



Tree species richness around urban red maples reduces pest density but does not enhance biological control

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ABSTRACT

Urban trees often host greater insect pest abundance than trees in rural forests. This may be due, in part, to differences in tree diversity and canopy cover between these settings. Urban trees are often planted in isolation or monoculture, which favors pest accumulation. Gloomy scale, *Melanaspis tenebricosa* Comstock, is a pest of urban red maples (*Acer rubrum* L.) that is abundant where impervious surfaces dominate the local landscape. Increasing tree diversity and canopy cover around urban red maples may reduce gloomy scale abundance by supporting natural enemy communities. We investigated the effect that surrounding tree species richness and tree canopy cover had on gloomy scale abundance, natural enemy abundance, and biological control in red maple trees in Raleigh, NC, USA. We collected scales and natural enemies from red maples that spanned a gradient of tree species richness, canopy cover, and impervious surface values. We also measured gloomy scale parasitism and predation of sentinel prey in red maple canopies. Greater tree species richness and canopy cover were associated with lower gloomy scale density. Red maples in diverse settings also hosted fewer scales per natural enemy. Parasitoids were less common in maples in diverse settings, but generalist predator abundance was unaffected by tree diversity. Finally, tree species richness and canopy cover did not increase biological control of scales or sentinel prey. Our findings suggest that higher tree diversity and greater canopy cover may reduce gloomy scale density, but this is not entirely explained by the effects of natural enemies and biological control.

1. Introduction

Urban tree plantings are often dominated by certain common species or genera (Raupp et al., 2006; Sjöman et al., 2012). For example, Raupp et al. (2006) found that 57% of trees in Toledo, Ohio, USA, were in the genus *Acer*. Low urban tree diversity can support the dispersal and proliferation of exotic pests with severe consequences for urban tree cover (Poland and McCullough, 2006; Raupp et al., 2006). Certain

native insect herbivores—sleeper species—that are innocuous in forests can become damaging pests in urban trees due to the unique abiotic conditions of cities, such as warmer temperatures (Dale and Frank, 2018; Frank and Just, 2020; Raupp et al., 2010). These sleeper species have characteristics of exotic invasive species, so similar management strategies, such as increasing tree diversity (e.g. Guyot et al., 2015), may help reduce their proliferation and damage to forests.

In the southeastern United States, gloomy scale (*Melanaspis*

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tenebricosa Comstock) has been recognized as a major native pest of urban red maples (*Acer rubrum* L.) for over 100 years (Frank, 2019; Just et al., 2020; Metcalf, 1922, 1912). Gloomy scales can feed on trees in at least 28 different genera, but gloomy scales are typically only pests on red maple (*A. rubrum* L.), silver maple (*A. saccharinum* L.), and freeman maple (*Acer x freemanii* A.E. Murray) (Just et al., 2020). Trees infested with gloomy scales exhibit leaf dieback and canopy thinning, which if severe, can result in tree death (Just et al., 2020). The urban heat island effect and drought conditions caused by impervious surface cover increase gloomy scale survival and fecundity, causing gloomy scales to reach damaging densities on urban red maples (Dale and Frank, 2017, 2014a, 2014b; Just et al., 2019). Red maples are often planted in monospecific patches, so low tree diversity could also facilitate gloomy scale establishment through multiple ecological mechanisms (Feeny, 1976; Root, 1973; Tahvanainen and Root, 1972). The enemies hypothesis states that increasing plant species richness can increase natural enemy abundance and diversity which can increase pest regulation (Root, 1973). Diverse plant communities provide resources such as supplemental nectar, diverse prey communities, and habitat refugia which can support natural enemy communities (Root, 1973; Russell, 1989). Gloomy scales are parasitized by wasps in at least three different families and are found in close association with many generalist predators (Dale and Frank, 2014a). Although it is uncertain which predators feed on gloomy scales, armored scales are consumed by generalists including lady beetles, tree crickets, harvestmen, lacewing larvae, and earwigs (Hanks and Denno, 1993; Tooker and Hanks, 2000). Tree diversity could support both parasitoids and predators and therefore biological control of gloomy scales.

Trees in species-rich forest stands often have lower pest abundance or damage compared to trees in monospecific patches (Grossman et al., 2018; Jactel et al., 2021; Jactel and Brockerhoff, 2007). However, few studies have examined how tree species richness influences herbivory by piercing-sucking insects such as scales. However, Jactel et al. (2006) found that bast scale, *Matsucoccus feytaudi* Ducas, a specialist pest of maritime pine (*Pinus pinaster* Aiton), was more abundant in pure stands of maritime pine than in mixed stands of maritime and Corsican pine. Some authors have also found beneficial effects of tree diversity on natural enemy abundance (Jactel et al., 2006; Staab et al., 2016; Stemmelen et al., 2022a). However, natural enemy responses to tree diversity often vary across enemy taxa (Ampoorter et al., 2020; Staab and Schuldt, 2020; Vehviläinen et al., 2008) and biological control services of enemies are seldom linked to tree diversity (but see Staab et al. 2016). Thus, the mechanisms by which tree diversity reduces pest damage and pest abundance remain unclear.

Greater tree abundance, regardless of species identity, may reduce pest abundance and support natural enemies. First, the leaf biomass provided by dense tree stands can increase herbivore biomass (Whitfield et al., 2012) which can support greater natural enemy abundance (Kagata and Ohgushi, 2006). Second, tree cover provides complex habitat structure which may weaken intraguild predation by increasing the availability of spatial refugia in which predators can avoid encounters with intraguild predators (e.g. Finke and Denno, 2006; Langelotto and Denno, 2006). Finally, trees cool the air through evapotranspiration and reduce temperatures by shading surrounding impervious surfaces (Shashua-Bar et al., 2009). Some enemy taxa may be unable to tolerate warmer temperatures resulting in homogenized community structure within urban heat islands (Meineke et al., 2017; Parsons et al., 2020; Youngsteadt et al., 2017). Therefore, shade provided by tree cover could reduce detrimental warming effects on natural enemies. These mechanisms may explain why scales are often less abundant in natural landscapes with greater tree cover than in planted ornamental landscapes (Hanks and Denno, 1993; Long et al., 2019; Tooker and Hanks, 2000). If tree species richness and tree density both influence natural enemy communities in red maples, these variables may interact to influence gloomy scale biological control. For example, natural enemies may be more abundant in red maples surrounded by

many trees represented by many species in comparison to red maples surrounded by the same number of species but fewer trees.

Our goal was to determine how tree species richness, tree canopy cover, and their interaction influence the abundance of gloomy scales and their natural enemies in red maples. We predicted that red maples surrounded by greater canopy cover and greater tree species richness would 1) have lower gloomy scale density, 2) higher natural enemy abundance, and 3) more biological control than red maples surrounded by less canopy cover, fewer tree species, or both. We also predicted that tree species richness and canopy cover will interact to influence gloomy scale density, natural enemy abundance, and biological control in red maples. Our findings indicate if the creation development and maintenance of urban tree cover and diverse urban forests is an effective strategy for managing scale density by increasing biological control.

2. Methods

2.1. Scale and natural enemy data collection

We collected gloomy scale count data from 95 red maples across the city of Raleigh, North Carolina, USA. Many of these trees were sampled for other research projects and scale data were collected between 2016 and 2020 (Long et al. 2019; Backe and Frank, 2019; unpublished data). Most maples were planted along roadsides, in parking lots, or in residential yards. Six trees were naturally occurring and were located at the edges of forest fragments. See Fig. S1 for a map of all tree locations and the Supplemental methods and table S1 for additional details on scale data sources.

Forty three of the 54 red maples sampled in 2020 had also been sampled in 2018. We used these recounted trees to assess changes in scale density over time. We used a non-parametric Kruskal-Wallis test to determine if total gloomy scale density differed on trees between 2018 and 2020. In both years scales were counted on four 30 cm twigs per tree, thus sampling intensity was the same. We found no significant difference in scale density between 2018 and 2020 ($\chi^2 = 0.359$, $df = 1$, $p = 0.549$). Therefore, we assumed gloomy scale density did not change appreciably in the time between sampling trees (2016–2020) and collecting data for this study (2020).

In June and September of 2020, we collected natural enemies from 90 red maples that had been sampled for scales using a funnel beat sampler. The sampler consisted of a 30.5 cm metal funnel attached to a 2.5 m long extendable pole with a wooden hinged lid (Meineke et al., 2017; Sperry et al., 2001). The lid of the funnel was attached to a string which was pulled to lift the lid. When the string was relaxed the lid fell and hit tree branches which dislodged arthropods and knocked them into the funnel. Arthropods then fell through the funnel into a 50 ml plastic tube that contained 10 ml of 70% ethanol. After beating tree limbs, the interior of the funnel was rinsed with 70% ethanol to wash all remaining arthropods into the tube. The 50 ml tube was attached to the outside of the funnel and was removed after sampling each tree. We collected arthropods from 12 branches per tree, each equally distributed around the lower canopy. We struck each branch five times with the lid, moving towards the trunk of the tree with each successive hit. In the lab, we sorted all natural enemies from these samples into the following categories: Ants (Formicidae), parasitic Hymenoptera (e.g. Aphelinidae), lady beetles (Coccinellidae), lacewings (Neuroptera), predatory thrips (Aelothripidae), predatory Hemiptera (e.g. Reduviidae), long-legged flies (Dolichopodidae), tree crickets (e.g. Mogoplistidae), Spiders (Araneae), and earwigs (Dermaptera).

2.2. Sample site characterization

We recorded the species richness and abundance of all trees and large shrubs (taller than 1.8 m) within a 25 m radius (including trees on the edge) of each red maple from February 26th – May 13th, 2020. All trees and shrubs were identified to species (82% of all trees and shrubs) or

morphospecies (18%). To ensure accurate boundaries of our 25 m radii, we created 25 m buffers using mapping software (Google Earth Pro v. 7.3.2.5776, Google Inc, 2020) which were projected on satellite imagery, printed, and brought on site to verify radius boundaries using landmarks in the image. We also measured 25 m from the focal tree and placed orange survey flags to delineate boundaries on publicly owned property. To avoid entering private property, certain trees were identified from the nearest sidewalk. These trees were at most 15 m away from observers, which is unlikely to have introduced substantial bias into our observations. The minimum nearest neighbor distance between trees in our dataset was 29 m while the mean nearest neighbor distance was 485 m.

We measured the percentage of impervious surfaces within the 25 m radii buffer from all 95 red maples using the packages ‘raster’ (Hijmans, 2019) and ‘rgdal’ (Bivand et al., 2019) from a 1 m unsupervised land-cover classification created by Long and Frank 2020. To measure percent canopy coverage within each 25 m buffer, we recorded the mean canopy cover percentage of all pixels within the buffer using the tree canopy layer from the 2016 National Land Cover Dataset (Yang et al., 2018).

2.3. Estimation of biological control services

To determine how tree diversity and canopy cover influenced predation by generalist predators, we conducted a biological control experiment over the months of June - July of 2020 in 30 red maples. We selected these trees to represent a gradient of tree species richness, percent canopy cover, and percent impervious surface values within a 25 m buffer. We glued 10 dead *Drosophila* spp. (Insecta: Diptera: Drosophilidae) adults to 4 cm² cardstock squares, and then sprinkled sand on these cards to provide traction for predators. *Drosophila* adults were a mixture of *D. melanogaster* and *D. suzukii* sourced from genetics laboratories at North Carolina State University. We placed cards on haphazardly selected leaves on the edge of the lower canopy of trees, and recorded prey removal at 48 h.

To determine how tree diversity and canopy cover influenced gloomy scale parasitism, we measured the proportion of parasitized gloomy scales (out of 50 individuals) on twigs from 27 red maples that spanned a gradient of surrounding tree species richness and tree canopy cover values. All twigs were removed from trees between December 9th - December 17th of 2020 when there are multiple parasitoid stages present within scales (Dale and Frank, 2014a). See the Supplemental methods and Figs. S2-S3 for additional details about both biological control experiments.

2.4. Statistical analyses

All analyses were conducted in R version 4.2.1 (R Core Team, 2022). Prior to fitting models, we rarefied our tree species richness data. We did this to separate the effects of species richness from tree abundance in our models. We rarefied our species richness data with the ‘iNEXT’ function in the ‘iNEXT’ package (Hsieh et al., 2020). We used the ‘cor.test’ function to determine if raw richness values recorded around each tree correlated with rarefied tree species richness and found a significant correlation ($r = 0.697$, $t_{93} = 9.376$, $p = 4.272 \times 10^{-15}$). Since rarefied tree species richness values were used for all analyses, we hereafter refer to ‘rarefied tree species richness’ as ‘tree species richness’. See supplemental methods for additional details on rarefaction.

We fit a generalized linear mixed model (GLMM) using the lme4 package (Bates et al., 2015) with tree species richness and percent canopy cover as predictors and raw counts of gloomy scale abundance as the response, to evaluate the effect of these predictors on gloomy scale density. We included the twig length as an offset term in the model. Offset terms account for variation in time or space over data were collected - in this instance, the variable twig lengths over which scales were counted. We also included an interaction term between tree species

richness and canopy cover in this model. We fit this model with a poisson distribution and log link function and included each tree as an observation-level random effect to account for overdispersion in our response variable (Harrison, 2014). We did not fit this model with a negative binomial distribution because of model convergence errors. For this analysis and all others, all predictor variables were z-score standardized prior to model fitting. To determine whether tree species richness and canopy cover might be correlated to impervious surface cover around each focal tree, we used the ‘cor.test’ function to fit correlations between tree species richness and percent impervious surface cover and between percent canopy cover and percent impervious cover. We also fit one more model with gloomy scale density (with an offset for twig length) as the response and impervious surface cover as the sole predictor variable (GLMM, poisson error distribution, log-link function). We fit this model because we found correlations between tree species richness and impervious surface cover (Pearson’s correlation $r = -0.272$, $t_{93} = -2.729$, $p = 0.0076$) and between canopy cover and impervious surface cover ($r = -0.538$, $t_{93} = -6.148$, $p < 1.942 \times 10^{-8}$). Due to these correlations, we did not include impervious surface cover as a predictor in the tree richness and canopy cover model. We calculated AIC values for these models using the ‘stats’ package (R Core Team, 2022) to determine if tree species richness, canopy cover, and their interaction explained more variation in gloomy scale densities compared to impervious surface cover.

We fit a generalized linear model to determine how tree species richness, canopy cover, and their interaction, influenced natural enemy abundance recorded in each tree (summed across both collection periods). We fit this model with a negative binomial distribution and log-link function. We ran an additional model (GLM, negative binomial, log-link function) to determine if natural enemy abundance was influenced by total scale density recorded from each focal tree. We ran this model separately because we had established previously that tree species richness and tree canopy cover influenced gloomy scales in our first analysis. Therefore, fitting this model separately prevented fitting a model with multiple correlated predictors. We fit these same two models (negative binomial, log-link) for all generalist predators and parasitoids collected from our beat samples to determine if these groups responded differently to our predictor variables. We calculated AIC values for all models.

We fit an additional GLM to determine if the ratio of scales to natural enemies collected in red maples was influenced by tree species richness, canopy cover, and their interaction. We included total twig length over which scales were counted into this model as a covariate. We $\ln(x + 1)$ transformed scale abundance per natural enemy for this model to normalize model residuals. We fit similar models where the response variables were scales per parasitoid and scales per generalist predator.

We fit a binomial GLMM with a logit link function to evaluate if the probability of *Drosophila* removal at 48 h was influenced by tree species richness, percent canopy cover, and their interaction. We ran an additional model to evaluate whether the probability of *Drosophila* removal at 48 h was influenced by gloomy scale density recorded in each tree. We calculated AIC values for both models to compare model fit. Finally, we ran another model to evaluate if the probability of *Drosophila* removal differed between open cards and cards in clip cages. All models included a random intercept term for each sampling period to account for the repeated measures data collected for this experiment.

To determine how tree diversity and canopy cover influenced gloomy scale parasitism, we fit a GLMM (binomial distribution, logit-link function) with the proportion of parasitized gloomy scales as the response variable. Our predictors were tree species richness, tree canopy cover, and their interaction. We included an observation-level random effect term for each tree in the model because our response variable was overdispersed. We ran a separate model to determine if scale density recorded in each maple influenced recorded parasitism values from each tree. We ran one final model to determine if gloomy scale parasitism was influenced by the number of parasitoids collected in beat samples in

each tree. These models all included an observation-level random intercept term for each tree. We calculated AIC values for these models to compare fit.

3. Results

Total gloomy scale density ranged from 0.0 to 35.2 scales per cm of twig length (mean \pm SEM = 2.5 ± 0.6) and total natural enemy abundance ranged from 2 to 52 individuals per tree when both samples were combined (18.5 ± 1.2). Across all samples we recorded a total of 1667 natural enemies represented by: 785 parasitoids (47.1% of all natural enemies), 647 spiders (38.8%), 125 ants (7.2%), 40 predatory hemipterans (2.4%), 25 Coccinellidae (1.5%), 24 Neuroptera (1.4%), 19 tree crickets (1.1%), 3 Dermaptera (0.2%), 3 predatory thrips (0.2%), and 1 Dolichopodidae (0.1%). Tree species richness at each site ranged from 1.0 to 18.2 species (8.1 ± 0.3), percent canopy cover at a 25 m radius ranged from 0.0% to 90.0% ($16.6 \pm 2.2\%$), and impervious surface coverage ranged from 0.0% to 86.2% ($40.3 \pm 2.0\%$). Additional summary statistics for data are listed in Table S2.

There was an interaction between tree species richness and canopy cover on gloomy scale density such that the slope of the negative relationship between tree species richness and scale density became less negative at higher canopy cover values (Fig. 1A). Similarly, the slope of the negative relationship between canopy cover and gloomy scale density became less negative at higher tree species richness values (Fig. 1B, Table 1). Impervious surface cover was positively related to gloomy scale density ($\beta = 1.631 \pm 0.357$, $z = 4.566$, $p = 4.98 \times 10^{-6}$, Fig. S4). Tree species richness, percent canopy cover, and their interaction explained more variation in gloomy scale densities (AIC = 917.007) than did impervious surface cover (AIC = 925.072). Maples surrounded by high impervious surface cover had low canopy cover (Pearson's correlation: $r = -0.538$, $t_{93} = -6.148$, $p = 1.942 \times 10^{-8}$) and low surrounding tree species richness ($r = -0.272$, $t_{93} = -2.729$, $p = 0.0076$). Both tree species richness and percent canopy cover were negatively related to natural enemy abundance, but these predictors did not interact (Fig. 2A,B, Table 1). Scale density in red maples increased with natural enemy abundance (Table 1). Tree species richness, canopy cover, and their interaction explained more variation in natural enemy abundance (AIC = 656.974) than did gloomy scale density (AIC = 671.240).

We analyzed the influence of surrounding tree species richness,

canopy cover, and scale density, on parasitoids and generalist natural enemies. Canopy cover and tree species richness were negatively related to parasitoid abundance, but there was no interaction (Fig. 2C,D, Table 1). Gloomy scale density was positively related to parasitoid abundance (Table 1). Tree species richness, tree canopy cover, and their interaction explained more variation in parasitoid abundance (AIC = 565.694) than did gloomy scale density (AIC = 574.080). There was no effect of tree species richness, canopy cover, or their interaction on generalist predator abundance (Fig. 2E,F, Table 1). Furthermore, gloomy scale density did not affect generalist natural enemy abundance (Table 1). Tree species richness, tree canopy cover, and their interaction explained more variation in generalist natural enemy abundance (AIC = 551.390) than did gloomy scale density (AIC = 553.734). Because parasitoids were the most abundant natural enemy group collected (47% of all collected enemies), the effects of tree species richness, canopy cover, and scale density on total natural enemy abundance appears to be driven by the prevalence of parasitoids in these samples.

Both tree species richness and canopy cover were negatively related to the ratio of gloomy scales to natural enemies, but these predictors did not interact (Fig. 3AB, Table 2). We fit these same models separately for the ratio of scales to parasitoids and the ratio of scales to generalist predators. Tree species richness and percent canopy cover interacted to influence the ratio of scales to parasitoids, such that the slope of the negative relationship of tree species richness on the ratio of scales to parasitoids became less negative at higher percent canopy cover values (Fig. 4A, Table 2). Both tree species richness and percent canopy cover had a negative main effects, but no interactive effect, on the ratio of scales to generalist predators (Fig. 4B,C, Table 2). The total twig length over which scales were counted did not influence the ratio of scales to natural enemies in any model (Table 2).

The probability of *Drosophila* removal was greater for open cards than closed cards at 48 h ($\beta = 3.352 \pm 0.341$, $z = 9.823$, $p = 2.000 \times 10^{-16}$). The effect of tree species richness on the probability of *Drosophila* removal depended on canopy cover such that the probability of *Drosophila* removal became more negative at higher canopy cover values (Fig. 5A, Table 3). Similarly, percent canopy cover was positively associated with the probability of *Drosophila* removal where tree species richness was low, and percent canopy cover was negatively associated with the probability of *Drosophila* removal where tree species richness was high (Fig. 5B, Table 3). Scale density in red maples had no influence on the probability of *Drosophila* removal (Table 3). Tree

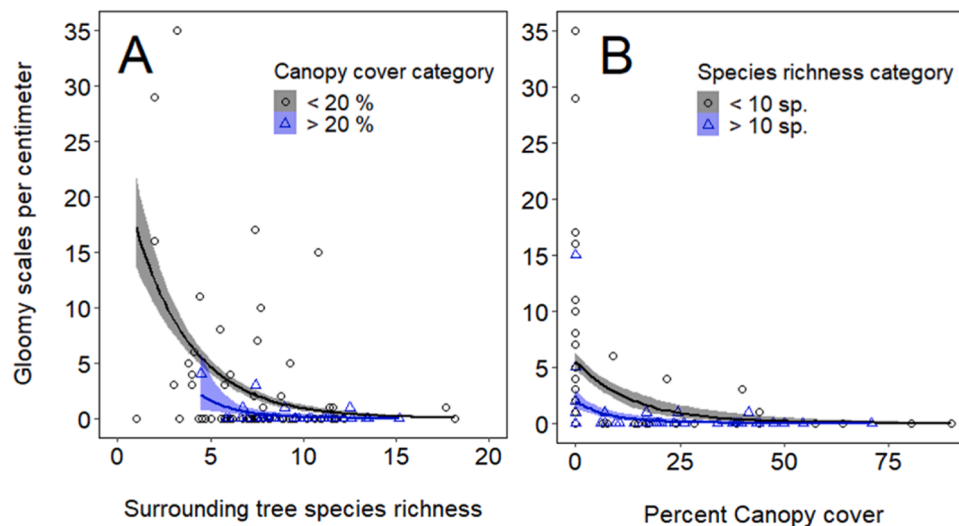


Fig. 1. The effect of tree species richness on gloomy scale density depended on the amount of canopy cover surrounding trees. (A) Tree species richness from all sites is separated into locations with higher and lower canopy cover values. (B) Canopy cover from all sites is separated into locations with higher and lower tree species richness values. In both graphs the predicted best fit lines (generalized linear models, poisson distribution, log-link) are plotted with shaded 95% confidence intervals.

Table 1

Results for gloomy scale and natural enemy models. Values in bold indicate statistically significant effects ($P < 0.05$). $N = 95$ for gloomy scale models and $N = 90$ for natural enemy models. Models that use scale density and impervious surface cover as predictors were fit separately from tree species richness and tree canopy cover due to the collinearity between these predictors. Estimates are shown below as predictors \pm standard errors.

Response	AIC	Intercept	Tree species richness	Percent canopy cover	Richness \times canopy cover	Scale density
Gloomy scale density (glmm)	917.007	-3.042 \pm 0.370 $z = -8.213$ $p < 2.000 \times 10^{-16}$	-0.450 \pm 0.356 $z = -1.264$ $p = 0.2062$	-1.801 \pm 0.415 $z = -4.343$ $p = 1.410 \times 10^{-5}$	0.778 \pm 0.396 $z = 1.964$ $p = 0.0495$	
Total natural enemy abundance (glm)	656.974	2.860 \pm 0.062 $z = 46.234$ $p < 2.000 \times 10^{-16}$	-0.170 \pm 0.065 $z = -2.620$ $p = 0.0088$	-0.198 \pm 0.063 $z = -3.126$ $p = 0.0018$	0.010 \pm 0.067 $z = 0.144$ $p = 0.8853$	
Total natural enemy abundance (glm)	671.240	2.906 \pm 0.063 $z = 46.246$ $p < 2.000 \times 10^{-16}$				0.150 \pm 0.060 $z = 2.504$ $p = 0.0123$
Parasitoid abundance (glm)	565.694	1.967 \pm 0.107 $z = 18.373$ $p < 2.000 \times 10^{-16}$	-0.260 \pm 0.112 $z = -2.318$ $p = 0.0204$	-0.337 \pm 0.112 $z = -3.002$ $p = 0.0027$	0.142 \pm 0.114 $z = 1.238$ $p = 0.2159$	
Parasitoid abundance (glm)	574.080	2.095 \pm 0.105 $z = 20.047$ $p < 2.000 \times 10^{-16}$				0.394 \pm 0.098 $z = 4.026$ $p = 5.680 \times 10^{-5}$
Generalist predator abundance (glm)	551.390	2.308 \pm 0.062 $z = 37.744$ $p < 2.000 \times 10^{-16}$	-0.058 \pm 0.065 $z = -0.897$ $p = 0.3695$	-0.105 \pm 0.062 $z = -1.675$ $p = 0.0940$	-0.122 \pm 0.070 $z = -1.743$ $p = 0.0814$	
Generalist predator abundance (glm)	553.734	2.281 \pm 0.059 $z = 38.500$ $p < 2.000 \times 10^{-16}$				-0.064 \pm 0.061 $z = -1.057$ $p = 0.2900$

species richness, canopy cover, and their interaction explained more variation in the probability of *Drosophila* removal (AIC = 148.845) than did gloomy scale density (AIC = 150.149). Tree species richness, percent canopy cover, and their interaction did not influence gloomy scale parasitism (Table 3). There was no effect of gloomy scale density (Table 3), or parasitoid abundance collected in each maple ($\beta = 0.002 \pm 0.223$, $z = -0.009$, $p = 0.993$) on gloomy scale parasitism. Parasitoid abundance (AIC = 121.371) and gloomy scale densities (AIC = 121.242) explained similar variation in gloomy scale parasitism, and both predictors explained more variation in gloomy scale parasitism than tree species richness, canopy cover, and their interaction (AIC = 123.306).

4. Discussion

We found limited support for the enemies hypothesis (Root, 1973) in our study system. Natural enemies were less abundant in maples surrounded by many tree species, and tree species richness did not strengthen biological control of scales or sentinel prey. However, we found that maples in locations with high tree diversity and canopy cover had low scale densities, and that these trees had fewer scales per natural enemy, which suggests that individual scales may be more likely to be parasitized or eaten by natural enemies in these locations. There is better support for the enemies hypothesis in forest diversity research, with many authors recording greater natural enemy abundance in locations with greater tree diversity (Ampoorter et al., 2020; Fornoff et al., 2019; Jouveau et al., 2020; Staab et al., 2016; Stemmelen et al., 2022a). Environmental differences (e.g. urban warming) between urban and forested settings can simplify enemy communities, making it difficult to predict how the effects of tree diversity on enemies found in forests translates to cities (Dale and Frank, 2018). In urban settings, woody plant diversity has been correlated with increases and decreases in pest abundance on focal plants (Raupp et al., 2001; Sperry et al., 2001). Woody plant diversity has also been associated with reduced pest management interventions in residential properties (Riley et al., 2022), increased parasitoid diversity in urban gardens (Burks and Philpott, 2017) and lower herbivory on urban trees (Stemmelen et al., 2022b). However, none of these studies quantify how pests, natural enemies, and biological control are all affected by tree diversity in cities, making it difficult to determine if the enemies hypothesis is the mechanism behind these findings. Future research investigating how these factors are affected by tree diversity will determine how generally applicable the

enemies hypothesis is for pest management in urban trees.

An alternative to the enemies hypothesis is the resource concentration hypothesis, which states that plants in diverse settings sustain less herbivory because it is harder for herbivores to locate and feed on them (Root, 1973; Tahvanainen and Root, 1972). This hypothesis may explain how tree diversity reduced gloomy scale density without strengthening biological control. Gloomy scale crawlers (immatures) are passively dispersed by wind and perhaps via phoresy (Just et al., 2020). Therefore, a red maple surrounded by many different species may not be colonized as readily as one surrounded by other red maples as dispersing crawlers may be more likely to colonize non-suitable hosts. Eighty four of the 95 trees we collected scales from had at least one red maple within 25 m, and these trees could have also harbored scales and influenced scale accumulation on focal trees. Future research is needed to determine if tree diversity supports red maple health by hindering scale colonization of new hosts.

Parasitoids were less common in maples in species-rich settings and tree diversity did not affect scale parasitism. Since scale density predicted parasitoid abundance, parasitoids are likely responding to the availability of their hosts, which are also less abundant in diverse settings, rather than to tree diversity directly. Our findings corroborate studies which have found more parasitoids and more scales in planted landscape trees than in forests (Hanks and Denno, 1993; Long et al., 2019) but no significant effect of scale abundance on parasitism in urban trees (Tooker and Hanks, 2000; Dale and Frank 2014b). Parasitoids appear to track the availability of their hosts, but tree diversity does not strengthen this form of biological control. However we did find more parasitoids per scale in diverse settings and thus individual scales in such locations may be more likely to be parasitized.

Tree diversity did not affect generalist predator abundance or strengthen generalist biological control. Therefore, in our system, generalist predators are ubiquitous in urban trees regardless of surrounding canopy cover or tree diversity. We also found that where canopy cover or tree species richness was high, there were fewer scales per generalist predator. These findings suggest that canopy cover and tree species richness may provide alternative prey to support natural enemy communities and that predators may be switching to more abundant prey when scales are less abundant. Both vegetation complexity and plant diversity are expected to support alternative prey resources to support natural enemies (Langellotto and Denno, 2004; Root, 1973). For example, Long and Frank (2020) found greater chewing

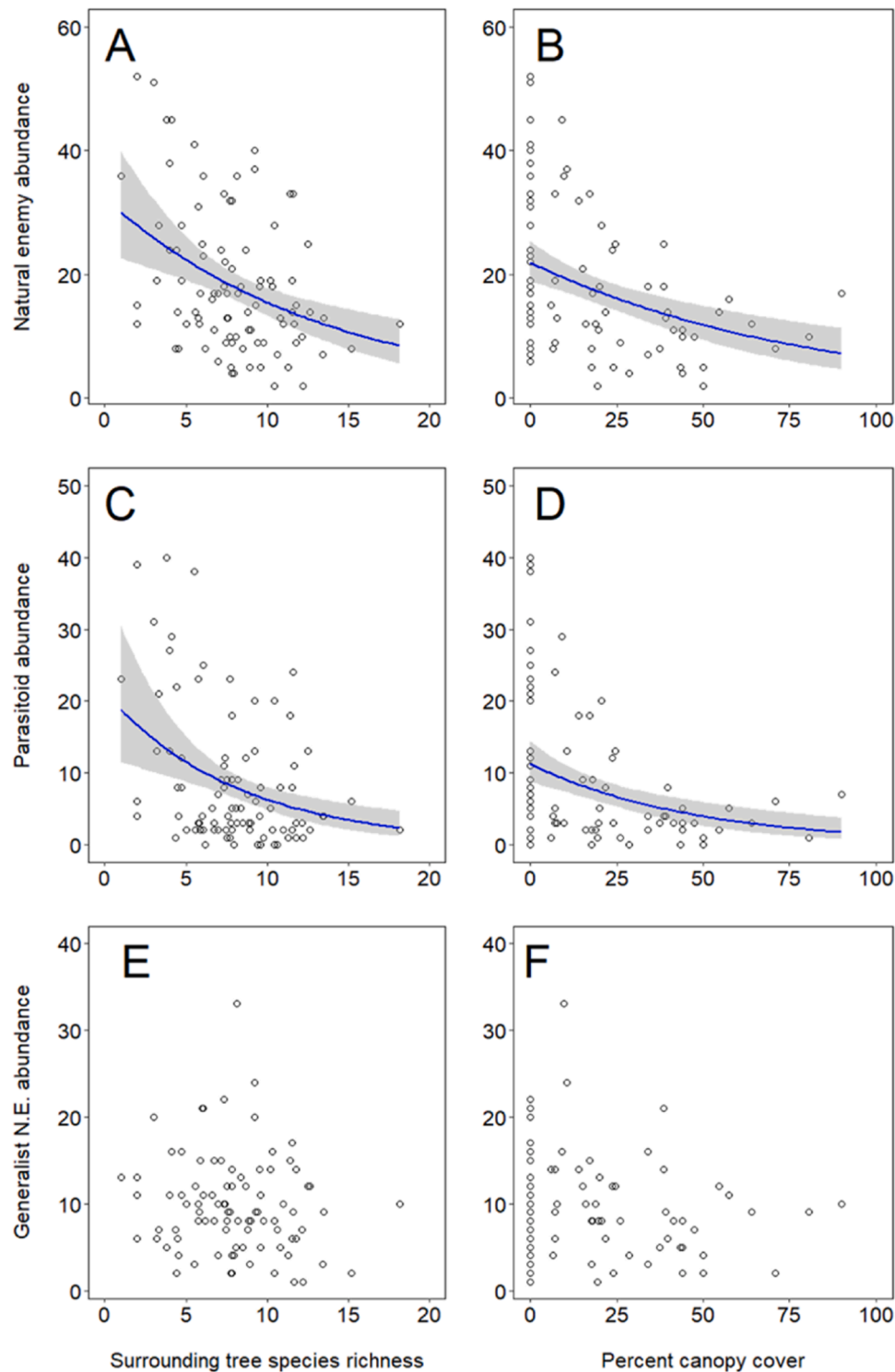


Fig. 2. Effect of tree species richness on A) all natural enemies C) parasitoids, E) generalist natural enemies, and effect of canopy cover on B) all natural enemies, D) parasitoids, and E) generalist natural enemies. Best fit lines and shaded 95% confidence intervals are plotted for significant effects (generalized linear models, negative binomial distribution, log-link).

herbivore richness and abundance in forest fragment trees than in planted landscape trees located in an urban center. Research conducted on heteropteran predators and spiders has shown that an increase in extraguild prey generally results in less intraguild predation (Lucas and Rosenheim, 2011; Rickers et al., 2006). Alternative prey in diverse settings may therefore stabilize predator populations in the absence of scales to serve as prey. Increased canopy cover also increases vegetation

complexity which reduces intraguild predation (Finke and Denno, 2006) and enhances natural enemy abundance (Langellotto and Denno, 2004; Shrewsbury and Raupp, 2006). Higher canopy cover around red maples may reduce the rate at which predators encounter and consume each other, offsetting the increase in intraguild predation that might otherwise be expected when prey such as scales are less available to predators.

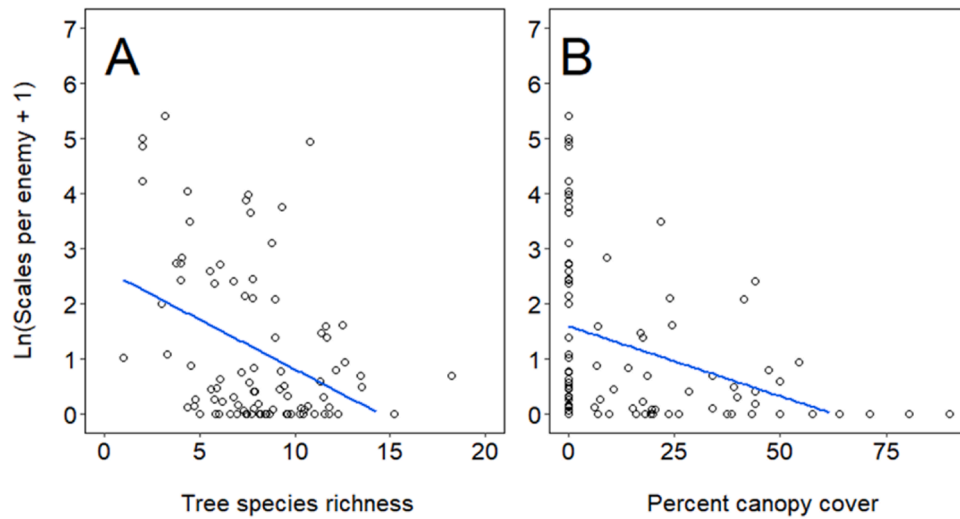


Fig. 3. A) Effect of tree species richness on the ratio of scales per natural enemy. B) The effect of canopy cover on the ratio of scales per natural enemy. The y-axis in both graphs was $\ln(x + 1)$ transformed to normalize model residuals. Best fit lines are plotted for each model.

Table 2

General linear model results from using the ratio of scales per natural enemy as a response variable. Values in bold indicate statistically significant effects ($P < 0.05$). Scales per natural enemy was log transformed to normalize residuals. Estimates are shown below as predictors \pm standard errors. Multiple R^2 values are reported for each model.

Response	R^2	Intercept	Tree species richness	Canopy cover	Richness x canopy cover	Total twig length
$\ln(\text{Scales per natural enemy} + 1)$	0.244	1.469 ± 0.400 $t = 3.672$ $p = 0.0004$	-0.421 ± 0.154 $t = -2.734$ $p = 0.0076$	-0.387 ± 0.148 $t = -2.615$ $p = 0.0106$	0.241 ± 0.153 $t = 1.570$ $p = 0.1202$	-0.003 ± 0.003 $t = -1.092$ $p = 0.2779$
$\ln(\text{Scales per parasitoid} + 1)$	0.225	2.035 ± 0.460 $t = 4.419$ $p = 2.970 \times 10^{-5}$	-0.389 ± 0.177 $t = -2.200$ $p = 0.0306$	-0.421 ± 0.173 $t = -2.434$ $p = 0.0171$	0.353 ± 0.176 $t = 2.001$ $p = 0.0486$	-0.005 ± 0.003 $t = -1.442$ $p = 0.1531$
$\ln(\text{Scales per generalist} + 1)$	0.263	-1.979 ± 0.514 $t = 3.852$ $p = 2.260 \times 10^{-4}$	-0.540 ± 0.198 $t = -2.732$ $p = 0.0077$	-0.554 ± 0.190 $t = -2.915$ $p = 0.0045$	0.319 ± 0.197 $t = 1.620$ $p = 0.1089$	-0.004 ± 0.004 $t = -1.127$ $p = 0.2628$

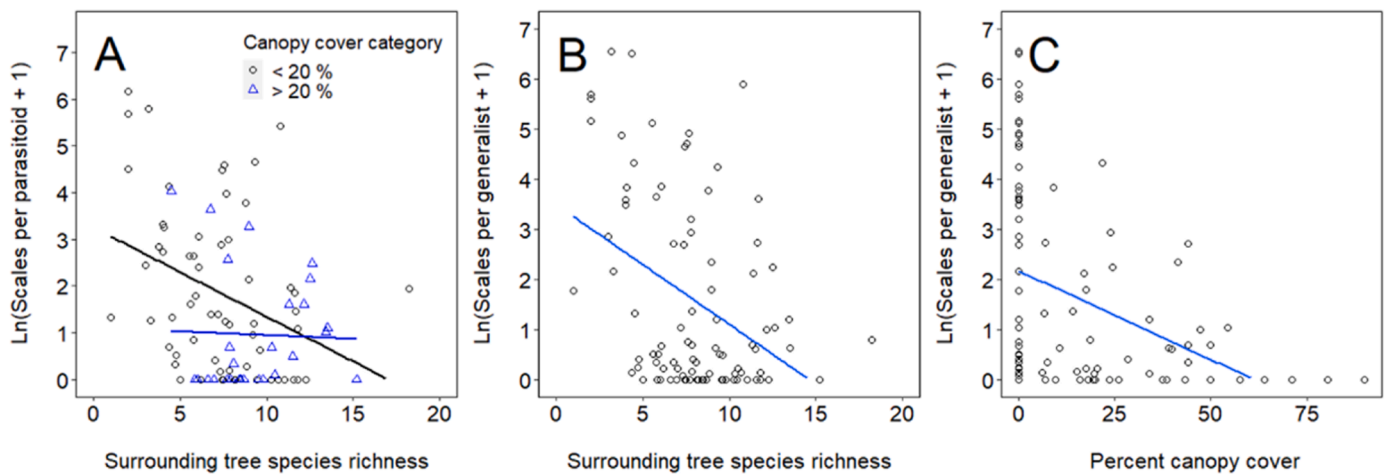


Fig. 4. A) Tree species richness and percent canopy cover interacted to affect the ratio of scales per parasitoid. B) Effect of tree species richness on the ratio of scales per generalist predator. C) Effect of canopy cover on the ratio of scales per generalist predator. The y-axes were $\ln(x + 1)$ transformed to normalize model residuals. Best fit lines are plotted for each model.

In line with previous work (e.g., Dale and Frank 2014b), gloomy scales were most abundant in locations with high impervious surface cover, which also tended to have fewer tree species and less canopy cover around them. Therefore, the observed benefit of canopy cover on gloomy scale density was likely linked to the abiotic effects associated with lower impervious surface cover. Accordingly, many authors have

found a positive relationship between impervious surface cover and scale density on red maples and other tree species (Backe and Frank, 2019; Dale et al., 2016; Just et al., 2019, 2018; Meineke et al., 2013; Speight et al., 1998). The cooling effects of additional tree cover likely act in conjunction with other canopy cover-mediated mechanisms (reduced intraguild predation) and diversity-mediated mechanisms

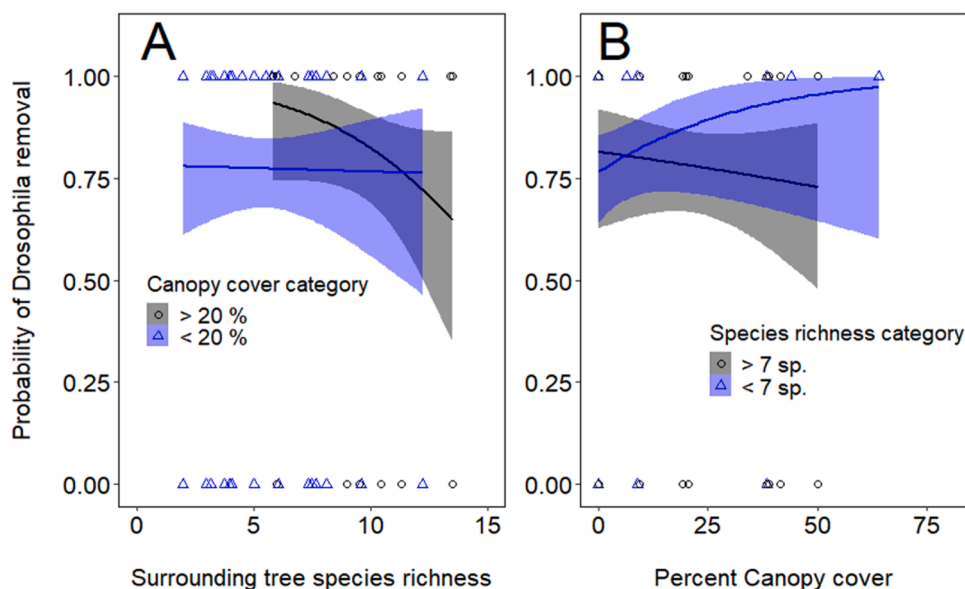


Fig. 5. The effect of tree species richness on the probability of *Drosophila* removal depended on the level of canopy cover surrounding trees. A) Tree species richness from all sites is separated into locations with higher and lower canopy cover values. (B) Canopy cover from all sites is separated into locations with higher and lower tree species richness values. Best fit lines are plotted with shaded regions displaying 95% confidence intervals (generalized linear mixed effect model, binomial distribution, logit-link).

Table 3

Biocontrol modelling results. Values in bold indicate statistically significant effects ($P < 0.05$). Estimates \pm SEM are shown below predictors. $N = 30$ for *Drosophila* models and $N = 27$ for the gloomy scale parasitism models.

Response	AIC	Intercept	Tree species richness	Canopy cover	Richness x canopy cover	Scale density
Probability of <i>Drosophila</i> removal (glmm)	148.845	1.885 \pm 0.471 $z = 4.001$ $p = 6.320 \times 10^{-5}$	-0.328 \pm 0.299 $z = -1.098$ $p = 0.2722$	0.578 \pm 0.370 $z = 1.534$ $p = 0.125$	-0.570 \pm 0.285 $z = -2.000$ $p = 0.0455$	
Probability of <i>Drosophila</i> removal (glmm)	150.149	1.461 \pm 0.370 $z = 3.952$ $p = 7.750 \times 10^{-5}$				-0.112 \pm 0.199 $z = -0.566$ $p = 0.5710$
Proportion of parasitized gloomy scales (glmm)	123.306	-3.132 \pm 0.236 $z = -13.288$ $p = 2.000 \times 10^{-16}$	0.094 \pm 0.239 $z = 0.395$ $p = 0.6930$	0.209 \pm 0.254 $z = 0.823$ $p = 0.4100$	-0.376 \pm 0.280 $z = -1.341$ $p = 0.1800$	
Proportion of parasitized gloomy scales (glmm)	121.242	-3.211 \pm 0.241 $z = -13.350$ $p = 2.000 \times 10^{-16}$				-0.084 \pm 0.234 $z = -0.360$ $p = 0.7190$

(resource concentration) that may reduce gloomy scale accumulation on urban red maples.

Diverse urban forests can prevent tree pests like gloomy scales from reaching high densities, but the enemies hypothesis alone may not adequately explain this relationship. Our work adds to a growing body of literature that demonstrates the beneficial effects of urban plant diversity on pest management outcomes. Our work suggests urban trees in diverse settings are less likely to host high scale abundance and that creating or maintaining diverse tree communities is an effective cultural control strategy.

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CRedit authorship contribution statement

CJW: Conceptualization, Methodology, Validation, Formal analysis, Investigation, Data curation, Writing - Original Draft, Writing - Review & Editing, Visualization, Supervision, Project administration. **KMB:** Investigation, Methodology, Writing - Review & Editing. **MGJ:** Methodology, Formal analysis, Investigation, Writing - Review & Editing. **ECL:** Investigation, Writing - Review & Editing. **AMN:** Investigation, Writing - Review & Editing. **LCL:** Investigation, Writing - Review & Editing. **AGD:** Conceptualization, Funding acquisition, Writing - Review & Editing. **SDF:** Conceptualization, Methodology, Resources, Writing - Review & Editing, Supervision, Project administration, Funding acquisition.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.ufug.2023.128093](https://doi.org/10.1016/j.ufug.2023.128093).

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