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Abstract Scale insects are common tree pests in urban ecosystems. Although severe scale infestations can worsen tree condition, trees can tolerate moderate scale densities. Scale insects are prey for many arthropod natural enemies that also feed on plant pests throughout urban landscapes. Because scale-infested trees support natural enemy communities, they may support biological control services on nearby plants and function analogously to banker plants in greenhouse production systems. In this study we tested if sentinel insect prey were more likely to be removed on shrubs below scale-infested trees compared to scale-uninfested trees. We conducted several biological control experiments from 2019 to 2021 using fruit flies, aphids, and caterpillars in potted and planted holly shrubs below scale-infested and scale-uninfested oak trees. We found that caterpillars in potted

shrubs and fruit flies in planted landscape shrubs were more likely to be removed underneath scale-infested trees compared to scale-uninfested trees. Caterpillars were also more likely to be removed from landscape *Ilex vomitoria* shrubs compared to *I. cornuta* shrubs. In all other experiments we found no effect of scale infestation status or shrub species on prey removal. Our results suggest that scale-infested trees can support biological control services in shrubs below them but that this effect can vary depending on prey and shrub species. The natural enemy communities in urban trees and shrubs appear to be linked and tolerating tree pests can favor conservation biological control services in urban landscapes.

Keywords Scale insect · Conservation biological control · Urban tree · Natural enemy · Banker plant

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Introduction

Scale insects (Hemiptera: Coccoidea) are often more prevalent on urban trees than trees in rural or natural areas (Hanks and Denno 1993; Tooker and Hanks 2000; Long et al. 2019). Scales and other pests thrive in urban sites, such as along streets and in parking lots with high temperatures, extensive impervious surface cover, and low vegetation diversity and complexity (Speight et al. 1998; Shrewsbury and Raupp 2000, 2006; Tooker and Hanks 2000; Meineke et al. 2013; Dale and Frank 2014a; Dale et al. 2016;

Parsons et al. 2020b). High scale densities can worsen tree condition and reduce their aesthetic value (Frank et al. 2013; Just et al. 2019). However, trees growing where less impervious surface cover is present, such as in yards and parks, host lower scale densities that tend not to cause damage or reduce growth (Dale et al. 2016; Just et al. 2018; Meineke and Frank 2018). Scale insects support a diverse array of natural enemies by serving as prey for predators and hosts for parasitoids (Hanks and Denno 1993; Tooker and Hanks 2000; Dale and Frank 2014b; Camacho et al. 2018; Long et al. 2019). Many scale insect species also produce honeydew which is used by insect predators, parasitoids, and pollinators as a supplemental food source (Konrad et al. 2009; Pfannenstiel 2015; Tena et al. 2016). However, the honeydew produced by scales could support ant species that protect scales and prevent other natural enemies from consuming scales or using them as hosts (Vanek and Potter 2010). Nonetheless, multiple studies have found that trees with scales host more diverse arthropod communities than trees without scales (Didham 1993; Hanks and Denno 1993; Tooker and Hanks 2000; Ewers 2002; Wilson and Frank 2022), which suggests that ant antagonism does not prevent scales from supporting natural enemy communities. Therefore, trees with scales likely bolster local populations of parasitoid wasps and generalist predators such as lady beetles, heteropterans, and lacewings (Hanks and Denno 1993; Tooker and Hanks 2000; Hodges and Braman 2004). A basic tenet of integrated pest management (IPM) is to maintain pests below economic or damaging thresholds rather than eradicate them, in part to support natural enemies (Stern et al. 1959). Moderate scale densities on urban trees may enhance biological control of nearby plant pests by sustaining natural enemy survival, reproduction, and recruitment without affecting tree health.

Scale-infested urban trees may function similarly to banker plants in greenhouse production systems if infestation levels are tolerable for the tree and residents. In banker plant systems, non-crop plants provide resources such as pollen, prey, or hosts to support natural enemies of crop pests (Frank 2010). When pest abundance in the crop is low, natural enemies survive and maintain high densities using banker plant resources. For example, grain plants infested with bird-cherry oat aphids (*Rhopalosiphum padi* (Linnaeus)), which are not pests of

most greenhouse crops, support parasitoid wasps that parasitize important aphid pests such as green peach aphids (*Myzus persicae* (Sulzer)) (Prado and Frank 2014). Likewise, flowering ornamental pepper plants are used as banker plants to provide pollen to *Orius* spp. (Hemiptera: Anthocoridae) that feed on thrips (Wong and Frank 2013). In urban ecosystems, scale-infested urban trees may function similarly by providing scales as prey for predators, hosts for parasitoids, and, in some cases, honeydew for omnivorous natural enemies. Natural enemy populations supported by scales may then increase natural enemy density and biological control in nearby plants, such as shrubs, which often host high pest densities (Raupp et al. 1985, 2010). However, the natural enemies supported by scale insects may not consume certain pest species present on shrubs underneath trees. Thus scale-infested trees may support biological control of certain pests in nearby plants over others.

Willow oaks (*Quercus phellos* L.) are common urban trees in the southeastern USA which often host high densities of oak lecanium scale (*Parthenolecanium quercifex* (Fitch) (Hemiptera: Coccidae)) and European fruit lecanium scale (*P. corni* (Bouché) (Hemiptera: Coccidae)) in urban locations (Schultz 1984; Meineke et al. 2013; Camacho et al. 2017). Oak lecanium scales produce copious honeydew and are eaten and parasitized by a diverse community of natural enemies (Schultz 1984; Meineke et al. 2014; Camacho et al. 2018) which may support conservation biological control of nearby plant pests. In a previous study, we found that willow oaks host more scales and more natural enemies than sawtooth oaks (*Quercus acutissima* Carruth.) and overcup oaks (*Quercus lyrata* Walter) which host few scales (Wilson and Frank 2022). Furthermore, shrubs planted below scale-infested willow oaks hosted more natural enemies than shrubs below scale-uninfested oaks (Wilson and Frank 2022). To expand that research, we conducted experiments to determine if sentinel insect prey representing different pest species were more likely to be removed from shrubs underneath scale-infested trees compared to scale-uninfested trees in Raleigh, NC, USA. Understanding how urban tree pests can strengthen conservation biological control on nearby plants is necessary for the development of sustainable urban landscapes.

Materials and methods

Selection of field sites and sentinel prey species

We conducted biological control experiments on shrubs below scale-infested and scale-uninfested oak trees during the summers of 2019, 2020, and 2021. We used willow oaks (*Quercus phellos* L.) to represent scale-infested trees and sawtooth (*Q. acutissima* Carruth.) and overcup (*Q. lyrata* Walter) oaks to represent scale-uninfested trees. In a previous study we found that scale densities on twigs from willow oaks averaged 11.3 ± 2.0 (mean \pm SE) scales per 30 cm while scale densities on twigs from scale-uninfested sawtooth and overcup oaks averaged 0.6 ± 0.2 scales per 30 cm (Wilson and Frank 2022). We also found that scale-infested oaks hosted significantly more non-natural enemy arthropods (represented primarily by the orders Hemiptera, Thysanoptera, and Psocodea) than scale-uninfested oaks (Wilson and Frank 2022). Because surrounding impervious surface cover can influence scale density on urban trees, we selected trees in similar landscaping settings to prevent differences in impervious surface cover from influencing scale densities on trees. All trees were mature landscape trees (mean diameter at breast height for trees used in 2019 experiments = 34.3 ± 2.1 cm) that had mulch at their base and were planted in turfgrass lawns or in landscaping beds adjacent to sidewalks, streets, or lawns. Ornamental plantings near our study trees consisted of herbaceous plants (e.g., *Itea virginica* L.), shrubs (e.g., *Ilex vomitoria* Sol. ex Aiton), and a few neighboring trees (e.g., *Lagerstroemia* spp. L.).

In all experiments we used sentinel prey including dead *Drosophila* spp. (Diptera: Drosophilidae) adults, crape myrtle aphids (*Tinocallis kahawaluokalani* (Kirkaldy) (Hemiptera: Aphididae)), corn earworm larvae (*Helicoverpa zea* (Boddie) (Lepidoptera: Noctuidae)), and fall armyworm larvae (*Spodoptera frugiperda* J.E. Smith (Lepidoptera: Noctuidae)) because they are consumed by many generalist predators and have been used by other researchers for assessing biological control (Isenhour et al. 1989; Parsons and Frank 2019; Nelson et al. 2020). In a previous study we found that scale-infested trees host more spiders, parasitoids, and lady beetles than scale-uninfested oaks (Wilson and Frank 2022). Therefore we selected sentinel prey items that are widely consumed by

generalist natural enemies commonly found in scale-infested trees. Dead *Drosophila* adults are consumed by predatory hemipterans and spiders (Krimmel and Pearse 2013), crape myrtle aphids produce honeydew which attracts predators such as ants, and crape myrtle aphids are consumed by lacewings, predatory hemipterans, syrphid fly larvae, and ladybeetles (Mizell and Schiffhauer 1987), finally both corn earworm and fall armyworm larvae are consumed by predatory hemipterans and spiders (Guillebeau and All 1990; Joseph and Braman 2009; García et al. 2022). In these experiments we did not directly quantify predation by natural enemies but rather removal of sentinel prey after set time periods. All experiments were conducted on the campus of North Carolina State University (NCSU).

Crape myrtle aphid biological control experiments—2019 and 2020

In 2019, we reared crape myrtle aphids on planted crape myrtle trees (*Lagerstroemia* spp. L.) on NCSU's campus for use in biological control experiments. To rear aphids, we located branches with aphids and covered the entire branch with a mesh bag to exclude predators and parasitoids. We left bags in place for two to four weeks to allow aphids to accumulate on leaves inside bags. For each experiment iteration, we removed infested crape myrtle leaves with approximately five cm of the basal twig remaining and placed them into water picks. We placed water picks into square pots that were filled with sand. We then placed these sand-filled pots with water picks into pots of the same size that had been hot glued on to 15 cm diameter circular plastic dishes below each study tree. We filled water dishes with soapy water to prevent ground-dwelling predators such as ants from entering pots and removing prey and held dishes in place with landscaping staples. This setup allowed flying arthropods and flightless arthropods that fell out of trees to access prey. The starting aphid density was reduced to approximately 50 nymphs per leaf using a paint brush and an OptiVISOR head lens (Donegan Optical Company, Inc. Lenexa, KS, USA). All crape myrtle aphid adults are alate (Alverson and Allen 1991), therefore we removed all alate aphids from leaves prior to beginning the experiment to reduce error associated with aphids dispersing to new leaves or producing more offspring. We recorded aphid abundance at

24 h after initiating the experiment. Because we did not directly observe predation on aphids by natural enemies, reductions in aphid abundance on leaves could be attributed to predation or death by other causes. This experiment was conducted six times during the months of July–September of 2019. To serve as controls, in the second iteration of the experiment, we placed a second aphid-infested leaf in a second pot below each tree in which contained the water pick inside of a mesh bag which was tied at the top and which had bamboo stakes in its corners to prevent the bag from falling on the leaf.

In the summer of 2020, we placed crape myrtle aphids on holly shrubs below 14 scale-infested and 15 scale-uninfested oaks (six *Q. acutissima*, nine *Q. lyrata*). We used nine *Ilex vomitoria* Sol. ex Aiton and six *I. cornuta* Lindl. shrubs below scale-uninfested oaks and five *I. vomitoria* and nine *I. cornuta* below scale-infested oaks. At each shrub we placed one leaf, with five cm of twig attached to it, into a water pick and used twist ties to secure these water picks to a holly shrub. On each leaf we reduced the abundance of aphids to approximately 50 individuals. We checked aphid abundance after 24 h to quantify prey removal. We conducted this experiment five times in August of 2020.

Drosophila biological control experiments on planted shrubs—2020

In 2020, we measured *Drosophila* adult removal at 24 h from planted holly shrubs below scale-infested and uninfested trees. We sourced *Drosophila* adults (a mixture of *Drosophila suzukii* (Matsumura) and *Drosophila melanogaster* Meigen) from genetics laboratories at North Carolina State University, USA. We glued ten dead *Drosophila* adults on four cm² cardstock squares (hereafter referred to as bait cards) and froze bait cards until placing them in the field. We created clip cages to cover bait cards and serve as controls in this experiment. Clip cages consisted of a hairclip attached to a four cm² foam base with a four cm plastic tube with fine mesh netting over the top (Parsons and Frank 2019). Control bait cards within cages were placed within 0.5 m of the open bait card. We placed bait cards and control cages on holly shrubs below 14 scale-infested and 15 scale-uninfested trees. These shrubs were below the same trees used for the crape myrtle aphid removal experiments

in 2020, but these experiments were conducted on different dates. We counted the number of *Drosophila* remaining on cards after 24 h. We repeated this experiment four times between June and July 2020. We excluded one round of data from analysis because heavy rainfall damaged many cards and removed most flies.

Potted and planted holly biological control experiments with caterpillars and *Drosophila*—2021

In 2021 we measured biological control in potted dwarf yaupon holly shrubs (*I. vomitoria* ‘schillings’, 3.8 l pots), with two placed below each of 14 scale-uninfested trees (six overcup oaks and eight sawtooth oaks) and 14 scale-infested trees (willow oaks). We placed the two shrubs below each tree such that the plants were located on opposite sides of the tree. We placed two shrubs under each tree so that we could run two predation experiments simultaneously. To deter ants from establishing colonies in pots, we placed potted hollies into pots of the same size (3.8 l) coated with a five cm band of Fluon® (Insect-a-Slip Insect Barrier—Fluon®, Bioquip Products, Rancho Dominguez, CA, USA) that were held in place with landscaping staples. We also treated the soil in all plants with permethrin.

On one shrub we pinned two fourth to fifth instar laboratory reared corn earworm larvae. We attached larvae to shrubs by pinning them with size zero insect pins to stems on opposite sides of the plant through the penultimate abdominal segment. This method of pinning does not result in caterpillar mortality after 24 h (Frank and Shrewsbury 2009). After 24 h we recorded if each caterpillar had been attacked (if partial remains of the caterpillar was present) or removed from its pin. This method of assessing caterpillar predation has been used in other studies and is considered effective for measuring predation by arthropods and not vertebrates like birds in urban landscape settings (Frank and Shrewsbury 2004, 2009; Frank et al. 2007). For the final two repetitions of this experiment, we used laboratory reared fall armyworm larvae in place of corn earworm larvae. We checked plants during the first round of the experiment after 24 h. However, due to the low rate of removal at this time point, we checked plants at approximately 30 h for the remaining experiment rounds.

On the second shrub, we attached *Drosophila* bait cards with a binder clip. As with the caterpillar experiment, we checked plants during the first round of the experiment after 24 h, and at 30 h for the remaining experiment rounds. We did not use *Drosophila* data from one experiment round where rain removed flies from cards. We used boxwood shrubs (*Buxus* sp. L.) at four sites to replace stolen or dead hollies for five iterations of both removal experiments. Both experiments were repeated ten times during the months of August and September of 2021. We switched which shrub received which prey (caterpillars or bait cards) for each round of experiments.

Finally, we conducted these predation experiments on planted landscape hollies below our scale-infested and scale-uninfested trees. We used hollies below 14 scale-infested oaks and 13 scale-uninfested oaks (six sawtooth oaks, seven overcup oaks) for this experiment. *I. cornuta* was below five scale-uninfested trees and six scale-infested trees, and *I. vomitoria* was below eight scale-infested and eight scale-uninfested trees. At each site we placed two corn earworm caterpillars on opposite sides of a randomly selected holly shrub and attached a *Drosophila* bait card to the middle of a neighboring shrub. Fall armyworm larvae were used in place of corn earworm larvae in the last two rounds of the experiment. We recorded how many flies and caterpillars had been removed after 24 h. We repeated this experiment ten times over the months of August and September of 2021.

Statistical analysis

All statistical analysis was conducted in R version 4.2.1 (R Core Team 2022). We fit general linear models to determine how average aphid abundance after 24 h was influenced by infestation status separately in 2019 and 2020. In 2019 tree infestation status was the only predictor while in 2020 tree infestation status, shrub species, and their interaction were the predictors. We included average initial aphid abundance as a covariate in both models because the starting abundance of aphids at all sites was not always 50 (2019: 49.3 ± 0.2 , 2020: 49.8 ± 0.04). We fit one additional general linear model to determine if average aphid abundance differed between open and caged twigs used in the second experiment iteration in 2019. In this model initial aphid

abundance was included as a covariate. We used type II ANOVAs to assess the significance of these models.

For the *Drosophila* removal experiment in 2020, we fit a generalized linear mixed effect model (binomial, logit link function) in package “lme4” (Bates et al. 2015) with a random intercept term for experiment round in all models. The response term was the presence or absence of *Drosophila* removal at 24 h and the predictors were tree infestation status (scale-infested vs. uninfested), shrub species (*I. cornuta* vs. *I. vomitoria*), and their interaction. We used an additional binomial glm to determine if *Drosophila* removal on open and closed bait cards differed at 24 h. The additional variation explained by the random effect term was zero and produced a singular fit in both models. Therefore, we removed the random effect term from both models. We used likelihood ratio tests to assess the significance of these models and all other generalized linear mixed effects models.

We analyzed *Drosophila* removal data separately from caterpillar removal data in both the potted plant and landscape removal experiments conducted in 2021. We also analyzed removal data from potted shrubs separately from removal data on planted shrubs. In each of these models we fit generalized linear mixed models (binomial error distribution, logit link function) where the presence or absence of *Drosophila* or caterpillar removal were the response terms. We included a random intercept term in all models for experiment round. In the potted plant models, we included tree infestation status, shrub species, and final time point as predictors. We included shrub species as a predictor because some holly shrubs were replaced with boxwoods over the course of the experiment. We included final time point as a predictor because we checked shrubs at 24 h for the first round of the experiment and at 30 h for all other rounds. In the planted holly removal models the predictor terms were tree infestation status, shrub species (*I. vomitoria* or *I. cornuta*), and their interaction. In the *Drosophila* removal experiment on planted shrubs we removed the random effect term from the model because the variance it explained was zero and resulted in singular fits.

Results

In both 2019 and 2020 tree infestation status did not influence average aphid abundance at 24 h (Fig. 1a,

b, Table 1). In 2020 there was no effect of shrub species on aphid abundance and shrub species did not interact with tree infestation status to influence aphid abundance (Fig. 2a, Table 1). In 2019 average aphid abundance was greater on caged leaves compared to open leaves ($F=8.303$; $df=1, 56$; $p=0.006$, Supp. Fig. S1, Supp. Table S1). Therefore cages were effective at excluding predators from crape myrtle leaves placed in pots.

In 2020, there was no effect of tree type or shrub species on *Drosophila* removal in planted shrubs (Figs. 1c, 2b, Table 1). *Drosophila* were also more likely to be removed from open bait cards compared to caged bait cards ($\chi^2=62.810$; $df=1$; $p<0.001$, Supp. Fig. S2, Supp. Table S1). Therefore, caged bait cards were effective at excluding predators in planted hollies.

In 2021, tree infestation status did not influence *Drosophila* removal in potted hollies and *Drosophila* removal did not differ between potted yaupon hollies and boxwoods (Fig. 1d, Table 1). Additionally, the final time point at which observations were recorded (24 h vs. 30 h) did not influence

Drosophila removal (Table 1). However, *Drosophila* were more likely to be removed in planted shrubs underneath scale-infested trees compared to scale-uninfested trees ($\chi^2=4.540$; $df=1$; $p=0.033$, Fig. 1e, Table 1). Shrub species did not influence *Drosophila* removal in planted shrubs and did not interact with tree infestation status (Fig. 2c).

In potted hollies, caterpillars were more likely to be removed underneath scale-infested trees compared to scale-uninfested trees (Fig. 1g, $\chi^2=8.106$; $df=1$; $p=0.004$). Caterpillar removal was not influenced by the final time point at which data were collected and caterpillar removal did not differ between potted yaupon hollies and boxwoods (Table 1). In planted hollies, caterpillars were more likely to be removed from *I. vomitoria* shrubs compared to *I. cornuta* shrubs (Fig. 2d, $\chi^2=6.886$; $df=1$; $p=0.009$), but there was no effect of tree infestation status on caterpillar removal in planted hollies (Fig. 1f, Table 1). Finally, tree infestation status and shrub species did not interact to influence caterpillar removal in planted hollies (Table 1).

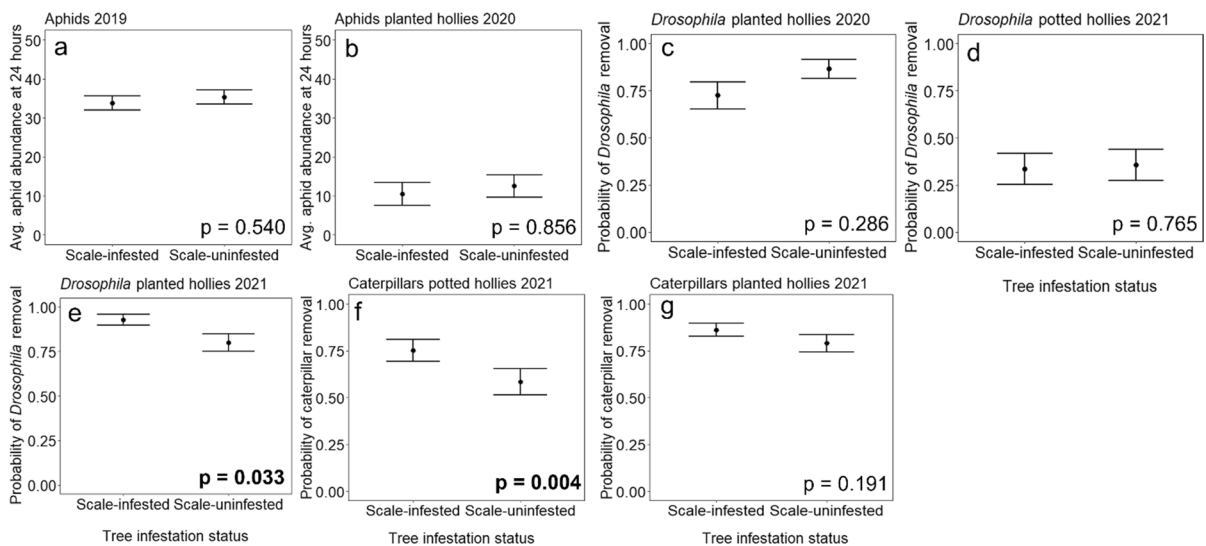


Fig. 1 Effect of tree infestation status (scale-infested or uninfested) on prey removal variables. In each graph the mean response (average abundance for **a**, **b**, probability of removal for **c–g**) is plotted with the SE. Significant p -values are in boldface text. **a** In 2019, tree infestation status did not influence average aphid abundance in pots placed below trees. **b** Average aphid abundance on crape myrtle leaves placed in planted hollies in 2020 was unaffected by tree infestation status. **c** *Drosophila* removal in planted hollies in 2020 was not influenced

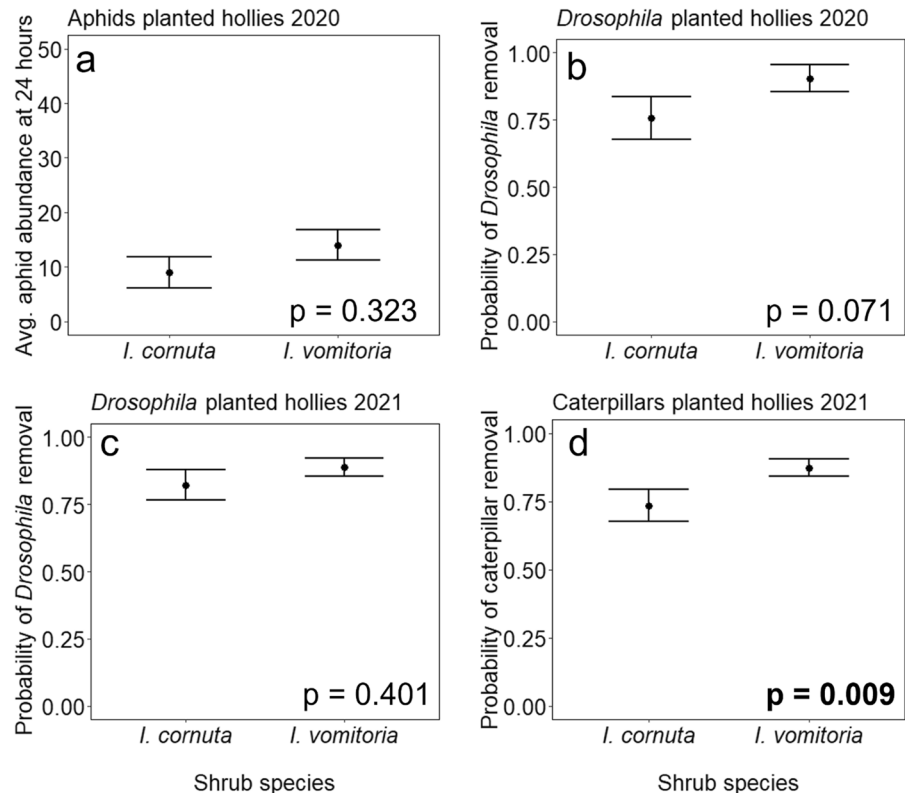
by tree infestation status. **d** In 2021, there was no effect of tree infestation status on *Drosophila* removal in potted hollies. **e** In 2021, *Drosophila* on planted hollies were more likely to be removed under scale-infested trees relative to scale-uninfested trees. **f** In 2021, caterpillars were more likely to be removed from potted hollies underneath scale-infested trees compared to scale-uninfested trees. **g** In 2021, caterpillar removal from planted hollies was not influenced by tree infestation status

Table 1 Model fitting results for biological control experiments

Response	Predictor	Estimate \pm SE	F/ χ^2	df	<i>p</i>
<i>2019 experiments</i>					
Average aphid abundance in pots at 24 h	Tree infestation status	Intercept: 67.601 \pm 69.696 Status: scale-uninfested: 1.589 \pm 2.557	0.386	1, 27	0.540
	Avg. initial aphid abundance	-0.687 \pm 1.414	0.236	1, 27	0.631
<i>2020 experiments</i>					
Average aphid abundance in holly shrubs at 24 h	Tree infestation status	Intercept: 358.203 \pm 441.946 Status: scale-uninfested: -2.919 \pm 6.231	0.034	1, 24	0.856
	Shrub species	Species: <i>I. vomitoria</i> : 0.364 \pm 6.562	1.020	1, 24	0.323
	Avg. initial aphid abundance	-6.984 \pm 8.858	0.622	1, 24	0.438
	Status \times shrub species	Status: S.U. \times shrub species: <i>I. vomitoria</i> : 7.610 \pm 9.085	0.702	1, 24	0.411
	Tree infestation status	Intercept: 0.406 \pm 0.408 Status: scale-uninfested: 1.466 \pm 0.862	1.140	1	0.286
Probability of <i>Drosophila</i> removal in planted hollies	Shrub species	Species: <i>I. vomitoria</i> : 2.234 \pm 1.113	3.271	1	0.071
	Status \times shrub species	Status S.U. \times shrub species: <i>I. vomitoria</i> : -2.234 \pm 1.450	2.785	1	0.095
	Tree infestation status	Intercept: -1.015 \pm 1.330 Status: scale-uninfested: 0.102 \pm 0.340	0.089	1	0.765
<i>2021 experiments</i>					
Probability of <i>Drosophila</i> removal in potted hollies	Shrub species	Species: <i>I. vomitoria</i> : 0.445 \pm 1.293	0.123	1	0.726
	Final time point	Time point: 24 h: -0.612 \pm 0.819	0.520	1	0.471
	Tree infestation status	Intercept: 1.723 \pm 0.860 Status: scale-uninfested: -0.773 \pm 0.275	8.106	1	0.004**
Probability of caterpillar removal in potted hollies	Shrub species	Species: <i>I. vomitoria</i> : -0.525 \pm 0.835	0.421	1	0.516
	Final time point	Time point: 24 h: -1.117 \pm 0.768	1.935	1	0.164
	Tree infestation status	Intercept: 1.735 \pm 0.626 Status: scale-uninfested: -0.348 \pm 0.801	4.540	1	0.033*
Probability of <i>Drosophila</i> removal in planted hollies	Shrub species	Species: <i>I. vomitoria</i> : 1.444 \pm 0.955	0.706	1	0.401
	Status \times shrub species	Status: S.U. \times species: <i>I. vomitoria</i> : -1.444 \pm 1.149	1.616	1	0.204
	Tree infestation status	Intercept: 1.174 \pm 0.461 Status: scale-uninfested: -0.266 \pm 0.489	1.713	1	0.191
Probability of caterpillar removal in planted hollies	Shrub species	Species: <i>I. vomitoria</i>: 1.033 \pm 0.494	6.886	1	0.009**
	Status \times shrub species	Status: S.U. \times species: <i>I. vomitoria</i> : -0.293 \pm 0.657	0.196	1	0.658

Experiments are listed based on the year they were conducted. F-tests were used to assess significance in models containing average aphid abundance as a response variable while likelihood ratio tests were used for all other models. For categorical predictors, F or χ^2 and *p*-values are reported for the predictor while estimates and SE are reported for each dummy variable of the predictor. Status: S.U. refers to the dummy variable for scale-uninfested trees. Significant predictors are in bold and significance is indicated with asterisks: **p* < 0.05; ***p* < 0.01

Fig. 2 Effect of shrub species on prey removal in planted hollies. In each graph the mean response (average abundance for **a**, probability of removal for **b–d**) is plotted with the SE. Significant *p*-values are in bold-face text. **a** Aphid abundance on planted hollies in 2020 was not influenced by shrub species. **b** In 2020, the probability of *Drosophila* removal was not influenced by shrub species. **c** Shrub species did not influence *Drosophila* removal on planted shrubs in 2021. **d** In 2021, the probability of caterpillar removal was greater on *I. vomitoria* shrubs compared to *I. cornuta* shrubs



Discussion

Scale-infested urban trees can act analogously to banker plants by supporting biological control on plants below them, but this effect appears to be context-dependent. Banker plant systems can vary considerably in their effectiveness of managing pest densities below damaging thresholds (Frank 2010; Huang et al. 2011). The variability in the ability of banker plants to support biological control services can be attributed to the banker plant species itself, the alternative prey/host species, and the natural enemy species used in the system (Frank 2010). Within our system, natural enemies present within scale-infested trees may prefer certain prey taxa over others which could lead to variable biological control efficacy of pests on plants underneath these trees. We previously found that scale-infested trees hosted more spiders and lady beetles than scale-uninfested trees and that shrubs underneath scale-infested trees hosted more ants, spiders, and predatory hemipterans (Wilson and Frank 2022). It is unclear which of these natural enemy groups could be driving the increased removal

of caterpillars and *Drosophila* under scale-infested trees while not affecting aphid removal. Future research which accounts for the prey preferences of these enemy groups could help explain which prey taxa are most likely to be managed by generalist natural enemies in scale-infested trees.

The activity of ground-dwelling predators may explain differences in caterpillar and *Drosophila* removal between planted and potted hollies. Turf-grasses can host diverse natural enemy taxa including ants, spiders, predatory beetles, predatory hemipterans, and parasitoid wasps (Heng-moss et al. 1998; Braman et al. 2000; Rochefort et al. 2006; Norton et al. 2014). Additionally, invasive ant species such as Argentine ants (*Linepithema humile* (Mayr) (Hymenoptera: Formicidae)) and red imported fire ants (*Solenopsis invicta* Buren (Hymenoptera: Formicidae)) are widely established in urban settings in southern USA (Jemal and Hugh-Jones 1993; Silverman and Brightwell 2008) and we frequently observed these species feeding on caterpillars and *Drosophila* prey in the landscape holly shrubs used in this study. In planted landscape shrubs, ground-dwelling

predators may remove prey before predators from trees can colonize shrubs to feed on prey. This may explain why tree infestation status influenced caterpillar removal in potted shrubs but not planted shrubs. Excluding ground arthropods from potted plants may better emphasize the effect that natural enemies dispersing from trees to shrubs have on sentinel prey. In comparison, increased *Drosophila* removal in planted, but not potted hollies, under scale-infested relative to uninfested trees may indicate that natural enemies entering shrubs from the ground readily utilize *Drosophila* as prey over natural enemies dispersing from trees. Shrubs underneath scale-infested trees can host significantly more non-natural enemy arthropods than shrubs under uninfested trees (Wilson and Frank 2022) and this higher abundance of arthropods may attract ground-dwelling predators to forage in shrubs. Finally, while we did not observe ants tending to and protecting the crape myrtle aphids on shrubs, ant antagonism could interfere with biological control services that natural enemies from trees might otherwise provide to naturally occurring aphid infestations in urban shrubs. For example, Wimp and Whitham 2001 found that removing aphids, and thus aphid-tending ants, from cottonwood trees (*Populus* sp.) resulted in a significant increase in generalist predators on these trees. Viewing urban landscapes as connected ecosystems in which the natural enemy communities in different vegetation strata are linked may better inform management strategies aimed at supporting conservation biological control (Hermes et al. 1984; Wilson and Frank 2022). Understanding natural enemy prey preferences and the relative contribution of biological control services from trees, turfgrass, and surrounding vegetation will aid in explaining the context-dependent effects of tree pests on biological control in urban shrubs.

The species of shrub planted underneath urban trees can influence biological control services and natural enemy communities. We found that the probability of caterpillar removal on planted landscape hollies in 2021 was higher on *I. vomitoria* compared to *I. cornuta* shrubs, regardless of overstory tree infestation status. Herbivores native to North America lack shared coevolutionary relationships with exotic species like *I. cornuta* which can prevent herbivores from exploiting exotic plant defenses (Keane and Crawley 2002). As a result, native plants often host higher herbivore abundance than exotic plants (Burghardt et al.

2010; Burghardt and Tallamy 2013). Natural enemies may be more likely to disperse from trees to shrubs below them to feed on herbivores if there is an abundance of herbivores within these shrubs. However, we only found an effect of shrub species on prey removal in one of the four experiments we conducted with landscape shrubs. While exotic trees and shrubs often host fewer herbivores than native species, they do not always host fewer natural enemies (Frank et al. 2019; Parsons et al. 2020a). Other factors besides herbivore abundance in shrubs may influence natural enemy dispersal from trees to shrubs such as avoiding competition for resources or escaping intraguild predation from other predators. Therefore, certain exotic shrubs may be as amenable as native congeners for supporting natural enemy communities and biological control services under urban trees.

The vegetation surrounding urban trees and shrubs also influences natural enemy communities, and likely influences biological control services. Urban plants with high surrounding vegetation complexity tend to host many natural enemies (Shrewsbury and Raupp 2006; Egerer et al. 2017; Parsons and Frank 2019; Dale et al. 2020; Parsons et al. 2020b; Nighswander et al. 2021). Vegetation complexity is expected to support natural enemy communities by increasing the availability of alternative food resources (such as nectar and pollen), prey, and shelter, as well as by providing ideal microclimate conditions and by reducing intraguild predation and cannibalism (Root 1973; Langelotto and Denno 2004; Finke and Denno 2006; Gurr et al. 2017). The trees and shrubs we used for this study were in managed landscapes, typically adjacent to parking lots or sidewalks. These trees had mulch at their base and were often surrounded by turfgrass, a few small shrubs, and in some cases small neighboring trees. While we did not manipulate vegetation complexity at our field sites, planting a diverse community of woody and herbaceous plants surrounding shrubs at these sites may increase natural enemy abundance and prey removal both within trees and in the shrubs below them. Future research which examines how increased vegetation complexity affects biological control services provided by scale-infested compared to scale-uninfested urban trees will better inform sustainable landscape design in urban ecosystems.

The development of pest tolerance thresholds for urban trees and shrubs may aid in natural enemy

conservation and prevent unintentional pest outbreaks due to overuse of pesticides (e.g., Raupp et al. 2001; Szczepaniec et al. 2011). Pest tolerance thresholds do not exist for most urban trees and shrubs, but consumer tolerances for pests in ornamental plants are stringent (e.g., Raupp et al. 1988, 1989; Coffelt and Schultz 1990). Our results suggest that tolerating scales in urban trees can support natural pest regulation and that establishing intervention thresholds for urban tree pests like scales may facilitate conservation biological control in urban landscapes. Our results indicate that natural enemy communities in urban trees and shrubs are linked and that disrupting this linkage could weaken biological control services. For example, treating the canopy of a tree with insecticides may alleviate pest issues in the tree, but could trigger pest outbreaks in shrubs planted below them by killing natural enemies that would normally disperse from trees to feed on pests in shrubs. Applying pesticides in the winter when natural enemies are not active or treating scales with insecticides that do not kill natural enemies may prevent such die-off. Increased tolerance for tree pests may synergize with other cultural management strategies such as increasing vegetation complexity around urban trees to support natural enemy communities and manage pests.

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Data availability The data used in this manuscript, and the R-script used to analyze the data, are available from the Dryad data repository at the following link: <https://doi.org/doi:10.5061/dryad.sbcc2frbm>.

Declarations

Conflict of interest The authors declare no conflicts of interest.

Human and animals rights Not applicable.

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