



# Scale insects contribute to spider conservation in urban trees and shrubs

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## Abstract

Urbanization filters arthropod communities and selects for species tolerant of urban conditions. Spiders are key generalist predators in urban ecosystems, but certain spider families are rare in cities compared to rural areas. The unique arthropod communities found in different tree species likely affects their ability to conserve spiders by providing different prey resources. If arthropods disperse from trees to plants growing below trees, the conservation benefits of the arthropod communities found in trees may also extend to plants growing beneath them. Certain urban tree species can host high densities of scale-insects and other arthropods that may provide important prey resources for spiders. To assess the conservation value of different arthropod communities in urban trees, we collected spiders from scale-infested and scale-uninfested trees and from shrubs under these trees. We also used hanging cup traps to collect spiders that fell from both tree types. Spider abundance was greater within, and in shrubs below, scale-infested compared to scale-uninfested trees. Scale-infested trees hosted more orb web weaving spiders than scale-uninfested trees. Shrubs under scale-infested trees hosted more hunting, orb web weaving, and space web weaving spiders than shrubs under uninfested trees. Our findings suggest that scale-infested urban trees, and the robust arthropod communities they support, conserve certain spider guilds, and these benefits extend to other plants in the landscape.

**Implications for insect conservation:** The ability of urban trees to conserve spider communities is in part attributable to the abundance of potential prey available within trees. Therefore, tolerating pests such as scale insects in urban trees can conserve spider communities both within trees and in shrubs planted below these trees.

**Keywords** Urban tree · Spider community · Conservation · Natural enemy

## Introduction

Spiders are common arthropod predators in urban ecosystems (Johnson et al. 2012; Gardiner et al. 2015; Lowe et al. 2016, 2018; Meineke et al. 2017). Spiders provide important predation services and regulate populations of economically important insect pests (Michalko et al. 2019). The biological control services that spiders provide can help manage pests in urban greenspaces as well (Riechert and Bishop 1990; Shrewsbury and Raupp 2006; Philpott and Bichier 2017).

However, urbanization filters arthropod communities by changing plant communities and local temperatures (McKinney 2006, 2008; Dale and Frank 2018; Martinson et al. 2020). As a result of these altered conditions, certain taxa become abundant in cities while others become rare or are extirpated (McKinney 2006; Youngsteadt et al. 2017; Hamblin et al. 2017, 2018; Dale and Frank 2018). The altered environmental conditions associated with urbanization can filter and homogenize spider communities (Shochat et al. 2004; Meineke et al. 2017; Lowe et al. 2018; Argañaraz and Gleiser 2020; Korányi et al. 2020). For example, Meineke et al. 2017 sampled spiders in willow oak (*Quercus phellos* L.) trees across an urban warming gradient. Spider abundance overall was not affected by urban warming, but Anyphaneidae spiders were less common in hot urban trees. Similarly, Argañaraz and Gleiser 2020 collected spiders from urban and suburban sites in Córdoba, Argentina and found that while overall spider abundance did not differ between site

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type, certain guilds—sheet web weavers, space web weavers, and stalker hunters—were more abundant in suburban sites while ambush hunters were more abundant in urban sites. Like many other arthropod taxa, spiders exhibit heterogeneous responses to environmental changes resulting from urbanization and these changes can have a disproportionate effect on one family or guild over others (Argañaraz et al. 2018; Lowe et al. 2018; Delgado de la flor et al. 2020). As cities are expected to continue growing (Seto et al. 2012) it is important to identify ways in which arthropod taxa, such as spiders, can be conserved within cities to protect the ecosystem services they provide.

Urban trees may conserve predatory arthropod communities by hosting herbivore prey. However, the communities of herbivores that survive on urban trees varies across tree species. For example, exotic trees are commonly planted in urban areas and exotic trees often host fewer herbivores relative to native species (Southwood et al. 2005; Hartley et al. 2010; Frank et al. 2019). Thus, the ability of urban trees to conserve predatory arthropods such as spiders may depend upon the arthropod communities they support. Sap-sucking insects, such as scale insects, aphids, and lace bugs are often more abundant on trees and shrubs in urban compared to rural areas, and sap-sucking insects are often abundant in locations with extensive impervious surface cover (Speight et al. 1998; Tooker and Hanks 2000; Shrewsbury and Raupp 2006; Meineke et al. 2013; Dale and Frank 2014a, b; Long et al. 2019; Backe and Frank 2019; Korányi et al. 2020; Parsons et al. 2020b). Scale insects, in particular, reach damaging densities in trees surrounded by extensive impervious surface cover and low vegetation density and diversity (Hanks and Denno 1993; Tooker and Hanks 2000; Dale and Frank 2014a, b). However, in urban greenspaces with low impervious surface cover and some vegetation cover, scales can be present on trees at lower densities without worsening tree condition (Dale et al. 2016; Just et al. 2018; Meineke and Frank 2018). Scale insects on urban trees are consumed by predators such as lady beetles, lacewing larvae, tree crickets, rove beetles, and spiders (Hanks and Denno 1993; Tooker and Hanks 2000; Hodges and Braman 2004; Camacho and Chong 2015). Additionally, the honeydew produced by scale insects and other sap sucking hemipterans is an alternative food source for many arthropod taxa (Hogervorst et al. 2008; Konrad et al. 2009; Tena et al. 2016). Therefore, urban trees that host high densities of scale insects may provide greater conservation benefit for predatory arthropods than trees with few scales.

The high scale densities found in certain urban tree species may be important for conserving spider communities. Spiders will eat scale insects on urban trees (Hodges and Braman 2004) and the honeydew produced by Sternorrhynchs (Pfannenstiel and Patt 2012; Pfannenstiel 2015).

Perhaps more importantly, scales and scale honeydew support diverse arthropod communities of herbivores, fungivores, predators, and parasitoids on trees that could, in turn, serve as prey for spiders (Didham 1993; Hanks and Denno 1993; Tooker and Hanks 2000; Ewers 2002; Dale and Frank 2014b; Camacho et al. 2018; Wilson and Frank 2022). Shrubs planted below scale-infested trees may also host high densities of the same spider guilds found in scale-infested trees due to spill-over effects. Spill-over effects occur when natural enemy communities or herbivores disperse from locations where their abundances are high to locations where additional prey or hosts are available. In urban ecosystems, maintaining diverse vegetation patches next to golf courses supports natural enemy dispersal into golf courses and supports biological control of turfgrass pests (Frank and Shrewsbury 2009; Dobbs and Potter 2016; Dale et al. 2020). Similarly, in a previous study we found that shrubs underneath scale-infested urban trees host higher natural enemy abundance than shrubs underneath scale-uninfested trees (Wilson and Frank 2022). To build upon this work, we studied the spider communities in scale-infested and scale-uninfested urban trees, and in shrubs below these trees, to determine which spider guilds are supported by the arthropod communities associated with scale insects in urban trees.

To determine the potential of scale-infested trees to conserve spider guilds within their canopies and in shrubs below them, we collected spiders in scale-infested and scale-uninfested urban trees and in holly shrubs underneath these two tree types in Raleigh, NC, USA. We hypothesized the following: (1) Scale-infested oaks host greater spider abundance than scale-uninfested oaks. (2) Shrubs below scale-infested oaks host greater spider abundance than shrubs below scale-uninfested oaks. (3) Scale-infested oaks host different spider guilds than scale-uninfested oaks. (4) Shrubs below scale-infested oaks host different spider guilds than shrubs below scale-uninfested oaks.

## Methods

### Study trees

We collected spiders from willow oaks, sawtooth oaks, and overcup oaks on the campus of North Carolina State University (NCSU) and the city of Raleigh, NC, USA. Willow oak [*Quercus phellos*, (L. Fagales: Fagaceae)] is a native species that is widely planted in urban areas as a shade tree (Schlaegel 1990). Willow oaks grow in moist alluvial soils in the southeastern United States (Schlaegel 1990). In urban areas Willow oaks can host high densities of scale insects such as oak lecanium scale [*Parthenolecanium quercifex*

(Fitch, Hemiptera: Coccidae)], obscure scale [*Melanaspis obscura* (Comstock, Hemiptera: Diaspididae)], and oak eriococcin scales [*Acanthococcus quercus* (Comstock, Hemiptera: Eriococcidae)] (Meineke et al. 2013; Wilson and Frank 2022). Sawtooth oak [*Quercus acutissima*, (Carruth, Fagales: Fagaceae)] is an exotic species that is native to open woodlands in eastern Asia (Whittemore 2004). Sawtooth oak is commonly planted in urban areas due to its fast growth and ability to tolerate urban conditions (Whittemore 2004). Overcup oak [*Q. lyrata* (Walter, Fagales: Fagaceae)] is a native species commonly found in poorly draining soils in bottom land forests in the southeastern United States and often grows in close association with willow oak (Solomon 1990). Both sawtooth and overcup oaks host few if any scales on their branches (Backe 2019; Frank et al. 2019; Wilson and Frank 2022). Willow, sawtooth, and overcup oaks are common landscape trees on the campus of NCSU. Previous work on these species documented that scale abundance was greater on Willow oaks (mean  $\pm$  S.E. =  $11.3 \pm 2.03$  scales per 30 cm twig length) than on sawtooth ( $0.4 \pm 0.2$  scales per 30 cm) and overcup oaks ( $0.7 \pm 0.2$  scales per 30 cm) (Wilson and Frank 2022). Therefore, we used willow oaks to represent scale-infested trees and sawtooth and overcup oaks to represent scale-uninfested trees in this study. All trees that we collected spiders from were mature landscape trees that were growing in mulched landscaping beds or in turfgrass lawns. Trees were typically adjacent to sidewalks or within parking lots. Plants growing beneath these trees included ornamental herbaceous plants [e.g. *liriope muscari* ((Decne.) L.H.Bailey, Asparagales: Asparagaceae)], small shrubs [e.g. *Ilex vomitoria* (Sol. ex Aiton, Aquifoliales: Aquifoliaceae)], and turfgrass. Commonly planted adjacent to our trees were small ornamental tree species such as crape myrtle [*Lagerstroemia spp.* (L. Myrtales: Lythraceae)].

### Spider collection in trees

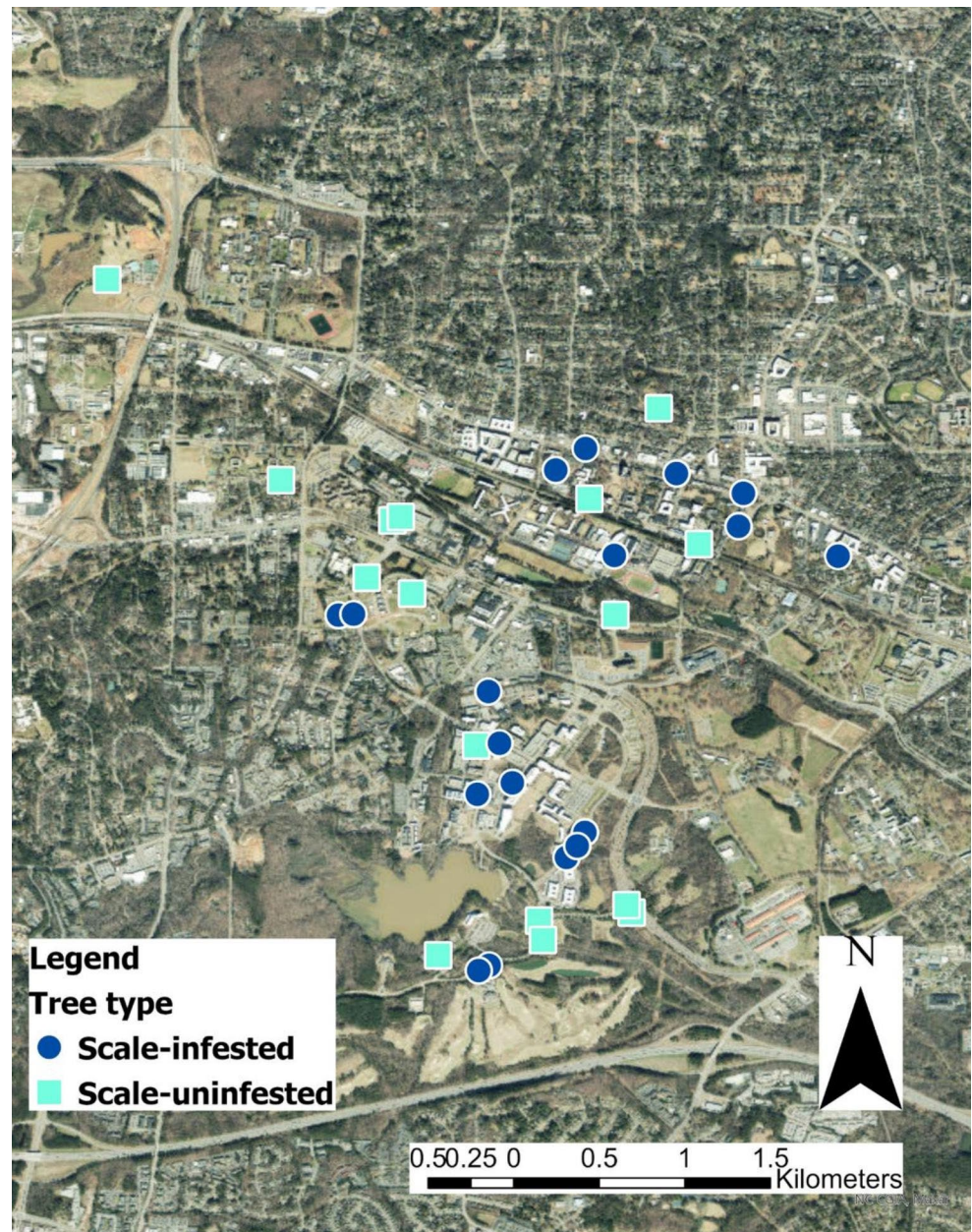
In June and September of 2020, we collected beat samples from 18 scale-infested willow oaks and 16 scale-uninfested oaks (9 sawtooth and 7 overcup oaks) on the campus of NCSU (Fig. 1). We collected spiders in these trees to determine how tree type (scale-infested v. scale-uninfested) influenced spider community composition. We used a funnel beat sampler to collect spiders (Sperry et al. 2001; Meineke et al. 2017). The funnel beat sampler consists of a 30.5 cm diameter wooden lid that is attached to a metal funnel on one side with a hinge. At the base of the funnel, we attached 50 ml plastic tubes that we filled with 10 ml of 70% ethanol to collect arthropods that fell into the tube. Attached to the funnel was a 2.5 m retractable pole. On top of the wooden lid, we attached a rope. At each site we pulled the rope to lift

the lid and then let go of the rope so that the lid would hit tree branches and knock arthropods into the metal funnel. After beating trees at each site, we washed all arthropods into the tube using 70% ethanol and then removed the tube so that we could later sort arthropods in the lab. We hit 12 branches on each tree with the sampler, each approximately evenly distributed around the lower canopy. Each branch was hit with the wooden lid 5 times to knock arthropods into the funnel, moving closer to the trunk with each consecutive hit. We collected spiders from trees in June and September of 2020 and identified all collected spiders to family using Ubick et al. 2017. To determine how tree type influenced the composition of spider guilds, we sorted all spider families into guilds based on the phylogenetic analysis by Cardoso et al. 2011. Families were sorted into the following guilds: active hunters (Anyphaneidae, Clubionidae, Salticidae, Philodromidae, Ctenidae), ambush hunters (Thomisidae), ground hunters (Lycosidae, Corinnidae), space web weavers (Theridiidae, Dictyniidae, Pholcidae), sheet web weavers (Linyphiidae), orb web weavers (Araneidae, Tetragnathidae, Uloboridae), and specialists (Mimetidae). We combined spider abundance values across both collection periods for statistical analysis.

### Spider collection from shrubs below trees

In June and September of 2020, we used a vacuum sampler to collect arthropods from one holly shrub (either *Ilex cornuta* or *I. vomitoria*) underneath 17 scale-infested (all willow oaks) and 16 scale-uninfested (9 overcup oaks and 7 sawtooth oaks) trees on the campus of NCSU. In July and October of 2021, we sampled 8 shrubs under scale-infested trees (all willow oaks) and 7 shrubs under scale-uninfested trees (2 sawtooth and 5 overcup oaks). This was done to determine if tree type (scale-infested or uninfested) influenced spider composition in shrubs planted below them. The vacuum sampler consisted of a modified Husqvarna 125BVx handheld blower created by Mitchell et al. in review. Inside the vacuum tube we placed an inverted cone of galvanized hardware cloth (2.6 cm<sup>2</sup> squares, 19 gauge galvanized steel, ACORN International) that we duct tapped to the inside of the tube. Before starting the vacuum at each site, we inserted a 38 cm x 28 cm mesh bag (sewn from organza fabric) inside the vacuum tube and attached it to the outside with a rubber band. We vacuumed each shrub for one minute and covered all sides of the shrub during that time. Because shrub size differed across sites, we measured the volume of each shrub using the formula for the volume of a cone ( $v = \pi * r^2 * h/3$ , where  $v$  = the volume of the shrub in cubic meters,  $r$  = the radius at the base of the shrub and  $h$  = the height of the shrub). Volume was used as an offset term in statistical analyses where spider abundance

**Fig. 1** The location of all oak trees that were beat sampled in 2020. Scale-infested trees are all willow oaks while scale-uninfested trees are a mixture of sawtooth and overcup oaks. Base map imagery comes from the ESRI World Imagery data layer (ESRI 2023)



was compared between tree types. We combined abundance values from both sampling periods for statistical analysis. All spiders in these samples were identified to family and sorted to guild.

### Measurement of spider dispersal from trees to shrubs

To determine if spiders fell out of scale-infested trees at a greater rate than scale-uninfested trees, we hung two plastic cup traps in 15 scale-infested (all willow oaks) and 15 scale-uninfested oaks (nine sawtooth and six overcup oaks) across the campus of NCSU in June and October of 2021.

Cup traps were 473 ml plastic deli cups (11.7 cm by 8.6 cm) filled with soapy water. At each tree we attached two cups on opposite sides of the tree's canopy. To attach cups, we drilled two holes approximately 90 degrees apart around the rim of each cup through which we tied 90 cm of fishing line which we attached with paper clips to branches in the outer third of the canopy. We then filled cups with soapy water and left them for two days. After two days we filtered the water from traps through a 150  $\mu\text{m}$  brass sieve and stored all arthropods in 70% ethanol. We identified all spiders to family and sorted families into guilds. We placed traps in trees once per week from May 31st – June 28th and from October 5th – October 27th of 2021 for a total of 5 replicates in May

and 4 replicates in October. We summed all spider data from all collection rounds per tree for analyses. We calculated the rate of spider accumulation per day for statistical analysis.

**Statistical analysis** All statistical analyses were conducted in R version 4.2.1 (R Core Team 2022). We fit generalized linear models with a negative binomial distribution and log link function to determine how tree type (scale-infested or uninfested) influenced spider abundance recorded from beat samples collected in 2020. We used a negative binomial distribution because our response variable was overdispersed count data. Because the scale-uninfested trees we sampled spanned two different species, we fit a subsequent model (negative binomial, log link function) to determine if spider abundance recorded in beata samples from scale-uninfested trees was influenced by tree species.

We used a Kruskal-Wallis test to determine if the daily accumulation rate of spiders into intercept traps differed based on tree type. For analysis, we summed these values across all collection periods for each tree. We used a follow-up Kruskal-Wallis test to determine if the daily accumulation rate of spiders into intercept traps below scale-uninfested trees differed between sawtooth and overcup oaks. Additionally, we fit generalized linear models (negative binomial, log-link) to determine if tree type, shrub species, and the interaction of these predictors, influenced spider abundance in landscape holly shrubs separately in 2020 and 2021. In these models we included total shrub volume as an offset term. We fit two additional models (negative binomial, log-link function) to determine if spiders collected from vacuum samples underneath scale-uninfested trees were influenced by tree species. As with the beat sample data, we used the negative binomial distribution for these models because our response variables were overdispersed counts. In these models we included an interaction term with shrub species and an offset term for shrub volume. In the 2021 model we removed the interaction term between tree species and shrub species due to convergence errors resulting from the smaller sample size in 2021. We used the package ‘mvabund’ (Wang et al. 2012) to determine if spider guild composition in beat, intercept trap, and vacuum samples differed by tree type. The mvabund package allows for the fitting of generalized linear models to determine if community composition is influenced by predictor variables. We used the “manyglm” function to fit a negative binomial glm with tree type as the sole predictor variable and the spider community recorded from beat samples as the response term. We tested for significance using wald tests and ran univariate tests to determine how each spider family was influenced by tree type. We adjusted p-values in the univariate tests using the default procedure in the anova.manyglm command. We fit an additional negative binomial glm to determine if spider guild composition recorded from scale-uninfested

trees was influenced by tree species. We repeated this same model fitting procedure using spider community data from intercept traps and vacuum sample data in 2020 and 2021. For intercept traps we used the total abundance of all spiders recorded at each site across all collection periods. For vacuum samples, we summed spider abundance data across both sampling rounds and included total shrub volume as an offset term in models. In the vacuum sample models we also included shrub species and the interaction of shrub species with tree type or tree species as covariates.

## Results

**Hypotheses (1) Scale-infested oaks host greater spider abundance than scale-uninfested oaks. (2) Shrubs below scale-infested oaks host greater spider abundance than shrubs below scale-uninfested oaks.**

We collected significantly more spiders in beat samples from scale-infested oaks (Mean  $\pm$  Std. error =  $9.7 \pm 0.9$ ) compared to scale-uninfested oaks ( $6.3 \pm 1.1$ ) ( $\chi^2 = 5.200$ ,  $p = 0.023$ ). In scale-uninfested oaks, spider abundance did not differ between sawtooth ( $6.1 \pm 1.3$ ) and overcup oaks ( $6.4 \pm 1.8$ ) (Table 1). Additionally, the daily input rate of spiders to intercept traps was significantly higher under scale-uninfested trees ( $0.1 \pm 0.02$  spiders/day) compared to scale-infested trees ( $0.04 \pm 0.01$  spiders/day) ( $\chi^2 = 4.07$ ,  $p = 0.044$ ). Underneath scale-uninfested trees, the daily input rate of spiders did not differ between sawtooth ( $0.8 \pm 0.2$  spiders/day) and overcup oaks ( $1.2 \pm 0.5$  spiders/day) ( $\chi^2 = 0.133$ ,  $p = 0.716$ ). We collected significantly more spiders from holly shrubs underneath scale-infested trees in both 2020 ( $\chi^2 = 3.972$ ,  $p = 0.046$ ) and 2021 ( $\chi^2 = 21.724$ ,  $p < 0.001$ ). In 2020 we collected  $111.0 \pm 26.7$  spiders per  $m^3$  and in 2021 we collected  $223.0 \pm 45.6$  spiders per  $m^3$  from shrubs under scale-infested trees. In shrubs below scale-uninfested trees, we collected  $84.0 \pm 30.7$  spiders per  $m^3$  in 2020 and in 2021 we collected  $76.8 \pm 10.8$  spiders per  $m^3$ . Tree type did not interact with shrub species to influence spider abundance in either year (Table 1). There was a significant main effect of shrub species on spider abundance in 2020 ( $\chi^2 = 5.271$ ,  $p = 0.022$ ), but not 2021 (Table 1), such that significantly more spiders were collected in *I. vomitoria* ( $134.2 \pm 11.2$  spiders per  $m^3$ ) compared to *I. cornuta* ( $63.7 \pm 7.6$  spiders per  $m^3$ ) shrubs in 2020 (Table 2). With respect to scale-uninfested trees, shrubs underneath overcup oaks hosted more spiders ( $122.5 \pm 50.8$  spiders per  $m^3$ ) than shrubs underneath sawtooth oaks ( $34.4 \pm 15.5$  spiders per  $m^3$ ) in 2020 ( $\chi^2 = 4.084$ ,  $p = 0.043$ ) but not 2021 (sawtooth:  $240.2 \pm 133.4$  spiders per  $m^3$ , overcup:  $493.4 \pm 134.1$  spiders per  $m^3$ ) (Table 1).

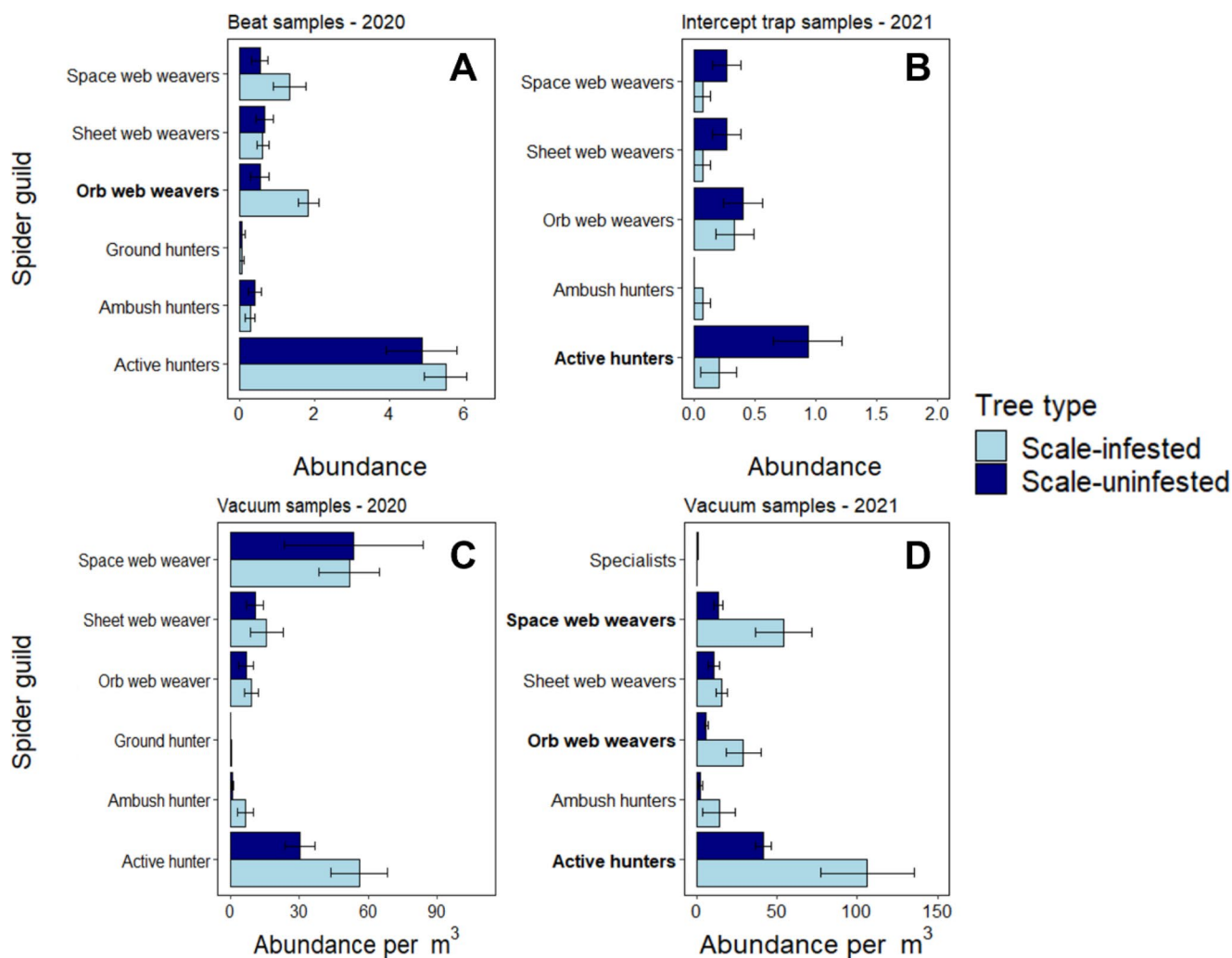
**Table 1** Results from negative binomial models that evaluated how spider abundance was influenced by tree type using data from beat samples in tree canopies and vacuum samples on planted landscape shrubs. Follow up models test how spider abundance recorded within and below scale-uninfested trees differed between sawtooth and overcup oaks. Model results are separated based on the year data were collected. Significance was evaluated with likelihood ratio tests. S.U. refers to scale-uninfested trees

Response	Predictor	Estimate ± SE	$\chi^2$	P
2020 data				
Spider abundance in beat samples	-	Intercept: 2.269 ± 0.122	-	-
	<b>Tree type</b>	<b>Tree type: S.U.: -0.426 ± 0.187</b>	<b>5.200</b>	<b>0.023</b>
Spider abundance in beat samples from scale-uninfested trees	-	Intercept: 1.815 ± 0.294		
	Tree species	Tree species: overcup: 0.048 ± 0.391	0.015	0.903
Spider abundance in shrubs	-	<b>Intercept: 4.385 ± 0.268</b>	-	-
	<b>Tree type</b>	<b>Tree Type: S.U.: -1.067 ± 0.451</b>	<b>3.972</b>	<b>0.046</b>
	<b>Shrub species</b>	<b>Shrub species: I. vomitoria: 0.666 ± 0.450</b>	<b>9.103</b>	<b>0.003</b>
	Type * species interaction	Type: S.U. * Species: I. vomitoria: -0.765 ± 0.641	1.345	0.246
Spider abundance in shrubs under scale-uninfested trees	-	<b>Intercept: 2.936 ± 0.416</b>	-	-
	<b>Tree species</b>	<b>Tree species: overcup: 0.880 ± 0.714</b>	<b>4.084</b>	<b>0.043</b>
	<b>Shrub species</b>	<b>Shrub species: I. vomitoria: 1.063 ± 0.629</b>	<b>5.271</b>	<b>0.022</b>
	Tree sp. * shrub sp. interaction	Tree species: overcup * shrub species: I. vomitoria: 0.078 ± 0.910	0.007	0.933
2021 data				
Spider abundance in shrubs	-	<b>Intercept: 5.010 ± 0.265</b>	-	-
	<b>Tree type</b>	<b>Tree Type S.U.: -0.704 ± 0.407</b>	<b>21.724</b>	<b>&lt;0.001</b>
	Shrub species	Shrub species: I. vomitoria: 0.578 ± 0.327	1.708	0.191
	Type * species interaction	Tree Type: S.U. * Species: I. vomitoria: -0.556 ± 0.491	1.283	0.257
Spider abundance in shrubs under scale-uninfested trees	-	Intercept: 4.066 ± 0.294	-	-
	Tree species	Tree species: overcup: 0.571 ± 0.298	2.794	0.095
	Shrub species	Shrub species: I. vomitoria: -0.254 ± 0.297	0.584	0.445

*Hypotheses 3) Scale-infested oaks host different spider communities than scale-uninfested oaks. 4) Shrubs below scale-infested oaks host different spider communities than shrubs below scale-uninfested oaks.*

Spider guild composition from beat samples was significantly different in scale-infested oaks compared to scale-uninfested oaks ( $\chi^2 = 3.949$ ,  $p = 0.013$ ). The difference in guild composition was driven by orb web weaving spiders ( $\chi^2 = 3.297$ ,  $p = 0.004$ ) which were more abundant in scale-infested oaks than scale-uninfested oaks (Fig. 2A; Table 2). Orb-web weaving spiders in beat samples were represented entirely by the family Araneidae. Within scale-uninfested trees, tree species did not influence spider guild composition recorded from beat samples, nor the abundance of any individual guild (Table 3). Spider guild composition in intercept traps differed between scale-infested and scale-uninfested trees ( $\chi^2 = 2.909$ ,  $p = 0.021$ , Table 2). Significantly more active hunters were collected from traps underneath scale-uninfested trees compared to scale-infested trees ( $\chi^2 = 2.300$ ,

$p = 0.023$ , Fig. 2B; Table 2). Active hunters collected in intercept traps were represented by the families Anyphaneidae (47% of active hunters in intercept traps), Clubionidae (24%), Philodromidae (18%), and Salticidae (12%). Underneath scale-uninfested trees, tree species did not influence guild composition recorded from intercept traps (Table 3). In 2020, spider guild composition in landscape holly shrubs was influenced by shrub species ( $\chi^2 = 5.998$ ,  $p = 0.006$ ) but not by tree type or the interaction of these predictors (Fig. 2C; Table 2). Guild composition differences were driven by the significantly higher abundance of sheet web weavers collected from *I. vomitoria* ( $21.8 \pm 7.3$  spiders per  $m^3$ ) compared to *I. cornuta* shrubs ( $5.3 \pm 2.9$  spiders per  $m^3$ ) ( $\chi^2 = 3.962$ ,  $p = 0.01$ ). Sheet web weavers were represented by the families Linyphiidae (91% of all sheet web weavers in beat samples) and Agelenidae (9%). Underneath scale-uninfested trees, spider guild composition differed between sawtooth and overcup oaks ( $\chi^2 = 5.060$ ,  $p = 0.004$ , Table 3). Sheet web weavers were more abundant in shrubs below



**Fig. 2** Effect of tree type on the abundance of spider guilds in (A) Beat samples, (B) Intercept trap samples, (C) Vacuum samples collected in 2020, and (D) Vacuum samples collected in 2021. Guilds in bold text

were significantly affected by tree type (see Table 2 for significance values). Means are plotted in all graphs and error bars show the standard error of the mean

overcup oaks ( $17.8 \pm 5.6$  spiders per  $m^3$ ) compared to sawtooth oaks ( $1.7 \pm 1.1$  spiders per  $m^3$ ) ( $\chi^2 = 3.795$ ,  $p = 0.038$ , Table 3).

In 2021, tree type, but not shrub species or their interaction, influenced spider guild composition in shrubs ( $\chi^2 = 6.731$ ,  $p = 0.003$ ). Guild differences were driven by active hunters ( $\chi^2 = 3.397$ ,  $p = 0.025$ ), orb web weavers ( $\chi^2 = 3.613$ ,  $p = 0.019$ ), and space web weavers ( $\chi^2 = 3.999$ ,  $p = 0.011$ ) which were all more abundant in shrubs under scale-infested trees (Fig. 2D; Table 2). Active hunters were represented by the families Salticidae (48% of all active hunters), Anyphaneidae (38%), Philodromidae (10%), and Clubionidae (4%). Orb web weavers were represented by the families Araneidae (57% of all orb web weavers), Uloboridae (41%), and Tetragnathidae (1%). Space web weavers were represented by the families Theridiidae (77% of all space web weavers), Pholcidae (15%), and Dictyniidae

(8%). In shrubs below scale-uninfested trees, guild community composition differed between sawtooth and overcup oaks ( $\chi^2 = 4.809$ ,  $p = 0.031$ , Table 3). This difference was driven by active hunters which were more abundant in shrubs below overcup oaks ( $46.9 \pm 2.9$  spiders per  $m^3$ ) compared to sawtooth oaks ( $27.6 \pm 12.4$  spiders per  $m^3$ ) ( $\chi^2 = 4.311$ ,  $p = 0.025$ , Table 3).

## Discussion

Trees are important for conserving predatory arthropod communities in cities (Smith et al. 2006a, b; Frank 2014; Meineke et al. 2017; Frank et al. 2019). Our results document that scale insects and their associated arthropod communities are particularly beneficial for spider conservation and that these benefits extend from trees to other nearby

**Table 2** Model fitting results that evaluated how tree type influenced spider guild composition recorded from trees, intercept traps, and holly shrubs. All models are fit with a negative binomial error distribution. Overall effects of model predictors on the entire community are presented first, then results from univariate tests on each family are presented second

Sample type	Predictor	Res. Df	Df. Diff.	Guild	Wald	P
Beat samples	Intercept	33	-	-	-	-
	<b>Tree type</b>	<b>32</b>	<b>1</b>	-	<b>3.949</b>	<b>0.013</b>
Beat samples	Tree type	-	-	Active hunter	0.889	0.733
	Tree type	-	-	Ambush hunter	0.485	0.878
	<b>Tree type</b>	-	-	<b>Orb web weaver</b>	<b>3.297</b>	<b>0.004</b>
	Tree type	-	-	Sheet web weaver	0.051	0.952
	Tree type	-	-	Space web weaver	1.921	0.198
	Tree type	-	-	Ground hunter	0.083	0.952
Intercept traps	Intercept	29	-	-	-	-
	<b>Tree type</b>	<b>28</b>	<b>1</b>	-	<b>2.909</b>	<b>0.021</b>
Intercept traps	<b>Tree type</b>	-	-	<b>Active hunter</b>	<b>2.300</b>	<b>0.023</b>
	Tree type	-	-	Ambush hunter	0.047	0.790
	Tree type	-	-	Orb web weaver	0.301	0.790
	Tree type	-	-	Sheet web weaver	1.240	0.289
	Tree type	-	-	Space web weaver	1.240	0.289
Vacuum samples – 2020	Intercept	32	-	-	-	-
	Tree type	31	1	-	3.319	0.229
	<b>Shrub sp.</b>	<b>30</b>	<b>1</b>	-	<b>5.998</b>	<b>0.006</b>
Vacuum samples – 2020	Type * shrub sp.	29	1	-	2.672	0.393
	Tree type	-	-	Active hunter	1.912	0.374
	Shrub sp.	-	-	Active hunter	1.941	0.187
	Type * shrub sp.	-	-	Active hunter	1.121	0.688
	Tree type	-	-	Ambush hunter	2.582	0.151
	Shrub sp.	-	-	Ambush hunter	1.518	0.231
	Type * shrub sp.	-	-	Ambush hunter	1.564	0.581
	Tree type	-	-	Orb web weaver	0.468	0.965
	Shrub sp.	-	-	Orb web weaver	2.766	0.090
	Type * shrub sp.	-	-	Orb web weaver	0.616	0.728
	Tree type	-	-	Sheet web weaver	0.598	0.965
	<b>Shrub sp.</b>	-	-	<b>Sheet web weaver</b>	<b>3.962</b>	<b>0.012</b>
	Type * shrub sp.	-	-	Sheet web weaver	0.896	0.728
	Tree type	-	-	Space web weaver	0.102	0.965
	Shrub sp.	-	-	Space web weaver	2.542	0.102
	Type * shrub sp.	-	-	Space web weaver	1.500	0.586
	Tree type	-	-	Ground hunter	0.328	0.965
	Shrub sp.	-	-	Ground hunter	0.311	0.551
	Type * shrub sp.	-	-	Ground hunter	0.046	0.728
Vacuum samples – 2021	Intercept	14	-	-	-	-
	<b>Tree type</b>	<b>13</b>	<b>1</b>	-	<b>6.731</b>	<b>0.003</b>
	Shrub sp.	12	1	-	2.726	0.415
Vacuum samples – 2021	Type * shrub sp.	11	1	-	2.216	0.475
	<b>Tree type</b>	-	-	<b>Active hunter</b>	<b>3.397</b>	<b>0.025</b>
	Shrub sp.	-	-	Active hunter	0.419	0.889
	Type * shrub sp.	-	-	Active hunter	0.601	0.856
	Tree type	-	-	Ambush hunter	1.948	0.180
	Shrub sp.	-	-	Ambush hunter	1.315	0.614
	Type * shrub sp.	-	-	Ambush hunter	0.237	0.856
	<b>Tree type</b>	-	-	<b>Orb web weaver</b>	<b>3.613</b>	<b>0.019</b>
	Shrub sp.	-	-	Orb web weaver	1.509	0.582
	Type * shrub sp.	-	-	Orb web weaver	1.774	0.404



**Table 2** (continued)

Sample type	Predictor	Res. Df	Df. Diff.	Guild	Wald	P
	Tree type	-	-	Sheet web weaver	0.963	0.355
	Shrub sp.	-	-	Sheet web weaver	0.521	0.889
	Type * shrub sp.	-	-	Sheet web weaver	1.061	0.769
	<b>Tree type</b>	-	-	<b>Space web weaver</b>	<b>3.999</b>	<b>0.011</b>
	Shrub sp.	-	-	Space web weaver	1.723	0.547
	Type * shrub sp.	-	-	Space web weaver	0.471	0.856
	Tree type	-	-	Specialist	0.036	0.612
	Shrub sp.	-	-	Specialist	0.080	0.889
	Type * shrub sp.	-	-	Specialist	0.017	0.856

plants in the landscape. Scale-infested trees hosted significantly more spiders and a different spider community than scale-uninfested trees and these effects spilled-over to the shrubs planted below them. Scale-infested trees hosted more orb web weaving spiders of the family Araneidae than scale-uninfested trees. Shrubs under scale-infested trees hosted more hunting, space web weaving, and orb web weaving spiders than shrubs under scale-uninfested trees. Tolerating moderate scale densities in trees could benefit urban arthropod conservation efforts both by reducing harmful management practices such as insecticide applications and by providing resources for spiders and their prey. The potential for urban trees to conserve important predatory arthropods such as spiders has thus far been unappreciated.

In 2021, but not 2020, we found that shrubs under scale-infested trees hosted more hunting, orb web weaving, and space web weaving spiders than shrubs under scale-uninfested trees. Our findings reflect a common theme in urban ecology—that certain taxa can exploit urban ecosystems to become highly abundant, urban exploiters, while others that cannot exploit urban ecosystems become less common—urban avoiders (Blair and Launer 1997). For example, Shochat et al. 2004 found that increased productivity in urban habitats supported Lycosid and Linyphiid spiders but that other families were less abundant, resulting in lower spider diversity compared to unmanaged low-productivity habitats. It remains unclear why hunting, orb web weaving, and space web weaving spiders, were more abundant underneath scale-infested trees compared to other guilds. However, our findings suggest that these guilds can exploit the increased prey abundance found in shrubs underneath scale-infested trees (Wilson and Frank 2022). Future work examining the diet and foraging preferences of common representatives of these guilds may better explain how scale-infested urban trees support certain spider guilds.

We found that intercept traps underneath scale-uninfested trees collected spiders at a greater rate compared to traps under scale-infested trees. Additionally, spider guild

composition differed in intercept traps between scale-infested and uninfested trees and this difference was driven by a higher abundance of active hunting spiders collected underneath scale-uninfested trees. Our results could suggest that the lower abundance of prey available in scale-uninfested oaks encourages active hunting spiders to disperse from these trees at higher rates to find prey elsewhere. Active hunting spiders disperse greater distances for prey and move more regularly than sit and wait and ambush-hunting spiders (Miller et al. 2014). Thus, active hunting spiders may be more likely to disperse from scale-uninfested trees to feed on prey in plants below trees than web building, sit and wait, or ambush hunters. In contrast, orb web weaving *Tetragnatha elongata* Walckenaer spiders have been found to remain in place when prey is rare to maximize the rate of prey capture (Gillespie and Caraco 1987). Since we did not find more spiders in shrubs below scale-uninfested trees in either 2020 or 2021, the greater dispersal of active hunting spiders from scale-uninfested trees does not appear to produce noticeable differences in shrubs below these trees.

The variability in herbivore abundance within urban tree species likely influences their ability to conserve natural enemy taxa like spiders. While native species often host more herbivores, and thus more prey for natural enemies than exotic species, certain native plant species can also host fewer herbivores than their exotic congeners (e.g. Parsons et al. 2020a). In our study system, both native overcup oaks and exotic sawtooth oaks host fewer scales and natural enemies than native willow oaks (Wilson and Frank 2022). Therefore, when assessing the conservation potential of urban tree species for spiders and other natural enemy taxa, native status may be less informative than herbivore abundance. Interspecific differences in host susceptibility to herbivores also likely influences the prey arthropods, and thus spiders, that colonize urban trees. The trees comprising our scale-infested and scale-uninfested tree category were different species and variation in plant defensive compounds between these species may affect the prey and

**Table 3** Model fitting results showing how tree species influences spider guild composition recorded from trees, intercept traps, and holly shrubs using data within and below scale-uninfested trees only. All models are fit with a negative binomial error distribution. Overall effects of model predictors on the entire community are presented first, then results from univariate tests on each family are presented second

Sample type	Predictor	Res. Df	Df. Diff.	Guild	Wald	P	
Beat samples	Intercept	15	-	-	-	-	
	Tree species	14	1	-	1.341	0.810	
Beat samples	Tree species	-	-	Active hunter	0.260	0.985	
	Tree species	-	-	Ambush hunter	0.038	0.985	
	Tree species	-	-	Orb web weaver	0.851	0.827	
	Tree species	-	-	Sheet web weaver	0.220	0.985	
	Tree species	-	-	Space web weaver	0.978	0.827	
	Tree species	-	-	Ground hunter	0.039	0.985	
	Intercept traps	Intercept	14	-	-	-	-
Intercept traps	Tree species	13	1	-	1.128	0.661	
	Tree species	-	-	Active hunter	0.707	0.797	
Intercept traps	Tree species	-	-	Ambush hunter	0	1.00	
	Tree species	-	-	Orb web weaver	0.497	0.797	
	Tree species	-	-	Sheet web weaver	0.600	0.797	
	Tree species	-	-	Space web weaver	0.405	0.797	
	Vacuum samples – 2020	Intercept	15	-	-	-	-
		<b>Tree species</b>	<b>14</b>	<b>1</b>	-	<b>5.060</b>	<b>0.044</b>
		Shrub sp.	13	1	-	4.440	0.064
	Tree sp. * shrub sp.	12	1	-	0.811	0.955	
Vacuum samples – 2020	Tree species	-	-	Active hunter	1.394	0.330	
	Shrub sp.	-	-	Active hunter	2.371	0.244	
	Tree sp. * shrub sp.	-	-	Active hunter	0.583	0.968	
	Tree species	-	-	Ambush hunter	0.183	0.685	
	Shrub sp.	-	-	Ambush hunter	0.432	0.538	
	Tree sp. * shrub sp.	-	-	Ambush hunter	0.032	0.968	
	Tree species	-	-	Orb web weaver	2.010	0.328	
	Shrub sp.	-	-	Orb web weaver	1.391	0.361	
	Tree sp. * shrub sp.	-	-	Orb web weaver	0.025	0.968	
		<b>Tree species</b>	-	-	<b>Sheet web weaver</b>	<b>3.795</b>	<b>0.038</b>
		Shrub sp.	-	-	Sheet web weaver	2.718	0.160
		Tree sp. * shrub sp.	-	-	Sheet web weaver	0.255	0.968
		Tree species	-	-	Space web weaver	2.275	0.328
		Shrub sp.	-	-	Space web weaver	2.141	0.282
		Tree sp. * shrub sp.	-	-	Space web weaver	0.501	0.968
		Tree species	-	-	Ground hunter	0.039	0.685
		Shrub sp.	-	-	Ground hunter	0.057	0.538
		Tree sp. * shrub sp.	-	-	Ground hunter	0.015	0.968
	Vacuum samples – 2021	Intercept	6	-	-	-	-
		<b>Tree species</b>	<b>5</b>	<b>1</b>	-	<b>4.809</b>	<b>0.031</b>
Shrub sp.		4	1	-	1.850	0.632	
Tree sp. * shrub sp.		3	1	-	3.339	0.058	
Vacuum samples – 2021	<b>Tree species</b>	-	-	<b>Active hunter</b>	<b>4.311</b>	<b>0.025</b>	
	Shrub sp.	-	-	Active hunter	1.331	0.642	
	Tree sp. * shrub sp.	-	-	Active hunter	2.662	0.070	
	Tree species	-	-	Ambush hunter	0.022	0.881	
	Shrub sp.	-	-	Ambush hunter	0.511	0.926	
	Tree sp. * shrub sp.	-	-	Ambush hunter	0.001	0.716	
	Tree species	-	-	Orb web weaver	1.075	0.640	
	Shrub sp.	-	-	Orb web weaver	0.502	0.926	
	Tree sp. * shrub sp.	-	-	Orb web weaver	1.014	0.390	

**Table 3** (continued)

Sample type	Predictor	Res. Df	Df. Diff.	Guild	Wald	P
	Tree species	-	-	Sheet web weaver	0.364	0.881
	Shrub sp.	-	-	Sheet web weaver	0.254	0.926
	Tree sp. * shrub sp.	-	-	Sheet web weaver	0.019	0.505
	Tree species	-	-	Space web weaver	1.804	0.373
	Shrub sp.	-	-	Space web weaver	1.033	0.756
	Tree sp. * shrub sp.	-	-	Space web weaver	1.742	0.202
	Tree species	-	-	Specialist	0.033	0.881
	Shrub sp.	-	-	Specialist	0.074	0.926
	Tree sp. * shrub sp.	-	-	Specialist	0.012	0.716

spider communities that colonized these trees. Additionally, larger trees likely host more arthropod prey for spiders than younger or smaller trees (e.g. Smith et al. 2006a) and larger trees may better conserve spider communities. Regardless of mechanism, when factors associated with urbanization favor prey proliferation, spiders are often more abundant as well (Heiling and Herberstein 1999; Voss et al. 2007; Lowe et al. 2016). However, tree species with higher herbivore abundance do not always host higher abundances of spiders or other predatory arthropods (Hartley et al. 2010; Meineke et al. 2017; Frank et al. 2019). Consideration of additional factors that could influence spider abundance in trees such as the configuration of tree branches and their effect on the availability of web attachment points (Rypstra et al. 1999), the cooling potential of tree canopies (Meineke et al. 2017), and availability of alternative resources such as nectar (Pfannenstiel and Patt 2012) could be measured in conjunction with herbivore abundance to evaluate the ability of a tree species to conserve spider communities.

We found that spider abundance and community composition did not differ in the canopies, nor in the intercept traps beneath scale-uninfested sawtooth and overcup oaks. In contrast, we found that spider abundance was greater underneath overcup oaks compared to sawtooth oaks in 2020 but that spider abundance did not differ in 2021. In 2020, sheet web weavers were more abundant below overcup oaks while in 2021 active hunters were more abundant below overcup oaks. These findings indicate that additional factors associated with these tree species besides prey abundance in their canopies influence the community of spiders found in shrubs below them. From our study it is unclear what these additional factors are, but one potentially important factor could be differences in shading potential resulting from different branching patterns between these species. The amount of shade that landscape shrubs receive can influence their susceptibility to sap-sucking pests (Shrewsbury and Raupp 2000) and the degree to which vegetation is shaded can affect oviposition behavior by lepidopteran

pests (Moore et al. 1988), and concentrations of plant defensive compounds (Louda and Rodman 1996). Furthermore, the shade produced by urban trees can effectively cool their local environment (Shashua-Bar et al. 2009) which could offset effects of urban warming on scale insect proliferation and fecundity (Meineke et al. 2013, 2014; Dale and Frank 2014a, b) in shrubs below trees. Factors such as shading potential likely influence the prey community available in holly shrubs which may in turn influence the spider guilds that colonize these shrubs.

Tolerating pests such as scale insects on urban trees can conserve spider communities and could offset the homogenizing effects of urbanization on spider communities reported in other studies. Our results suggest that multiple spider guilds benefit from scale insects and their associated arthropod communities and that these benefits can be found in trees with scales and in the shrubs planted below them.

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**Data Availability** All data reported in this paper are available for download from the Dryad data repository at the following link: <https://doi.org/10.5061/dryad.wh70rxws7>.

## Declarations

**Competing interests** The authors have no conflicts of interest to declare.

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