolina, South Carolina, and Tennessee.

State	Species Richness	Shannon Index	Simpson Index	Pielou's Evenness
Georgia	25	1.671	0.6994	0.5190
2014–2015	9	1.931	0.8349	0.8789
2016–2023	23	1.955	0.7968	0.6226
North Carolina	25	1.766	0.7102	0.5824
2014–2020	22	2.039	0.8081	0.6597
2021–2023	21	2.174	0.8515	0.7142
South Carolina	24	1.673	0.7012	0.5264
2014–2020	21	2.032	0.8249	0.6673
2021–2023	21	1.906	0.7868	0.626
Tennessee	22	1.8	0.7139	0.5824
2014–2020	20	2.103	0.8317	0.702
2021–2023	20	2.229	0.8597	0.744
Alabama	26	1.796	0.7134	0.5512
Kentucky	20	1.685	0.7044	0.5625
Ohio	20	1.723	0.7071	0.5751
Virginia	23	1.777	0.7116	0.5666

significantly in 2018 and has been increasing annually (Loarie 2023). If this trend of increasing spider observations continues, especially the trend of more observers and identifiers, then the increased attention is likely to benefit spider communities by building support for conservation practices. An exception was noted in Georgia. In Georgia, where *T. clavata* has been observed for the longest, the number of spider and araneid observations, observers, identifiers, and sampling effort all declined in 2023 compared with 2022; for example, the *T. clavipes* observations declined by >50%. There are several possible explanations for this. First, Georgia observers might have been less inclined to photograph araneids by 2023 due to the ubiquity of *T. clavata* and lack of novelty observing it. For example, potential Georgia community scientists could have assumed the presence of *T. clavata* at a given site had already been exhaustively documented (Bowler et al. 2022). Second, potential Georgia community scientists might have stopped searching for araneids under the assumption *T. clavata* had excluded most other species. And third, some community scientists in Georgia might have decided by 2023 to post their *T. clavata* observations

to alternate platforms such as Joro Watch (jorowatch.org), which was created in 2022 and promoted by University of Georgia Cooperative Extension Service. Continued monitoring of araneid communities might be particularly meaningful in Georgia, where *T. clavata* is the dominant species.

Insights about the effects of T. clavata on native spider observations can be gained from comparing two other dominant species, A. aurantia and T. clavipes. Both A. aurantia and T. clavipes are among the largest araneids in the eastern United States and build conspicuous webs in habitats where they are likely to be seen by community observers (Enders 1973, Moore 1977). Both species may potentially compete with T. clavata (Chuang et al. 2023). Argiope aurantia was the most-often observed araneid in each state except Georgia, which was dominated by spiders identified as T. clavata. Argiope aurantia is native to North America and is a large, easily identifiable orb-weaver with eye-catching stabilimenta in its webs (Blackledge 1997); thus, many observers might have already been familiar with this species. No decline in observed A. aurantia relative abundance occurred in the four states with T. clavata present. The observed relative abundance of spiders identified as T. clavipes was negatively correlated with that of spiders identified as T. clavata in Georgia. This correlation could have multiple causes. First, although they largely niche partition both by habitat type and active season (Davis and Frick 2022), it is possible these two species compete for web-building sites or prey where both are present. Trichonephila species share web-building strategies such as debris decorations that Argiope spp. do not (Hénaut et al. 2010, Walter 2024), further suggesting that T. clavata and T. clavipes might compete more with each other than with other araneid genera where they geographically overlap. Experimental or observational studies can determine the intensity of potential competition. Second, T. clavipes is the most likely species a community scientist identifier could confuse with T. clavata; in Georgia, where both are densely populated, early-season misidentifications could affect the records for both species. Although it is outside the scope of this study, future research on the rate of misidentifications is recommended.

Conclusions drawn from community scientist data must be considered with caution. Community scientists tend to be concentrated in urban areas and biased toward large, charismatic species (Deitsch et al. 2024, Ward 2014) or specialize in a single taxonomic group (Di Cecco et al. 2021). A recent study similar to this one found that *T. clavata* is frequently observed on iNaturalist due to its size and coloration, especially by inexperienced users (Deitsch et al. 2024). Although *T. clavata* seems to be anthropophilic to some extent (Davis et al. 2024), community scientist data are likely lacking in regard to its presence and potential ecological impacts in rural areas. In this study, county-level observations could not be compared because of a lack of observations in counties without major urban areas. Community scientists might also upload a frequently observed species only once to build a personal species list, which limits the ability to track species abundance and community makeup over time (Di Cecco et al. 2021). More information about *T. clavata*'s impacts on araneid communities can be revealed as more observations are made and repeated observations of *T. clavata* and other araneids are recommended.

This study found minimal effects of *T. clavata* on observed araneid community makeup; however, empirical research is needed to identify realized effects on araneid

communities. A recent field survey by Nelson et al. (2023) in Georgia found that *T. clavata* was the dominant orb weaver at several field sites and that orb weaver species diversity was lower closer to the *T. clavata* point of introduction. The decline in species diversity observed by Nelson et al. (2023) is likely due to *T. clavata* outcompeting other species due to its abundance and dietary niche overlap. Continuing field surveys during the next decades, as *T. clavata* continues to establish itself and potentially naturalizes, will be vital to understanding its ecological impacts. Removal experiments are the standard method to determine whether an organism is beneficial, harmful, or neither to its ecosystem and interaction strengths within the community (Díaz et al. 2003). Although *T. clavata* might prove difficult to remove due to their sheer abundance and ability to disperse back into ecosystems in both urban environments and natural, forested habitats are recommended. These field surveys and experiments can be used to validate data from community scientists.

In conclusion, professional and community scientists alike are in the preliminary stages of discovering the ecological impacts of *T. clavata* on araneid communities in the eastern United States. Data from community scientists is beneficial for initiating field research and identifying conservation needs. Entomologists, arachnologists, and conservation biologists are encouraged to communicate with community scientists about best practices for observing *T. clavata* and other araneids to better inform ecological research. These best practices include repeated observations by both experienced and newcomer community scientists in a variety of habitats, especially rural habitats both near the introduction point in Georgia and at the edges of *T. clavata*'s expanding range.

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