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Research

Biological Control - Parasitoids and Predators

Scale Insects Support Natural Enemies in Both Landscape Trees and Shrubs Below Them

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Abstract

Scale insects are frequently abundant on urban trees. Although scales can worsen tree condition, some tree species tolerate moderate scale densities. Scales are prey for many natural enemies. Therefore, scale-infested trees may conserve natural enemies in their canopies and in nearby plants. We examined if scale-infested oaks—*Quercus phellos* L.—hosted more natural enemies than scale-uninfested oaks—*Q. acutissima* Carruth. and *Q. lyrata* Walter in Raleigh, NC. USA. We also tested if natural enemies were more abundant in holly shrubs (*Ilex spp.*) planted below scale-infested compared to scale-uninfested oaks. We collected natural enemies from the canopies of both tree types and from holly shrubs planted below these trees. To determine if tree type affected the abundance of natural enemies that passively dispersed to shrubs, we created hanging cup traps to collect arthropods as they fell from trees. To determine if natural enemies became more abundant on shrubs below scale-infested compared to scale-uninfested trees over short time scales, we collected natural enemies from holly shrubs below each tree type at three to six-day intervals. Scale-infested trees hosted more natural enemies than scale-uninfested trees and shrubs below scale-infested trees hosted more natural enemies than shrubs under scale-uninfested trees. Natural enemy abundance in hanging cup traps did not differ by tree type; however, shrubs underneath scale-infested trees accumulated more natural enemies than shrubs under scale-uninfested trees in six to nine days. Tolerating moderate pest densities in urban trees may support natural enemy communities, and thus biological control services, in shrubs below them.

Key words: urban tree, natural enemy, scale insect, conservation biological control

Herbivorous insects are often more abundant on trees and shrubs in cities compared to rural areas (Raupp et al. 2010). Scale insects in particular, tend to be more abundant on urban trees than forest trees (Hanks and Denno 1993a, Tooker and Hanks 2000, Long et al. 2019). Urban features, such as impervious surface cover, cause warm temperatures and dry soil that increase water stress for trees and improve their quality as hosts to scale insects (Dale and Frank 2017, Meineke and Frank 2018). Urban warming can also increase scale insect densities by increasing scale fecundity, interrupting interactions with natural enemies, and through other mechanisms (Dale and Frank 2014, 2017; Meineke et al. 2014; Frank 2021). In locations with extensive impervious surfaces and little vegetation cover, scale insects can reach damaging densities that worsen tree condition (Dale and Frank 2014, Dale et al. 2016, Just et al. 2018). However, in locations with low to moderate impervious cover, scale density is often below damaging levels (Dale et al. 2016, Just et al. 2018). In these situations, Integrated Pest Management (IPM) would suggest that intervention for these pests is not necessary and that they may even be beneficial.

A core tenet of IPM is that pest densities should be maintained below damaging thresholds, rather than eradicated, to support natural enemy communities and reduce wasteful insecticide applications (Stern et al. 1959). Scale insects on urban trees are parasitized by many parasitoid wasp species (Hanks and Denno 1993a Tooker and Hanks 2000; Meineke et al. 2013, 2014; Dale and Frank 2014; Camacho et al. 2018). For example, Hanks and Denno found that white peach scale (*Pseudaulacaspis pentagona* Targioni-Tozzetti) is parasitized by at least 64 species in 6 families (Hanks and Denno 1993b). Scale insects are also consumed by many specialists and generalist predators including harvestmen (Opiliones, earwigs (Dermaptera), tree crickets (Orthoptera: Grylloidea), lady beetles (Coleoptera: Coccinellidae), lacewing larvae (e.g., Neuroptera: Chrysopidae), ants (Hymenoptera: Formicidae), rove beetles (Coleoptera: Staphylinidae), and spiders (Araneae) (Hanks and Denno 1993a, Tooker and Hanks 2000, Hodges and Braman 2004). In addition, many scale insect species produce honeydew that is a source of nutrition for, and attractive to, many predators, parasitoids, and non-natural enemy arthropods (Didham 1993, Ewers 2002, Hogervorst et al. 2008, Pfannenstiel and Patt 2012). Therefore, urban trees with low to moderate scale densities may support natural enemy communities, and thus biological control services, within their canopies and the surrounding landscape.

Conservation biological control is the practice of supporting arthropod natural enemies to suppress plant pests in managed ecosystems. This is frequently accomplished by modifying vegetation structure and diversity to increase the availability of alternative hosts and prey, floral resources, nesting sites, and ideal microclimate conditions for natural enemies (Begg et al. 2017, Gurr et al. 2017). Scale-infested trees may provide greater prey abundance, via scales and their associated arthropods, to support natural enemies than trees without scales. In this way scale-infested trees may function like banker plants that have been used to support natural enemies in greenhouses and other agricultural systems (Frank 2010, Huang et al. 2011). The natural enemies that are attracted to the prey and resources in scale-infested trees may also forage in nearby plants to manage other insect pests. This is similar to conservation biological control in agricultural settings, wherein natural enemies disperse from field margins, banker plants, or other installations into fields to feed on crop pests (e.g., Woodcock et al. 2016). By providing resources to natural enemies, scale infested urban trees may contribute to conservation biological control more effectively than uninfested trees.

Willow oaks [Quercus phellos (L. Fagales: Fagaceae)] are commonly planted along streets and in landscapes throughout the eastern United States. They frequently host high densities of oak lecanium scale [Parthenolecanium quercifex (Fitch, Hemiptera: Coccidae)], European fruit lecanium scale [*P. corni* (Bouché)], and other scales in locations with extensive impervious surface cover (Meineke et al. 2013, Frank 2019). However, willow oaks are able to maintain growth even with high scale densities if they are not water stressed (Meineke and Frank 2018). Therefore, willow oaks in landscapes with low impervious surface cover may support scale densities that do not reduce tree growth or appearance. *Parthenolecanium spp.* on willow oaks are parasitized by wasps in at least four families and are found in close association with generalist predators including lady beetles spiders, minute pirate bugs (Hemiptera: Anthocoridae), lacewing larvae, carabid beetles (Coleoptera: Carabidae), and long-legged flies (Diptera: Dolichopodidae) (Meineke et al. 2013, 2014; Camacho et al. 2018; Frank et al. 2019). If natural enemies actively or passively disperse from tree canopies willow oaks may increase natural enemy abundance in plants growing below them. However, natural enemies could remain in tree canopies, where resources are abundant, and even recruit natural enemies from other parts of the landscape. In this case natural enemy abundance could be lower on plants below scale infested trees.

Our goal was to determine if scale-infested trees support natural enemies and other arthropod communities in urban trees and the shrubs planted below them. We conducted experiments in landscapes containing scale-infested willow oaks and scale-uninfested sawtooth and overcup oaks (*Q. acutissima* Carruth., *Q. lyrata* Walter) which host low scale abundance compared to willow oaks (Backe 2019, Frank et al. 2019). Therefore, for all experiments we compared arthropod communities found within and below scale-infested trees—willow oaks—to arthropods found within and below scale-uninfested trees—sawtooth and overcup oaks. Our hypotheses were that, compared to uninfested oak species, scale-infested willow oaks will 1) support more natural enemies and non-natural enemy arthropods 2) have more natural enemies and non-natural enemies that passively disperse from trees; 3) increase natural enemy and non-natural enemy accumulation rate and abundance in shrubs below trees. Understanding the role of trees in supporting natural enemies throughout urban landscapes will improve the development of IPM strategies for these complex ecosystems.

Methods

All experiments were conducted during 2019 – 2021 on the campus of North Carolina State University (NCSU) in Raleigh, NC. USA. All trees and shrubs were owned by either North Carolina State University or the City of Raleigh, NC. USA.

Hypothesis 1: Scale-Infested Willow Oaks Support More Scales, Natural Enemies, and Non-natural Enemy Arthropods Than Scale-Uninfested Oaks

We identified 32 willow oaks (*Quercus phellos)*, 12 sawtooth oaks (*Quercus acutissima)*, and 14 overcup oaks (*Quercus lyrata)* oaks on the campus of NCSU to collect scale insects and natural enemies from in 2019. All trees were planted in turfgrass lawns or in mulched landscape beds, often with shrubs or herbaceous plants below them. Willow oaks were selected as the scale-infested trees because they can host high densities of *Parthenolecanium* spp. scales (Meineke et al. 2013, 2014). Sawtooth oaks and overcup oaks were selected to represent scale-uninfested oak trees because these species tend to host few scale insects (Backe 2019, Frank et al. 2019). We used both species to represent scale-uninfested trees because there were not enough of either tree species on the campus of NCSU to allow for comparable sampling of tree branches between scale-infested and scale-uninfested trees.

To determine if scale abundance differed between scale-infested and scale-uninfested trees, we collected 8 twigs from each tree between March and June of 2019. At each tree, we removed one 30 cm twig from each cardinal direction in the lower canopy (3.29 m from the ground) and four 30 cm twigs from the upper canopy (5.08 m from the ground), each from a different cardinal direction. We pruned twigs to the most recent bud-scar before measuring 30 cm lengths from the distal end. Twigs were placed into a refrigerator until scales were counted. Within one week of collecting twigs all living scales were counted and identified to the following groups: obscure scales [Melanaspis obscura (Comstock, Hemiptera: Diaspididae)], all other armored scales (Hemiptera: Diaspididae), lecanium scales (*P. quercifex*/ *P. corni*), oak eriococcin scales [Acanthococcus quercus (Comstock, Hemiptera: Eriococcidae)], all other soft scales (Hemiptera: Coccidae), and pit scales (Hemiptera: Asterolecaniidae).

To determine if natural enemy and non-natural enemy arthropod abundance was greater in scale-infested compared to scale-uninfested trees, we used a funnel beat sampler to collect natural enemies from the canopies of our three tree species (Sperry et al. 2001, Meineke et al. 2017). The sampler consists of a 30.5 cm diameter metal funnel attached to a 2.5m extendable pole. A 50 ml plastic tube filled with 10 ml of 70% ethanol is attached at the base of the funnel. The funnel is topped with a hinged wooden lid attached to a rope, with which the user can use to move the lid up and down to dislodge arthropods from tree branches into the plastic tube.

In June and August of 2019, we collected natural enemies with the funnel beat sampler from 23 scale-infested (willow oaks), and 17 scale-uninfested oaks (11 overcup oaks, and six sawtooth oaks) on which we had counted scales. We hit each branch five times with the lid of the sampler. We started at the outermost leaves and moved towards the trunk of the tree with each successive hit. We hit 12 branches per tree with the sampler, approximately equally distributed around the lower canopy of the tree. After we had hit all 12 branches, we rinsed the funnel with 70% ethanol to collect specimens into the 50 ml plastic tube. We removed the tube afterwards and replaced it with a new tube. In June and August of 2020, we repeated this procedure and collected arthropods with the beat sampler in 18 scale-infested and 16 scale-uninfested oaks (nine overcup, seven sawtooth oaks). In the lab we sorted all natural enemies collected from trees in 2019 and 2020 into eight categories: Ants (Hymenoptera: Formicidae), parasitoid wasps (such as Hymenoptera: Aphelinidae), lady beetles (Coleoptera: Coccinellidae), lacewings (Neuroptera: Chrysopidae, Hemerobiidae, and Coniopterygidae), predatory hemipterans, (such as Hemiptera: Reduviidae), Spiders (Araneae), earwigs (Dermaptera), and long-legged flies (Diptera: Dolichopodidae). In addition, we sorted all natural enemy and nonenemy arthropods collected from trees in 2020 to order.

All statistical analyses were conducted in R v. 3.6.1 (R Core Team 2019). We used the Kruskal-Wallis test to determine if scale abundance per 30 cm was significantly different between scale-infested trees and scale-uninfested trees. We then used the Kruskal-Wallis test followed by the post-hoc Steel-Dwass test [in package ‘PMCMRplus’ (Pohlert 2022)] test to determine if scale abundance per 30 cm differed significantly between willow, sawtooth, and overcup oaks.

We used Kruskal-Wallis tests to determine if scale-infested trees hosted greater natural enemy abundance than scale-uninfested trees separately for 2019 and 2020. For both years we combined beat sample data collected from early summer and late summer for these analyses. If we found significant differences, we ran post-hoc Kruskal-Wallis tests where we compared the abundance of the four most abundant natural enemy groups between each tree type. We also used Kruskal-Wallis tests to compare non-natural enemy arthropod abundance collected in 2020 from beat samples between both tree types. To determine if scale abundance influenced enemy abundance in willow oaks, we fit a negative binomial GLM with total natural enemy abundance measured in all willow oaks in 2019 as the response, and scale abundance per 30 cm as a predictor.

Hypothesis 2: More Natural Enemies and Non-natural Enemies Passively Disperse From Scale-Infested Compared to Scale-Uninfested Trees

To determine if natural enemies and non-natural enemy arthropods fell from scale-infested trees at a greater rate than scale-uninfested trees, we created intercept traps to collect arthropods as they fell from trees. Intercept traps were 473 ml, 11.7 cm by 8.6 cm plastic deli cups filled with soapy water that we hung from 15 scale-infested (all willow oaks) and 15 scale-uninfested (six overcup oaks and nine sawtooth oaks) trees for two days. We drilled two small holes approximately 90° apart around the rim of each cup through which we strung 90 cm of fishing line that we attached with paper clips to tree branches in the outer third of the canopy. We hung two cups per tree, each on opposite sides of the canopy. After two days, we poured cup contents into a 150 µm brass sieve and transferred debris and arthropods into a 50 ml plastic tube with 70% ethanol. We repeated this procedure once per week between May 31st–June 28th and October 5th–27th of 2021 for a total of five replicates in early summer and four replicates in late summer. By collecting several samples in early and late summer from each tree we aimed to limit the effect that seasonal variation in arthropod dispersal would have on our results. We identified all arthropods to order and counted and classified natural enemies with the same categories used for beat samples.

To calculate the rate that natural enemies and non-natural enemies fell out of trees we first calculated the total area from which arthropods were collected. Each intercept trap was 107.51 cm^2 for a total area of 215.08 cm^2 per tree. We divided enemy and non-natural enemy counts by 215.08 and then by two to calculate the rate of natural enemy and non-natural enemy deposition per square centimeter per day. We fit two general linear mixed effects models [using the ‘lme4’ package (Bates et al. 2015)] with deposition rate of natural enemies and non-natural enemy arthropods as the response variables and tree type as the predictor. We included a random effect term for each experiment round to account for repeated measures. If we found a significant effect of tree type on the deposition rate of natural enemies we conducted post-hoc analyses to determine which of the 4 most abundant natural enemy groups were more abundant in traps below each tree type.

Hypothesis 3: Shrubs Under Scale-Infested Trees Accumulate More Natural Enemies and Non-natural Enemies Than Shrubs Below Scale-Uninfested Trees

To determine if shrubs below scale-infested trees hosted more natural enemies and non-natural enemy arthropods than shrubs below scale-uninfested trees we used a vacuum sampler to collect arthropods from holly shrubs below both tree types in 2020 and 2021. Since there were not enough planted holly shrubs of the same species for sufficient replication, we used two similar and commonly planted species: *Ilex cornuta* (Lindl. Aquifoliales: Aquifoliaceae) and *I. vomitoria* (Sol. ex Aiton. Aquifoliales: Aquifoliaceae). We included shrub species as a covariate in our analyses to account for the effect that differences in plant chemistry could have on arthropod communities. Holly shrubs were in maintained landscape beds (often surrounded by turfgrass) that contained mulch, neighboring shrubs, and small herbaceous plants. In June and August 2020, we sampled 12 *I. cornuta* and six *I. vomitoria* shrubs below scale-infested oaks and six *I. cornuta* and 10 *I. vomitoria* shrubs below scale-uninfested oaks. In July and October of 2021, we sampled five *I. vomitoria* and three *I. cornuta* below scale-infested trees, and five *I. vomitoria* and three *I. cornuta* below scale-uninfested trees. In total, we sampled hollies below 18 scale-infested and 16 scale-uninfested oaks in 2020 and below eight scale-infested and seven scale-uninfested oaks in 2021. In both years we collected vacuum samples in early and late summer to account for seasonal variation in arthropod abundance within shrubs.

The vacuum sampler was created from a Husqvarna 125BVx handheld blower and was modified so that the inside of the vacuum tube had galvanized mesh hardware cloth (2.6 cm^2 squares, 19 gauge galvanized steel, ACORN International) which held sampling bags in place (Mitchell et al. in review). We placed 38 × 25 cm fine mesh bags (organza fabric, 41,290 holes per cm^2) over the vacuum opening and secured bags with a rubber band. To collect arthropods, we vacuumed the entirety of each shrub for one minute. After sampling, bags were tied shut and placed in a five-gallon bucket containing a 50 ml plastic tube with paper towels doused in ethyl acetate to kill the arthropods. Bags were stored in a freezer before processing. We also recorded the basal diameter and height of each shrub. We used these measurements to estimate the volume of each shrub using the equation 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 in meters and h = the height of the shrub in meters). We used shrub volume as an offset term in analysis to account for the size differences in shrubs that we collected arthropods from.

To process samples, we poured sample bags into a 2.0 mm brass sieve placed on top of a 150 µm sieve. We poured water over samples in the top sieve to wash small arthropods into the lower sieve and separate plant material. We collected large arthropods from the top sieve with tweezers and collected arthropods and debris from the bottom sieve into a 50 ml plastic tube with 70% ethanol. We identified all arthropods to order and recorded and classified natural enemies to the same categories used for beat and intercept trap samples.

We fit a generalized linear model (negative binomial, log-link) to determine if natural enemy abundance was greater in shrubs below scale-infested trees compared to scale-uninfested trees. We used vacuum samples from landscape shrubs in 2020 and 2021 for these models. In both years shrubs were sampled in early and late summer so we pooled both samples but analyzed data from each year separately. We included tree type, shrub species, and their interaction as predictor variables. We also included an offset term for the total volume over which arthropods were sampled in both models. If we found a significant effect of tree type on enemy abundance in either year, we ran four separate negative binomial GLMs which evaluated the effect of tree type on the abundance of the four most abundant natural enemy groups. These models also included an offset term for shrub volume.

To determine if natural enemies and non-natural enemy arthropods accumulated more quickly on shrubs below scale-infested compared to scale-uninfested trees, we measured arthropod accumulation on potted and planted holly shrubs below both tree types in 2021. We placed one gallon potted dwarf yaupon holly shrubs (*I. vomitoria* 'Schillings') below 14 scale-infested (willow oaks) and 14 scale-uninfested trees (six overcup oaks and eight sawtooth oaks) in July and October of 2021. Two shrubs were placed on opposite sides of each tree within the outer third of the canopy. Shrubs were secured in place with landscaping staples and bungee cords. Before deploying shrubs we removed all arthropods by vacuuming shrubs with a vacuum sampler for one minute.

After the initial removal event, we vacuumed one of the shrubs after three days and did not vacuum the other shrub. After six days, we vacuumed the second shrub to get a six-day sample. After three more days we vacuumed both shrubs to collect an additional three-day and six-day sample. Finally, after nine more days we vacuumed both shrubs again. Thus, we collected arthropods from two shrubs each site at three-, six-, and nine-day increments. We later sorted all arthropods from all three, six, and nine-day samples to order and natural enemy group. Arthropods from these samples were preserved and processed in the same way as vacuum samples collected from planted shrubs in 2020 and 2021. Because six shrubs were stolen or vandalized in August and September, we replaced them with boxwood shrubs [Buxus sp. (L. Buxales: Buxaceae)] in one-gallon pots or changed our site selection for the sampling round in October of 2021. One holly shrub was replaced with a boxwood underneath two scale-infested and two scale-uninfested trees while both holly shrubs were replaced with boxwoods underneath one scale-infested tree. We used the Kruskal-Wallis test to determine if natural enemy and non-natural enemy abundance recorded in 3, 6, and 9 day boxwoods and hollies at the four trees where only one shrub was replaced. We found no significant differences in the abundance of either group at any time point (Supp Table 1 [online only]). Because no boxwoods were sampled in July, we analyzed the July data separately from the October data.

To measure natural enemy and non-natural enemy accumulation on planted hollies, we measured arthropod accumulation on *I. cornuta and I. vomitoria* hollies planted below the two tree types after six days in July and October of 2021. We selected eight hollies below scale-infested trees (five *I. vomitoria*, three *I. cornuta*), and seven hollies below scale-uninfested trees (five *I. vomitoria*, two *I. cornuta*) for sampling. On the first day, we vacuumed all shrubs for one minute to remove arthropods from the plant. We then revisited shrubs after six days to vacuum shrubs once more for one minute to collect arthropods. Arthropods from these samples were preserved and processed in the same way as vacuum samples from potted hollies. We measured the volume of all shrubs to use as an offset term in statistical analysis.

We used the Kruskal-Wallis test to determine if the abundance of natural enemies and non-natural enemies collected on potted holly shrubs at three, six, and nine day intervals differed significantly based on tree type. We analyzed samples from July and October separately. If we found a significant effect of tree type on enemy abundance at any time point we ran post-hoc Kruskal-Wallis tests to determine which of the four most abundant natural enemy groups were influenced by tree type at that time point.

We used generalized linear models to determine if natural enemy and non-natural enemy abundance differed on planted shrubs at six days based on tree type, shrub species, and the interaction of these predictors. We included an offset term for shrub volume in these models. We analyzed data from July and October separately because one shrub was not sampled in October. If we found a significant effect of tree type on natural enemy abundance in either July or October we ran negative binomial GLMs to determine how tree type influenced the four most abundant enemy groups collected from our samples.

Results

Hypothesis 1: Scale-Infested Willow Oaks Support More Scales, Natural Enemies, and Non-natural Enemies Arthropods Than Scale-Uninfested Oaks

Scale density per 30 cm was significantly higher on scale-infested oaks (mean ± S.E. = 11.3 ± 2.0 scales per 30 cm) than on scale-uninfested oaks (0.6 ± 0.2 scales per 30 cm) (Fig. 1A, $\chi = 27.138$, $p < 0.001$). Scale density differed significantly across the three oak species (Supp. Fig. 1 [online only], $\chi = 29.199$, $p < 0.001$). Scale density was significantly different between overcup and willow oaks ($p < 0.001$) and between sawtooth and willow oaks ($p < 0.001$). Scale density was also significantly different between sawtooth and overcup oaks (sawtooth: 0.4 ± 0.2, overcup: 0.7 ± 0.2 scales per 30 cm) ($p = 0.03$). The most abundant scale group we recorded were obscure scales—*Melanaspis obscura* (58% of all counted scales), followed by oak lecanium scales (*Parthenolecanium quercifex*) (29%), and Oak eriococcin scales (*Acanthococcus quercus*) (11%).

Natural enemies were significantly more abundant in beat samples from scale-infested oaks than scale-uninfested oaks in 2019 ($\chi = 12.408$, $p < 0.001$) and 2020 ($\chi = 8.723$, $p = 0.003$) (Fig. 1B). The most common natural enemies in scale-infested oaks in 2019 were spiders (49% of all natural enemies), parasitoids (23%), ants (7%), and lady beetles (7%) while the most common natural enemies in scale-uninfested oaks were spiders (54%), ants (25%), and parasitoids (13%). In 2019, Scale-infested oaks hosted significantly more spiders ($\chi = 8.186$, $p = 0.004$), parasitoids ($\chi = 8.968$, $p = 0.003$), and lady beetles ($\chi = 5.189$, $p = 0.004$) than scale-uninfested oaks (Supp Fig. 2, Supp Table 2 [online only]). In 2020 the most

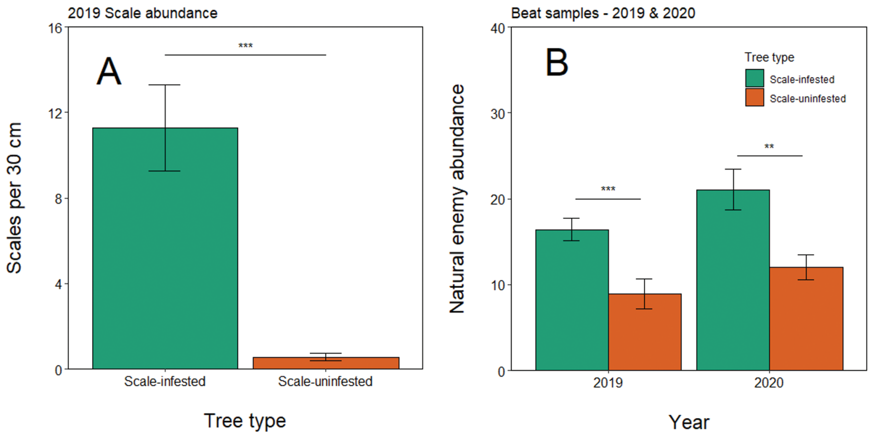

Fig. 1. A) The effect of tree type on scale abundance per 30 cm twig lengths. B) The effect of tree type on natural enemy abundance recorded from beat samples in 2019 and 2020. Significance is indicated as follows: NS: $p > 0.05$, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$. Error bars indicate standard error of the mean.

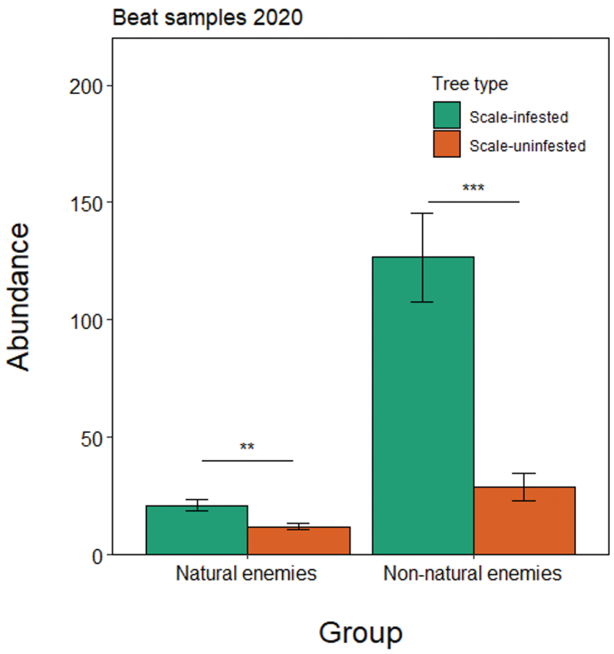

Fig. 2. The effect of tree type on natural enemy and non-natural enemy abundance recorded from beat samples in 2020. Significance is indicated as follows: NS: $p > 0.05$, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$. Error bars indicate standard error of the mean.

common natural enemies in scale-infested oaks were spiders (46%), parasitoids (35%), and ants (6%), in scale-uninfested oaks the most abundant natural enemies were spiders (52%), parasitoids (27%), and predatory hemipterans (6%). In 2020 scale-infested oaks hosted significantly more spiders ($\chi = 4.197$, $p = 0.026$) than scale-uninfested oaks (Supp Fig. 3, Supp Table 2 [online only]). In 2020, scale-infested oaks hosted significantly more non-natural enemy arthropods (126.6 ± 18.8) than scale-uninfested oaks (28.8 ± 5.8) ($\chi = 20.430$ $p < 0.001$, Fig. 2). The most abundant non-natural enemy arthropod orders in scale-infested oaks were Hemiptera (48% of all non-natural enemies), Thysanoptera (27%), and Psocodea (25%), and the most abundant non-natural enemy arthropod orders in scale-uninfested oaks were Hemiptera (43%), Psocodea (35%), and Thysanoptera (21%). Scale density in willow oaks did not significantly predict natural enemy abundance ($\beta = 0.011 \pm 0.006$, $z = 1.748$, $p = 0.081$).

Hypothesis 2: More Natural Enemies and Non-natural Enemies Passively Disperse From Scale-Infested Compared to Scale-Uninfested Trees

There was not a significant difference in the number of natural enemies collected in traps hung from scale-infested oaks (0.01 ± <0.01 natural enemies/cm^2/day or 1.5 ± 0.1 natural enemies/day) compared to scale-uninfested oaks (0.01 ± <0.01 natural enemies/cm^2/day or 1.4 ± 1.8 natural enemies/day) ($\chi = 0.58$, $p = 0.44$). Similarly, there was not a significant difference in the number of non-natural enemy arthropods collected in traps below scale-infested oaks (0.02 ± <0.01 arthropods/cm^2/day or 5.0 ± 0.54 arthropods/day) compared to scale-uninfested oaks (0.02 ± <0.01 arthropods/cm^2/day or 3.9 ± 0.4 arthropods/day) ($\chi = 2.78$, $p = 0.10$).

Hypothesis 3: Shrubs Under Scale-Infested Trees Accumulate More Natural Enemies and Non-natural Enemies Than Shrubs Below Scale-Uninfested Trees

In 2020, there were significant main effects of tree type ($\chi = 7.160$, $p = 0.007$) and shrub species ($\chi = 14.125$, $p < 0.001$) on natural enemy abundance in planted shrubs wherein shrubs below scale-infested oaks hosted more natural enemies than shrubs below scale-uninfested oaks and *I. vomitoria* shrubs hosted significantly more natural enemies and non-natural enemy arthropods than *I. cornuta* shrubs (Supp Figs. 3A and 4 [online only], Table 1). Only shrub species had a significant effect on non-natural enemy abundance ($\chi = 14.137$, $p < 0.001$), wherein *I. vomitoria* shrubs hosted more non-natural enemy arthropods than *I. cornuta* shrubs (Fig. 4, Table 1). Spiders, parasitoids, and ants were the most abundant natural enemies in shrubs below scale-infested (41, 34, and 14% of all arthropods respectively) and scale-uninfested (42, 36, and 11% respectively) trees in 2020. Ants were significantly more abundant below scale-infested trees ($z = 2.225$, $p = 0.026$) while the 3 other most abundant enemy groups did not differ based on tree type (Supp Fig. 4, Supp Table 3 [online only]). Acari, Psocodea, and Diptera were the most abundant non-natural enemy arthropod orders in shrubs below scale-infested (26 25, 14% of all non-natural enemy arthropods respectively) and scale-uninfested (38, 17, and 15% respectively) trees. In 2021 tree type ($\chi = 20.882$, $p < 0.001$), but not shrub species, had a significant main effect on natural enemy and non-natural enemy abundance in landscape shrubs, wherein shrubs below scale-infested trees hosted significantly more natural enemies and non-natural enemy arthropods (Fig. 3B, Table 1).

Table 1. Model fitting results evaluating the effect of tree type and shrub species on natural enemy and non-natural abundance collected from vacuum samples on planted holly shrubs. All models are negative binomial generalized linear models with the abundance of each arthropod group as the response term. All models contain an offset term for shrub volume. Significant differences are bolded. NE = natural enemies, NNE = non-natural enemy arthropods

Response	Predictor	Estimate ± SE	χ	*p*
2020 samples				
NE abundance in holly shrubs	**Tree type**	**Intercept: 4.066 ± 0.335** **Type: Scale-infested: 1.124 ± 0.431**	**7.160**	**0.007**
	Shrub species	**Species: *I. vomitoria*:1.483 ± 0.438**	**14.125**	**< 0.001**
	Type * species interaction	Type: Scale-infested * species: *I. vomitoria*: −0.518 ± 0.614	0.690	0.406
NNE abundance in holly shrubs	Tree type	Intercept: 5.005 ± 0.402 Type: Scale-infested: 1.013 ± 0.500	3.362	0.067
	Shrub species	**Species: *I. vomitoria*: 1.765 ± 0.508**	**14.137**	**< 0.001**
	Tree type * Species interaction	Type SP * Species: *I. vomitoria*: −0.643 ± 0.712	0.787	0.375
2021 Samples				
NE abundance in holly shrubs	**Tree type**	**Intercept: 4.619 ± 0.284** **Type: Scale-infested: 1.214 ± 0.368**	**20.882**	**< 0.001**
	Shrub species	Species: *I. vomitoria*: 0.529 ± 0.335	2.099	0.147
	Tree type * species interaction	Type SP * species: *I. vomitoria*: −0.348 ± 0.445	0.600	0.439
NNE abundance in holly shrubs	**Tree type**	**Intercept: 5.218 ± 0.435** **Type: Scale-infested: 1.789 ± 0.560**	**13.594**	**< 0.001**
	Shrub species	Species: *I. vomitoria*: 0.791 ± 0.513	0.824	0.364
	Tree type * species interaction	Type SP * species: *I. vomitoria*: −0.780 ± 0.680	1.273	0.259

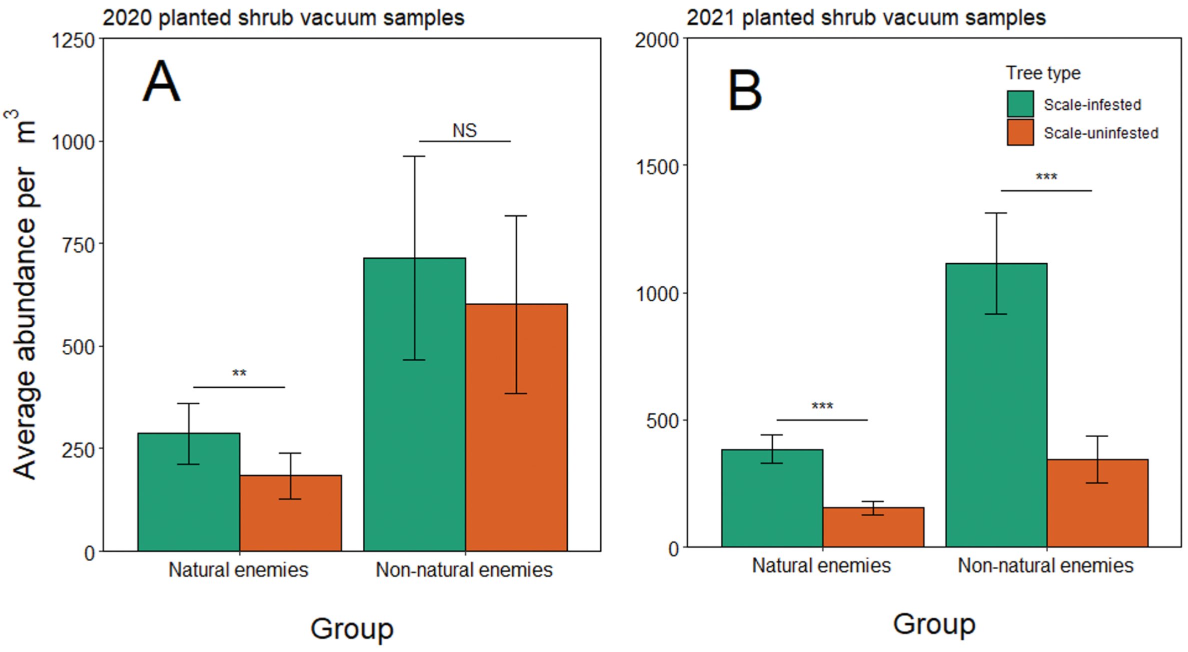

Fig. 3. The effect of tree type on natural enemy and non-natural enemy arthropod abundance recorded from vacuum samples collected from planted shrubs in A) 2020 and B) 2021. Significance is indicated as follows: NS: $p > 0.05$, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$. Error bars indicate standard error of the mean.

In 2021 spiders, parasitoids, and ants were the most abundant enemy groups in shrubs below scale-infested (62, 16, 10% of all natural enemies respectively) and scale-uninfested trees (51, 26, 8% respectively). Spiders ($z = 4.395$, $p < 0.001$) and predatory hemipterans ($z = 5.380$, $p < 0.001$) were significantly more abundant in shrubs below scale-infested trees than scale-uninfested trees (Supp Fig. 5, Supp. Table 3 [online only]). In 2021 Acari, Diptera, and Collembola were the most abundant non-natural enemy arthropod orders in shrubs under scale-infested (48, 13, 13% of all nonenemy arthropods respectively) and scale-uninfested trees (45, 24, 6% respectively).

In July of 2021 we found no significant effect of tree type on natural enemies or non-natural enemy arthropod abundance in potted

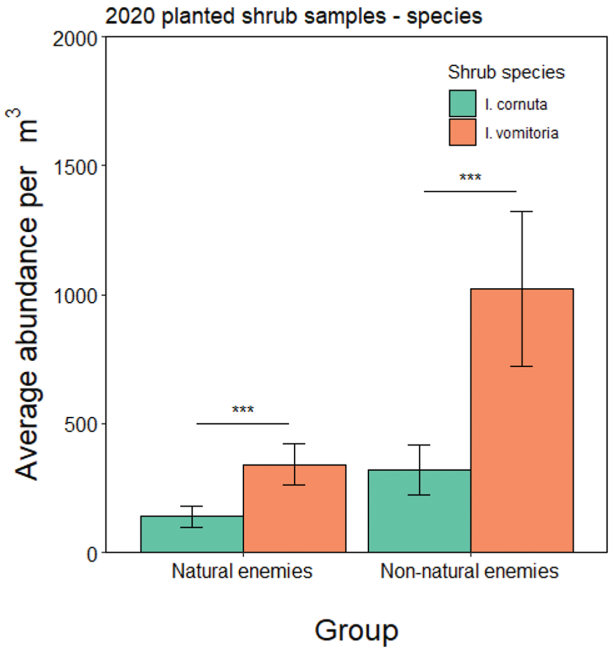

Fig. 4. The effect of shrub species on average natural enemy and non-natural enemy abundance collected from vacuum samples in 2020. Significance is indicated as follows: NS: $p > 0.05$, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$. Error bars indicate standard error of the mean.

hollies at three days (Fig. 5A, Table 2). At six days, potted hollies below scale-infested oaks hosted significantly more non-natural enemy arthropods than hollies below scale-uninfested oaks ($\chi = 10.465$, $p = 0.001$), but natural enemy abundance was not significantly different (Fig. 5A, Table 2). At nine days, potted hollies below scale-infested oaks hosted significantly more natural enemies ($\chi = 9.742$, $p = 0.002$) and non-natural enemy arthropods ($\chi = 3.952$, $p = 0.049$) than scale-uninfested oaks (Fig. 5A, Table 2). Of the four most abundant natural enemy groups, spiders ($\chi = 4.417$, $p = 0.036$) and ants ($\chi = 7.664$, $p = 0.006$) were significantly more abundant in potted hollies below scale-infested trees compared to scale-uninfested trees at nine days (Supp Fig. 6, Supp Table 2 [online only]). In October, we did not find a significant difference in natural enemy abundance or non-natural enemy arthropod abundance in potted hollies below either tree type in the three-, six- or nine-day sample periods (Fig. 5B Table 2).

In six-day accumulation samples from planted holly shrubs, we found that natural enemy [$\chi = 19.236$, $p < 0.001$ (July); $\chi = 21.365$, $p < 0.001$ (October)] and non-natural enemy abundance [$\chi = 11.112$, $p = 0.001$ (July), $\chi = 17.902$, $p < 0.001$ (October)] was significantly higher in hollies below scale-infested trees than scale-uninfested trees in July and October of 2021 (Fig. 6, Table 3). There was no significant effect of holly species on natural enemy abundance in July and October and no effect of holly species on non-natural enemy abundance in July (Table 3). In October, tree type interacted with shrub species to influence non-natural enemy abundance at six days ($\chi = 16.383$, $p < 0.001$, Table 3). Non-natural enemy abundance was higher in *I. vomitoria* shrubs under scale-infested trees compared to scale-uninfested trees and non-natural enemy abundance was higher on *I. cornuta* shrubs under scale uninfested compared to scale-infested trees (Supp Fig. 7 [online only]). In July, spiders were significantly more abundant in planted hollies below scale-infested trees ($z = 5.225$, $p < 0.001$) and in October spiders ($z = 4.929$, $p < 0.001$) and predatory hemipterans ($z = 1.980$, $p = 0.048$) were significantly more abundant in planted hollies below scale-infested trees (Supp Figs. 8 and 9, Supp Table 3 [online only]).

Discussion

Urban trees host diverse communities of natural enemies and non-natural enemy arthropods. Here we demonstrate that a group of insects commonly considered to be tree pests can support natural enemy communities in urban trees and the shrubs below them. In only six to nine days, shrubs below scale-infested trees accumulated more natural enemies than shrubs below scale-uninfested trees. Therefore, plants growing below scale-infested urban trees may receive associational resistance to pest damage due to regular visitation, and thus herbivore population regulation by, natural enemies. Our work suggests that the enemy communities in urban trees and shrubs are linked so management in one plant type could affect arthropod communities, including pests, in the other.

We found that scale-infested oaks hosted more natural enemies than scale-uninfested oaks and this may be due to scales serving as hosts for parasitoids and prey for predators. Dense scale populations on urban vegetation are often associated with abundant parasitoid communities (Hanks and Denno 1993a, Tooker and Hanks 2000, Dale and Frank 2014, Long et al. 2019, Nighswander et al. 2021). Although we found more parasitoids in scale-infested than scale-uninfested trees in 2019, we did not find a similar effect in 2020. However, we collected significantly more spiders in 2019 and 2020 from scale-infested compared to scale-uninfested oaks and spiders outnumbered parasitoids in all samples in both years. In our study system, scales may better support generalist predators such as spiders instead of parasitoid wasps. In addition, generalists may be more important in conservation biological control since they feed on many pests whereas parasitoids may be more specialized. Spiders feed on scales in urban landscape settings (Hodges and Braman 2004), and spiders can regulate populations of economically important scales (e.g., Mansour and Whitecomb 1986). However, they also consume other natural enemies such as parasitoids that are abundant in scale-infested trees. Intraguild predation of parasitoids by spiders can hinder biological control of pests normally controlled by parasitoids (Heimpel et al. 1997, Traugott et al. 2012). Thus, spider predation may reduce scale parasitism and could explain why some scale species are not adequately controlled by parasitoids in urban trees (e.g., Dale and Frank 2014, Long et al. 2019). Future research which examines if scale-infested urban trees support natural enemies like spiders directly by serving as prey or indirectly by attracting intraguild prey, such as parasitoid wasps, may indicate the exact mechanism by which scales recruit natural enemies.

Beyond serving as prey, certain scale insect species produce honeydew, which is an important resource for spiders, ants, parasitoids, lacewing larvae, solitary bees, and many other arthropod taxa (Ewers 2002, Hogervorst et al. 2008, Konrad et al. 2009, Pfannenstiel and Patt 2012, Tena et al. 2016). In scale-infested trees the most abundant scale species we recorded was obscure scale which does not produce honeydew, however, the second and third most abundant species—oak lecanium scales and oak eriococcin scales—do. Since scale-infested trees hosted more non-natural enemy arthropods than scale-uninfested trees, the supplemental honeydew produced by scales may provide resources to support non-natural enemies, and thus alternative prey to support natural enemies. The most abundant non-natural enemy arthropod orders in scale-infested trees were Hemiptera, Thysanoptera, and Psocodea. These arthropods orders are primarily herbivores (or fungivores in the case of Psocodeans) and are eaten by many arthropod natural enemies. The honeydew produced by scales may indirectly support natural enemy communities by supporting non-natural enemy arthropods, and thus alternative prey. Therefore, the ability of scale insects to serve

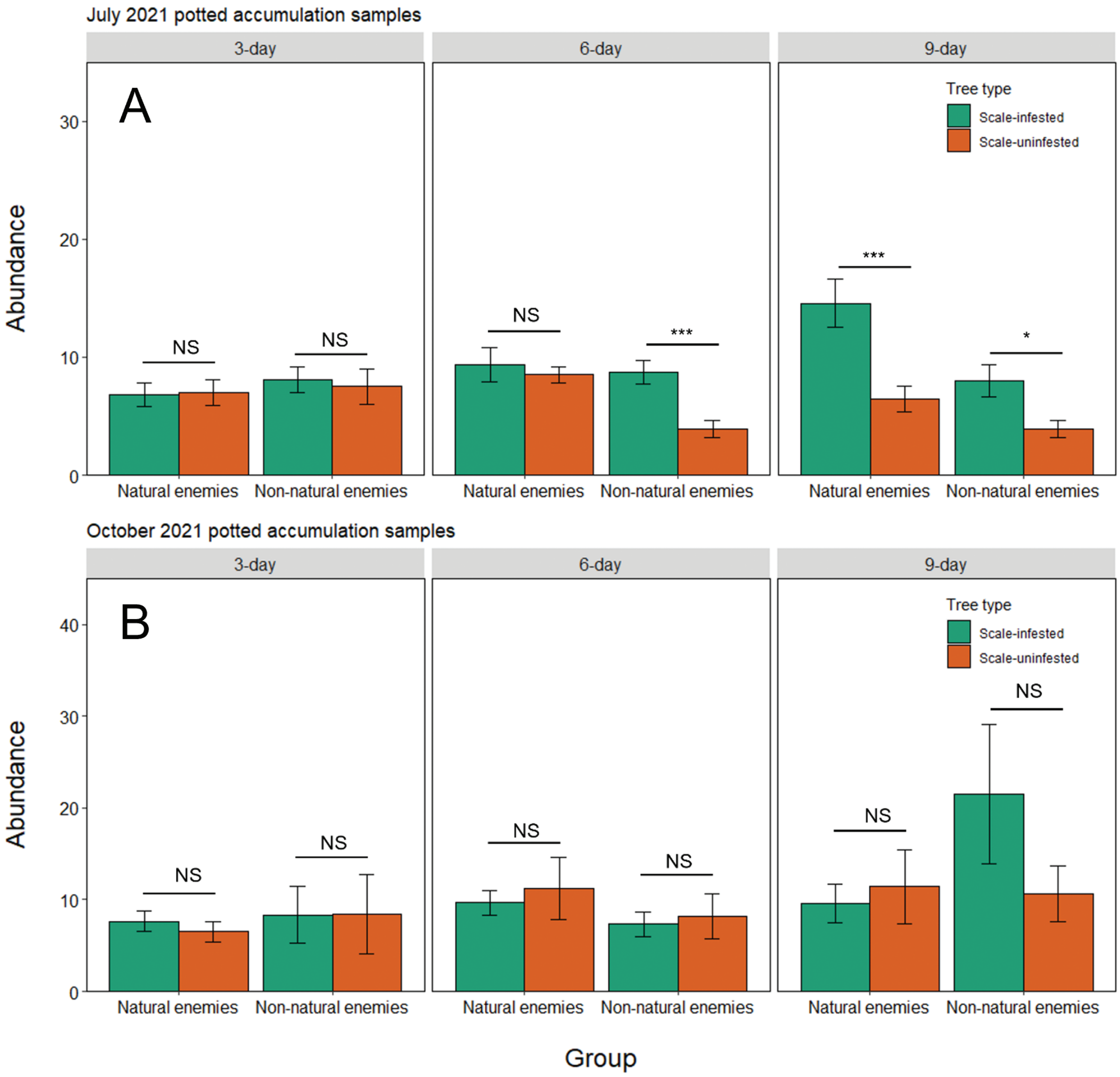

Fig. 5. The average abundance of arthropods, natural enemies, and spiders are shown from 3, 6, and 9-d accumulation samples collected from potted hollies in July and October of 2021. Significance is indicated as follows: NS: $p > 0.05$, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$. Error bars indicate standard error of the mean.

as prey, support alternate prey, and produce honeydew may act together to support natural enemy communities in urban trees.

Scale-infested oaks may also host high abundances of other herbivores which could also attract natural enemies to scale-infested trees. High scale abundance in urban trees could therefore act as an indicator of total herbivore abundance. For example, Nighswander et al. 2021 collected pests and natural enemies from vegetation in ornamental gardens in central Florida, USA. They found that scale insects constituted 77% of all pests identified and that seasonal changes in total pest abundance were driven by scale dispersal and mortality. Similarly, we found that scale-infested trees hosted more non-natural enemy arthropods compared to scale-uninfested trees. These findings indicate that quantifying the abundance of scales on trees may serve as an effective proxy for total herbivore abundance. Additionally, since we used different tree species to represent scale-infested and uninfested trees due to logistical constraints, interspecific differences in tree susceptibility to herbivores could influence herbivore abundance and thus natural enemy abundance collected in trees. It is uncertain if scale abundance, nonenemy abundance, or interspecific variation in tree susceptibility to herbivores, or the combination of these factors are what attract natural enemies to scale-infested trees, but future work which disentangles these relationships will better define the role of scales for natural enemy recruitment.

We found that shrubs below scale-infested trees tended to host greater natural enemy and non-natural enemy abundance than shrubs below scale-uninfested trees. However, we did not record a higher rate of natural enemy or non-natural enemy collection in intercept traps hanging from scale-infested trees. Our results suggest that arthropod movement from trees to shrubs occurs primarily through active rather than passive dispersal. However, the timing of our trap placement may have influenced our results. For example, certain arthropods only fall out of trees as juveniles when they cannot fly (e.g., lacewings or lady beetles) but would actively disperse as adults. The timing of when we placed our traps in trees—June and October—may have occurred at times when arthropods that would normally passively disperse into shrubs as juveniles had already reached adulthood. Additionally, the area

Table 2. Means and significance testing results for three-, six-, and nine-day accumulation samples collected from potted holly shrubs below scale-infested and scale-uninfested trees. Data are presented separately for July and October. Significant differences are bolded. NE = natural enemies, NNE = non-natural enemy arthropods

Sample	Tree type	Mean ± SE	χ	*p*
July				
Three-day NE abundance	Scale-infested	6.8 ± 1.0	0.019	0.890
	Scale-uninfested	7.0 ± 1.1		
Three-day NNE abundance	Scale-uninfested	7.5 ± 1.5	0.360	0.549
	Scale-infested	8.1 ± 1.1		
Six-day NE abundance	Scale-infested	9.4 ± 1.5	0.000	1.000
	Scale-uninfested	8.5 ± 0.7		
Six-day NNE abundance	**Scale-infested**	**8.7 ± 1.0**	**10.465**	**0.001**
	Scale-uninfested	3.9 ± 0.7		
Nine-day NE abundance	**Scale-infested**	**14.6 ± 2.0**	**9.742**	**0.002**
	Scale-uninfested	6.4 ± 1.1		
Nine-day NNE abundance	**Scale-infested**	**8.0 ± 1.4**	**3.952**	**0.049**
	Scale-uninfested	3.9 ± 0.9		
October				
Three-day NE abundance	Scale-infested	7.6 ± 1.1	0.388	0.533
	Scale-uninfested	6.5 ± 1.1		
Three-day NNE abundance	Scale-infested	8.4 ± 3.0	0.527	0.468
	Scale-uninfested	8.4 ± 4.3		
Six-day NE abundance	Scale-infested	9.6 ± 1.2	0.043	0.836
	Scale-uninfested	11.2 ± 3.4		
Six-day NNE abundance	Scale-infested	7.4 ± 1.3	0.282	0.595
	Scale-uninfested	8.2 ± 2.5		
Nine-day NE abundance	Scale-infested	9.6 ± 2.1	0.119	0.730
	Scale-uninfested	11.4 ± 4.0		
Nine-day NNE abundance	Scale-infested	21.5 ± 7.6	1.128	0.288
	Scale-uninfested	10.6 ± 3.0		

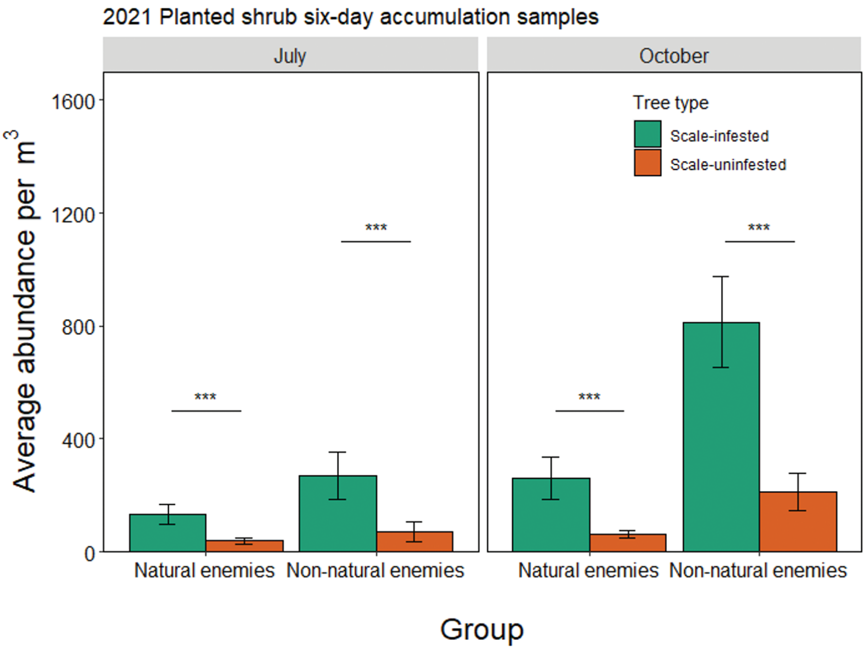

Fig. 6. Average abundance of each arthropod group per cubic meter collected from plated holly shrubs after 6 d in July and October of 2021. Significance is indicated as follows: NS: $p > 0.05$, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$. Error bars indicate standard error of the mean.

covered by our intercept traps was small compared to the total area of each tree's crown where arthropods could have fallen out, and as a result we may have not collected many arthropods as they fell out of trees. Therefore, placing larger intercept traps in trees in early summer (April to June) may further determine if more arthropods passively disperse from scale-infested trees than scale-uninfested trees.

Shrubs below scale-infested trees hosted more non-natural enemies in 2021. The higher abundance of non-natural enemies provides more alternative prey resources and may attract more

Table 3. Model fitting results for 6-d accumulation samples collected from landscape holly shrubs planted on the campus of NC-State University in 2021. All models are negative binomial generalized linear models with the abundance of each arthropod group as the response term. All models contain an offset term for shrub volume. NE = natural enemies, NNE = non-natural enemy arthropods

Response	Predictor	Estimate ± SE	χ	*p*
July				
Six-day NE abundance	**Tree type**	**Intercept: 3.861 ± 0.399** **Type: Scale-infested: 1.110 ± 0.501**	**19.236**	**<0.001**
	Shrub species	Species: *I. vomitoria*: −0.434 ± 0.470	0.961	0.327
	Tree type * shrub species	Type SP * Species: *I. vomitoria*: 0.223 ± 0.607	0.127	0.722
Six-day NNE abundance	**Tree type**	**Intercept: 4.948 ± 0.561** **Tree type: Scale-infested: 0.391 ± 0.727**	**11.112**	**0.001**
	Shrub species	Shrub species: *I. vomitoria*: −1.262 ± 0.671	0.803	0.370
	Tree type * shrub species interaction	Type: scale-infested * Species: *I. vomitoria*: 1.638 ± 0.887	3.366	0.067
October				
Six-day NE abundance	**Tree type**	**Intercept: 3.793 ± 0.578** **Tree type: Scale-infested: 1.247 ± 0.676**	**21.365**	**<0.001**
	Shrub species	Shrub species: *I. vomitoria*: 0.371 ± 0.637	3.003	0.083
	Tree type * shrub species interaction	Tree type: scale-infested * shrub species: *I. vomitoria*: 0.380 ± 0.768	0.249	0.618
Six-day NNE abundance	**Tree type**	**Intercept: 3.23 ± 0.534** **Type: scale-infested: 3.791 ± 0.592**	**17.902**	**<0.001**
	Shrub species	Shrub species: *I. vomitoria*: 2.195 ± 0.571	1.004	0.316
	Tree type * shrub species interaction	**Type: Scale-infested * Species: *I. vomitoria*: −2.978 ± 0.658**	**16.383**	**<0.001**

natural enemies to shrubs as a result (Gratton and Denno 2003, Langellotto and Denno 2004, Frank and Shrewsbury 2009). In our accumulation experiment with potted shrubs, we found that non-natural enemies, but not natural enemies, were more abundant below scale-infested trees at six days. At nine days, both non-natural enemies and natural enemies were more abundant below scale-infested trees which suggests the abundance of non-natural enemies supported natural enemy accumulation. Of the 4 most abundant enemy groups in landscape shrubs, we found more spiders, predatory hemipterans, and ants in shrubs below scale-infested trees. Orb-weaving spiders re-locate more frequently in habitats with high prey availability to reduce the variability in prey capture and minimize reproductive failure (Caraco and Gillespie 1986, Gillespie and Caraco 1987). In contrast, when prey availability is low, orb weaving spiders tend to stay in place to maximize the rate of prey capture (Caraco and Gillespie 1986, Gillespie and Caraco 1987). Orb-weaving spiders in scale-infested urban trees (where prey is abundant) may be more likely to relocate to shrubs below them to minimize variability in prey capture while spiders in scale-uninfested trees (where prey is less abundant) may stay in place to maximize the rate of prey capture. *Orius insidiosus* (Say), a common predatory hemipteran in urban trees (e.g., Parsons et al. 2020a), exhibits a direct density dependent response to prey availability, and preferentially oviposits in locations with high prey abundance (Coll and Ridgway 1995, Seagraves and Lundgren 2010). Thus, hemipterans such as *O. insidiosus* may disperse from trees to lay eggs in shrubs and *O. insidiosus* may be attracted to shrubs below scale-infested trees from nearby vegetation due to the high abundance of prey in these shrubs. Ants are common in turfgrass and garden environments in urban landscapes (e.g., Uno et al. 2010, Yadav et al. 2012). High ant abundance in shrubs below scale-infested trees may result from ants dispersing from nearby turfgrass to forage for prey in shrubs instead of dispersing from trees into shrubs. Thus, shrubs below scale-infested trees likely benefit from both active foraging of predators dispersing from scale-infested trees, but also from predators entering shrubs from surrounding vegetation to prey on high densities of non-natural enemies. Future research which determines how natural enemy communities in other vegetation strata such as turfgrass influence biological control within shrubs may further indicate the degree to which natural enemy communities are linked across urban vegetation strata.

The species of shrub planted below scale-infested trees likely influences habitat suitability for natural enemies and herbivores or alternative prey (e.g., Harris et al. 2016, Parsons et al. 2020b). We found more natural enemies and non-natural enemies in *I. vomitoria* shrubs than *I. cornuta* shrubs in 2020. Because *I. cornuta* is an exotic species, it does not have shared evolutionary relationships with herbivores native to the eastern United States. This absence of shared evolutionary relationships prevents certain herbivores from overcoming plant defenses and allows exotic plant species to escape herbivory in novel habitats (Keane and Crawley 2002). If herbivores prefer to use *I. vomitoria* as hosts over *I. cornuta*, then *I. cornuta* shrubs may generally host lower alternative prey abundance to support natural enemies. Both *I. cornuta* and *I. vomitoria* may be visited similarly by natural enemies dispersing from scale-infested trees, but natural enemies may be less likely to reside in *I. cornuta* shrubs due to lower prey abundance. Since we found an effect of shrub species on natural enemy and non-natural enemy abundance in 2020 but not in 2021, the effect of shrub species on natural enemy abundance may vary depending on what herbivores are colonizing shrubs. If broad generalists are the primary herbivores dispersing from trees to shrubs, then the native status of the shrub may not matter for retaining these herbivores and both native and exotic shrubs may be visited similarly by natural enemies.

We have documented a beneficial effect of scale insects on natural enemy communities in urban trees which spills over to shrubs planted below these trees. Our findings emphasize the importance of tolerating pest densities in urban trees to conserve natural enemy communities, and treating urban landscapes as ecosystems in which trees and shrubs are linked (Hermes et al. 1984, Shrewsbury and Raupp 2000, Frank 2014, Parsons and Frank 2019). Our results suggest that natural enemy communities in shrubs depend upon pests present within trees for survival. Trees with moderate pest densities ensure that natural enemies in the landscape have prey available to them when prey is lacking in shrubs below trees. Conversely, when prey is lacking within trees, natural enemies can rely on prey found within shrubs for survival. Treating trees with pesticides to control pests such as scale insects may reduce scale density, but treating trees could also kill off natural enemies that would otherwise feed on shrub pests below these trees. As a result, treating trees with pesticides could worsen pest issues in shrubs below trees. If urban landscapes are viewed as ecosystems in which arthropods in trees, shrubs, turfgrass, and herbaceous plants are linked, pesticide applications in any of these vegetation strata may affect natural enemy communities and produce pest outbreaks in other strata as a result. Viewing urban landscapes as ecosystems may prevent unnecessary pesticide applications and unintended pest outbreaks as a result.

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Conflict of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data used in this project are available from the Dryad data repository using the following link: https://doi.org/10.5061/dryad.83bk3j9vm.

Supplementary Data

Supplementary data are available at *Environmental Entomology* online.

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