Exotic urban trees conserve similar natural enemy communities to native congeners but have fewer pests

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ABSTRACT

Urban trees serve a critical conservation function by supporting arthropod and vertebrate communities but are often subject to arthropod pest infestations. Native trees are thought to support richer arthropod communities than exotic trees but may also be more susceptible to herbivorous pests. Exotic trees may be less susceptible to herbivores but provide less conservation value as a consequence. We tested the hypotheses that native species in Acer and Quercus would have more herbivorous pests than exotic congeners and different communities of arthropod natural enemies. The density of scale insects, common urban tree pests, was greatest on a native Acer and a native Quercus than exotic congeners in both years of our research (2012 and 2016) and sometimes reached damaging levels. However, differences in predator and parasitoid abundance, diversity, and communities were not consistent between native and exotic species in either genus and were generally similar. For example, in 2012 neither predator nor parasitoid abundance differed among native and exotic Acer congeners but in 2016 a native species, A. saccharum, had the least of both groups. A native, Q. phellos, had significantly more predators and parasitoids in 2012 than its native and exotic congeners but no differences in 2016. Parasitoid communities were significantly different among Acer species and Quercus species due in each case to greater abundance of a single family on one native tree species. These native and exotic tree species could help conserve arthropod natural enemies and achieve pest management goals.

INTRODUCTION

Urban trees serve a critical conservation function by supporting herbivorous arthropod communities that, in turn, support vertebrate and invertebrate communities at higher trophic levels (Burghardt, Tallamy & Gregory Shriver, 2009; Morse, 1971; Tallamy, 2004). However, herbivorous arthropods can also be serious pests of urban trees that reduce...
tree health and the ecosystem services trees provide (Raupp, Shrewsbury & Herms, 2010). Thus, a potential conflict exists between the conservation value and aesthetic value of urban trees. To balance any such tradeoff and manage urban trees for the benefit of wildlife and people, it is important to understand factors that influence the arthropod communities they support.

Cities contain many native tree species that share an evolutionary history with local herbivores and many exotic tree species that do not (Aronson et al., 2015; Raupp, Cumming & Raupp, 2006; Riley, Herms & Gardiner, 2018). The evolutionary history between plants and arthropods in a habitat is an important factor influencing herbivore diversity and herbivory (Ehrlich & Raven, 1964; Farrell, Mitter & Futuyma, 1992). The “enemy release hypothesis” predicts that, because native herbivores are not adapted to exotic plant defenses, exotic plants should have fewer herbivores and be subject to less herbivory than are native plants (Keane & Crawley, 2002). This outcome would fulfill pest management objectives, as pest damage to trees would be minimal, but would make exotic plants less useful for supporting biodiversity. Alternatively, the “biotic resistance hypothesis” predicts that exotic plants can be consumed by native herbivores against which they are not defended (Hokkanen & Pimentel, 1989; Parker & Hay, 2005). This outcome may fulfill conservation goals, as trees would support arthropod communities, but only if trees do not require insecticide applications and are not severely damaged or killed. Both hypotheses have received mixed support, with research finding that herbivore abundance or herbivory on exotic plants can be more than, less than, or equal to that of native plants (Keane & Crawley, 2002; Zuefle, Brown & Tallamy, 2008).

The composition and effects of herbivore communities supported by exotic tree species in cities are difficult to predict. Cities are relatively recent human constructions and have many unnatural characteristics to which few animal species have evolved (Grimm et al., 2008; Shochat et al., 2006). For example, the urban heat island effect can alter natural enemy communities, insect and plant phenology, and affect host tree susceptibility to herbivory (Dale & Frank, 2017, 2018; Meineke, Dunn & Frank, 2014; Raupp, Shrewsbury & Herms, 2010). In addition, many native and exotic urban tree species have chronic or outbreak pest populations that are greater than for the same species in natural areas (Conway & Vander Vecht, 2015; Long, D’Amico & Frank, 2018; Raupp, Shrewsbury & Herms, 2010). For these reasons, ecological theories developed in natural ecosystems may not predict herbivore responses in cities (Dale & Frank, 2018).

Scale insects (Hemiptera: Coccoidea) are among the most common and abundant herbivores on urban trees (Dale & Frank, 2014b; Meineke et al., 2013; Raupp, Shrewsbury & Herms, 2010; Tooker & Hanks, 2000; Wu, Jamieson & Kielbaso, 1991). Scales are sedentary for most of their lifecycle. They insert flexible styles into host plants to feed on phloem, xylem, or other tissue. Feeding by scales and other hemipterans reduces plant growth by removing carbohydrates and reducing photosynthesis (Cockfield & Potter, 1990; Cockfield, Potter & Houtz, 1987; Dixon, 1971; Zvereva, Lanta & Kozlov, 2010). Scale insects often reach high populations on urban trees due to factors such as high temperature (Dale & Frank, 2014a, 2014b; Meineke et al., 2013), drought (Dale & Frank, 2017), plant stress (Meineke & Frank, 2018; Speight et al., 1998),
and diminished natural enemy communities (Hanks & Denno, 1993; Luck & Dahlstein, 1975; McClure, 1977; Meineke, Dunn & Frank, 2014; Tooker & Hanks, 2000). Our goal was to determine if exotic and native tree species common in urban plantings support similar arthropods, with a specific focus on scale insects and natural enemy communities of arthropod predators and parasitoids (Fig. 1). To achieve this, we examined scale insect and natural enemy abundance on native and exotic tree species in the genera Quercus and Acer. These genera contain some of the most common trees in urban landscapes (Raupp, Cumming & Raupp, 2006), and native trees in both genera are hosts to many scale species (Frank et al., 2013; Johnson & Lyon, 1976). Our first objective was to compare scale insect abundance on native and exotic species within each genus. Our second objective was to determine if natural enemies of scales and other herbivores were more abundant, diverse, or had different community structure on native or exotic species within each genus.

**METHODS**

All study trees were located on the grounds of North Carolina State University, an urban campus in Raleigh, NC, USA (35.786°N, 78.672°W). In 2012, we located 10 or 15 trees
Table 1 2012 and 2016 scale insect abundance.

| 2012          | Species          | Origin | n  | Scale insects | BH |
|---------------|------------------|--------|----|---------------|----|
| 2012          | Acer palmatum    | exotic | 15 | 0.92          | (0.27) | ab |
| 2012          | Acer platanoides | exotic | 10 | 0.22          | (0.18) | c  |
| 2012          | Acer rubrum      | native | 10 | 28.48         | (22.33) | a  |
| 2012          | Acer saccharum   | native | 10 | 0.22          | (0.08) | bc |
| 2012          | Quercus acutissima | exotic | 15 | 0.33          | (0.11) | a  |
| 2012          | Quercus alba    | native | 15 | 106.01        | (46.00) | b  |
| 2012          | Quercus phellos | native | 15 | 3.55          | (1.10) | c  |
| 2016          | Acer buergerianum | exotic | 10 | 0.10          | (0.07) | a  |
| 2016          | Acer palmatum    | exotic | 10 | 0.15          | (0.08) | a  |
| 2016          | Acer rubrum      | native | 10 | 65.75         | (31.77) | b  |
| 2016          | Acer saccharum   | native | 10 | 0.90          | (0.31) | c  |
| 2016          | Quercus acutissima | exotic | 10 | 0.30          | (0.17) | a  |
| 2016          | Quercus alba    | native | 10 | 11.65         | (5.24) | b  |
| 2016          | Quercus phellos | native | 10 | 8.75          | (3.89) | b  |

Note:
Mean scale insect abundance per 30 cm of branch in 2012 (top) and 2016 (bottom), reported as mean (± standard error) with n indicating the number of trees. 2016 counts include live scale insects only. Within each year-genus pair, tree species that share a letter are not different (α = 0.05) based on a Kruskal–Wallis test with a Benjamini–Hochberg (BH) post hoc comparison. Tree species are ordered alphabetically within each year-genus pair.

(Table 1) of each of the following species: *Acer palmatum* (Japanese maple), *A. platanoides* (Norway maple), *A. rubrum* (red maple), *A. saccharum* (sugar maple), *Quercus acutissima* (sawtooth oak), *Q. alba* (white oak), and *Q. phellos* (willow oak). *Acer palmatum* is native to Japan, South Korea, and eastern China. The other exotic maple, *A. platanoides*, is native to eastern Europe and western Russia from Sweden south to Greece. It is also an invasive species that has become established in parts of the eastern and northwestern US and Canada. *Acer rubrum* is native throughout the eastern half of North America from Quebec, Canada south to Florida, US. *Acer saccharum* is native throughout much of eastern North America south to North Carolina and Tennessee, US and cool regions further south. *Quercus acutissima* is native to eastern Asia including China, Korea, and Japan but has become established in some regions of eastern and southern US. *Quercus alba* is native throughout eastern North America from Quebec, Canada south to Florida and Texas, US. *Quercus phellos* is native throughout the southern and eastern US north to New Jersey. North Carolina State University campus is comprised of many land cover types including impervious surfaces, like roads and buildings, lawn and ornamental landscapes, sports fields,
and small forest patches. Study trees were in growing in lawn areas surrounded by turf or in mulched landscape beds surrounded by ornamental shrubs.

In October 2012, we pruned five 30 cm branches from each tree and used a dissecting microscope to identify and count scale insects on the branches. Many scale insects, especially those in the family Diaspididae, leave behind waxy covers that can persist on trees after the soft-bodied scale insect has died. In 2012, we counted all scales insects, live or dead, on the branches and identified armored scales (Hemiptera: Diaspididae), soft scales (Hemiptera: Coccidae), and pit scales (Hemiptera: Astrolecaniidae) to family. In May 2012, we used 7.6 × 12.7 cm yellow sticky cards (Great Lakes IPM, Inc., Vestaburg, MI, USA) to capture scale insect natural enemies in the canopy of each tree. Sticky cards were placed in the interior of the canopy, above the first lateral branches, to avoid attracting insects from other areas and incidental capture of insects flying in the vicinity of the trees. Arthropods were sampled for 7–13 days in each tree. We identified common predators to family or order and counted parasitoid wasps without identifying them. One sticky card was lost during sampling.

In 2016, we used ArcMap 10.2.2 (Esri, Redlands, CA, USA) to randomly select 10 study trees of each species from a geo-referenced inventory of trees maintained by the North Carolina State University Facilities Division. We included the same tree species as in 2012 except we replaced the exotic species A. platanoides, which was no longer present in sufficient numbers on campus, with another exotic, A. buergerianum (trident maple) which is native to eastern Asia. Trees of each species were at least 100 m apart, with the exception of three white oaks (Q. alba) which, out of necessity, were at least 50 m apart. From late February through early May 2016, we collected two terminal branches that were at least three m high from each tree to count scale insect abundance. We used a dissecting microscope to identify and count scale insects on the terminal 30 cm of each branch. We used metal probes to determine which scale insects were alive and included only live scale insects in 2016 data analysis. We counted all live scales and identified live armored scales (Hemiptera: Diaspididae), soft scales (Hemiptera: Coccidae), and pit scales (Hemiptera: Astrolecaniidae) to family. We used 7.6 × 12.7 cm yellow sticky cards (Great Lakes IPM, Inc., Vestaburg, MI, USA) to survey natural enemy abundance. We placed a single card in the canopy of each tree for two weeks in June 2016, and we repeated this in July and August 2016. Four sticky cards were lost. We used a dissecting microscope to identify parasitoid wasps to family and to identify common scale insect predators (Goulet & Huber, 1993). Here, we report on the six predator taxa that were collected and identified in both 2012 and 2016. Insect taxa were identified to family (Hemiptera: Anthocoridae, Coleoptera: Carabidae, Coleoptera: Coccinellidae, Diptera: Dolichopodidae) and spiders to order (Araneae).

**Analyses**

We conducted all statistical analyses in R version 3.3.2 (R Core Team, 2016) and conducted separate tests for maples and oaks. Because we used different data collection methods in 2012 and 2016, we do not compare results across years. We pooled scale insect counts from all sampled branches on each tree and calculated mean scale insect...
abundance per 30 cm of branch for use in analyses. To compare scale insect abundance between tree species, we performed four separate Kruskal–Wallis tests, one for each year-genus pair, using R package agricolae (De Mendiburu, 2016). We used the Benjamini–Hochberg method for post hoc multiple comparisons when overall tests indicated significant differences ($\alpha < 0.05$) between tree species (Benjamini & Hochberg, 1995). For each year, we compared total predator and, separately, total parasitoid wasp abundance between tree species using Kruskal–Wallis tests with Benjamini–Hochberg post hoc comparisons as above. For consistency and to account for differences in sampling duration (2012) and lost sticky cards (2016), we converted all predator and parasitoid counts to abundance per 7-day sampling period prior to analysis.

We used R package mvabund (Wang et al., 2014) to test whether the abundance of the six predator taxa varied across tree species. mvabund fits generalized linear models to multivariate abundance data to test the effects of a predictor variable on both community-level response and the responses of individual taxa (Warton et al., 2015). Distance-based analyses sometimes confound location and dispersion effects, but mvabund avoids this problem by allowing the user to specify a mean-variance relationship, for example by using poisson or negative binomial regressions (Warton, Wright & Wang, 2012). We fit negative binomial regressions to each predator taxon using raw counts and offset terms to account for differences in sample durations (oaks in 2012) or numbers (oaks and maples in 2016). To test whether the community of these six predator taxa differed across tree species, we used the anova.manyglm function with a Wald test statistic, 1,000 bootstrap iterations, and the default step-down $p$-value adjustment method in mvabund. When this test indicated an overall significant effect of tree species, we used the summary.manyglm function to test pairwise contrasts of tree species following the methods in Ji et al. (2013) and Bruce (2013). To account for multiple comparisons, we adjusted $p$-values in R’s base package using the Benjamini–Hochberg correction.

To obtain univariate statistics for the pairwise comparisons, we used the default step-down $p$-value adjustment method in the anova.manyglm function, changing the baseline tree species as necessary.

We used the R package vegan (Oksanen et al., 2010) to calculate the Shannon diversity index of the parasitoid wasp communities at the family level. In R’s base package, we used ANOVA to compare the diversity indices between tree species. We used mvabund to analyze 2016 parasitoid wasp communities following the same procedures we used for predators. Prior to analysis, we removed parasitoid wasp families that were represented by only a single individual (two families each for maples and oaks).

RESULTS
Scale insects
In 2012, we collected 9,757 scale insects, with a mean (± SD) of 21.68 (± 83.74) scale insects per 30 cm of branch per tree. Scale insect abundance varied by tree species for maples ($\chi^2 = 15.11, p < 0.002$), with the native A. rubrum having the highest abundance and the exotic A. platanoides having the lowest abundance (Table 1). A total of 94.98% of the scales we collected on maples were armored scales (Hemiptera: Diaspididae),
and the remaining 5.01% were soft scales (Hemiptera: Coccidae). Differences were also apparent between oak species ($\chi^2 = 23.69, p < 0.001$), with highest abundance on the native Q. alba and lowest abundance on the exotic Q. acutissima (Table 1). A total of 92.17% of the scales we collected on oaks were armored scales (Diaspididae) 5.39% were pit scales (Hemiptera: Asterolecaniidae), and 1.89% were soft scales (Coccidae).

In 2016, we collected 1,752 live scale insects, with a mean (± SD) of 12.51 (± 43.25) live scale insects per 30 cm of branch per tree. Scale insect abundance was less than in 2012 since we only counted live scales in 2016. Scale abundance varied by tree species for maples ($\chi^2 = 17.11, p < 0.001$) and oaks ($\chi^2 = 11.79, p < 0.003$); both native species of each genus had significantly more scale insects than their exotic congener(s) (Table 1). On maples, 98.87% of the scales we collected were armored scales (Hemiptera: Diaspididae), and the remaining 1.13% were soft scales (Hemiptera: Coccidae). On oaks, 40.58% of the scales we collected were soft scales (Coccidae), 22.46% were pit scales (Hemiptera: Asterolecaniidae), and 21.50% were armored scales (Diaspididae).

**Predators**

In 2012, we collected 207 predators in the five predator taxa reported here. Abundance per sample did not differ among maple species ($\chi^2 = 2.08, df = 3, p = 0.555$) or oak species ($\chi^2 = 2.27, df = 2, p = 0.321$) (Table 2). In 2016, we collected 1,074 predators in the five taxa which is more than in 2012 since we sampled three times instead of once. The number of predators per sample differed among maple species ($\chi^2 = 13.22, df = 3, p = 0.004$), with lower total predator abundance within the exotic A. palmatum than in the other maple species (Table 2). There was no difference in total predator abundance among oak species ($\chi^2 = 4.02, df = 2, p = 0.134$) (Table 2).

In 2012, the composition of predator communities was not different among tree species for maples (Wald statistic = 3.64, $p = 0.134$) or oaks (Wald statistic = 3.92, $p = 0.074$). In 2016, the predator community differed among maple species (Wald statistic = 5.15, $p < 0.049$); the exotic A. palmatum had a different community than all other Acer species (Fig. 2). This difference was driven by the significantly lower Dolichopodidae abundance within A. palmatum (Fig. 2; Table S1). The predator community also differed between oak species in 2016 (Wald statistic = 5.125, $p = 0.029$) (Fig. 2). The exotic Q. acutissima had a different overall predator community than the two native species, which was not driven by significant differences in any individual taxa (Fig. 2; Table S2).

**Parasitoid wasps**

In 2012, we collected 4,676 parasitoid wasps from 89 samples, with a mean (± SD) of 52.5 (± 47.2) parasitoid wasps per 7-day sample. The number of parasitoid wasps per 7-day sample was not different among maple species ($\chi^2 = 4.64, df = 3, p = 0.200$) but differed among the oak species ($\chi^2 = 17.26, df = 2, p < 0.001$), with highest abundance within a native, Q. phellos, and lowest abundance within the exotic, Q. acutissima (Table 2). In 2016, we collected 12,520 parasitoid wasps in 25 families from 206 samples. There was a mean (± SD) of 30.35 (± 13.12) parasitoid wasps per 7-day period. The number of parasitoid wasps per sample differed among maple species, with lower total...
abundance within a native, *A. saccharum*, than the other maple species ($\chi^2 = 9.96$, df = 3, $p = 0.019$), and did not differ among oak species ($\chi^2 = 1.68$, df = 2, $p = 0.431$) (Table 2).

The Shannon diversity index did not differ among maple species ($F_{3,36} = 2.168$, $p = 0.109$) or oak species ($F_{2,27} = 2.502$, $p = 0.101$). Parasitoid community compositions differed among maple species (Wald statistic = 15.33, $p = 0.001$; Fig. 3), with pairwise tests showing differences between each pair of maple species ($p < 0.05$), driven primarily by high Signiphoridae abundance within *A. rubrum* and high Aphelinidae abundance within *A. palmatum* (Table S3). Parasitoid community composition also differed among oak species (Wald statistic = 9.40, $p = 0.007$; Fig. 3), with *Q. phellos* having a different composition than the other two species (Table S4). The abundance of parasitoid wasps in the family Dryinidae was higher on *Q. phellos* than on the other oak species ($p < 0.05$).

**DISCUSSION**

Trees are critical for sustaining invertebrate and vertebrate diversity in urban habitats (Smith et al., 2006a, 2006b; Stagoll et al., 2012). Native trees, in particular, are often thought to be critical for supporting local herbivores and the predators and parasitoids that consume them (Goddard, Dougill & Benton, 2010; Isaacs et al., 2009; McKinney, 2002; Tallamy, 2004; Zueflle, Brown & Tallamy, 2007). Thus, increasing the proportion of native

| Table 2 2012 and 2016 predator and parasitoid abundance. |
|---|
| **2012** |
| Species | Origin | $n$ | Predators | BH | Parasitoids | BH |
| *Acer palmatum* | exotic | 14 | 1.93 (1.03) | – | 22.36 (4.57) | – |
| *Acer platanoides* | exotic | 10 | 2.00 (0.77) | – | 33.50 (5.93) | – |
| *Acer rubrum* | native | 10 | 0.90 (0.31) | – | 22.90 (3.61) | – |
| *Acer saccharum* | native | 10 | 0.90 (0.59) | – | 30.50 (15.49) | – |
| *Quercus acutissima* | exotic | 15 | 1.26 (0.29) | – | 24.49 (1.77) | a |
| *Quercus alba* | native | 15 | 1.64 (0.37) | – | 42.58 (4.37) | b |
| *Quercus phellos* | native | 15 | 3.25 (1.16) | – | 67.03 (7.27) | c |
| **2016** |
| Species | Origin | $n$ | Predators | BH | Parasitoids | BH |
| *Acer buergerianum* | exotic | 10 | 2.30 (0.60) | a | 30.23 (3.29) | a |
| *Acer palmatum* | exotic | 10 | 0.72 (0.14) | b | 34.87 (4.91) | a |
| *Acer rubrum* | native | 10 | 3.15 (0.61) | a | 34.73 (4.13) | a |
| *Acer saccharum* | native | 10 | 2.83 (1.32) | a | 20.48 (2.13) | b |
| *Quercus acutissima* | exotic | 10 | 4.86 (1.14) | – | 30.25 (5.29) | – |
| *Quercus alba* | native | 10 | 2.28 (0.31) | – | 28.28 (4.36) | – |
| *Quercus phellos* | native | 10 | 1.98 (0.34) | – | 33.63 (3.40) | c |

Note: Mean predator and parasitoid wasp abundance per 7-day sample from sticky cards in 2012 (top) and 2016 (bottom), reported as mean (± standard error) with $n$ indicating the number of trees. Predator tests were performed separately from parasitoid tests for each year-genus pair. Within each year-genus pair, tree species that share a letter are not different ($\alpha = 0.05$) based on a Kruskal–Wallis test with a Benjamini–Hochberg (BH) post hoc comparison. Letters are provided only when the overall Kruskal–Wallis test indicated a significant difference between species. Tree species are ordered alphabetically within each year-genus pair.
Tree species is often recommended as a measure to conserve urban animal diversity and reduce homogenization between cities (Alvey, 2006; Clark et al., 1997; Herrmann, Pearse & Baty, 2012; McKinney, 2006). In support of this recommendation and the enemy

**Figure 2 2016 predator communities.** Abundance of predators in five taxa in 2016 for (A) maples and (B) oaks. Colored boxes mark the interquartile range (IQR), and whiskers extend to the largest value within 1.5 * IQR. Values beyond 1.5 * IQR are marked as points. Exotic species are outlined in black. Predator taxa that differed significantly between tree species in univariate tests are marked with * (Tables S1 and S2). Global tests indicated significant differences in the predator communities of maples and oaks ($p < 0.05$), where *A. palmatum* was different than other maple species and *Q. acutissima* was different than other oak species (Tables S1 and S2).
release hypothesis, native species we sampled in the genera Acer and Quercus had higher scale insect density than exotic congeners. The scale insect community on maples and oaks in Raleigh includes many species native to the Southeastern US including Melanaspis tenebricosa, M. obscura, Parthenolecanium quercifex, and Mesolecanium nigrofasciatum, in addition to exotic species such as Lopholeucus japonica and P. corni. Native A. rubrum, Q. phellos, and Q. alba had scale insect densities two to three orders of magnitude higher than any exotics or the native A. saccharum. In terms of supporting native herbivores, and herbivores in general, native tree species in cities are beneficial. However, from the perspective of aesthetics or the ecosystem services (such as carbon fixation) carried out by trees, the densities of scale insects observed on A. rubrum, Q. phellos, and other urban trees are potentially detrimental. At such densities, scale insects can reduce photosynthesis (Cockfield, Potter & Houtz, 1987), growth (Meineke et al., 2016; Meineke & Frank, 2018; Speight, 1991; Vranjic & Ash, 1997), and the aesthetic or structural condition of trees (Dale & Frank, 2014a; Just, Frank & Dale, 2018;
Speight et al., 1998; Sperry et al., 2001). Conversely, in the urban sites we studied, exotic trees had fewer pests and may be more likely to maintain growth and services such as temperature reduction and carbon sequestration with fewer management costs (Chalker-Scott, 2015; Hitchmough, 2011).

Scale insects and other hemipteran herbivores are prey or hosts for hundreds of predatory and parasitic arthropods as well as prey for birds and other vertebrates (Brennan, Morrison & Dahlsten, 2000; Clout & Hay, 1989; Evans, Towns & Beggs, 2015; Moed & Fitzgerald, 1982; Morse, 1971; Witmer, 1996). In our study, the abundance and community composition of predators and parasitoid wasps, as sampled by sticky cards, were generally similar between native and exotic congeners. In 2012, both predator and parasitoid wasp abundance were highest within the native species Q. phellos. Parasitoid wasp abundance was lowest within the exotic species Q. acutissima. Parasitoid wasp abundance overall was greatest in Q. phellos but the family Dryinidae was the only family that was significantly more abundant. Dryinid wasps parasitize Hemipterans in the suborder Auchenorrhyncha which includes leafhoppers, planthoppers, lace bugs, and others but not scale insects (suborder Sternorrhyncha) (Klejdysz et al., 2018). Oaks support many Auchenorrhyncha that could be hosts for Dryinid wasps including specialists like oak lace bug (Corythucha arcuata) and oak treehopper (Platycotis viitata) and many generalists (Johnson & Lyon, 1976; Southwood, 1961; Southwood, Moran & Kennedy, 1982; Southwood et al., 2004, 2005). The most abundant parasitoid families within oaks were Aphelinidae, Platygatridae, and Mymaridae. Most Aphelinids are parasitoids of Sternorrhyncha which includes scale insects, aphids, and mealybugs (Viggiani, 1984). Coccophagus lycimnia is a common Aphelinid parasitoid of Parthenolecanium spp. scale which is the most common scale on Q. phellos in our region (Meineke, Dunn & Frank, 2014; Meineke et al., 2013; Robayo Camacho et al., 2018). A total of 21 parasitoid species have been reared from Parthenolecanium scales from Q. phellos (Meineke, Dunn & Frank, 2014; Meineke et al., 2013; Robayo Camacho et al., 2018). Most Platygastids parasitize flies in the family Cecidomyiidae many of which are herbivorous leafminers and gall makers but the family also includes predatory flies that prey on scales, aphids, and other Hemipterans (Hagen et al., 1999). All species within the family Mymaridae parasitize eggs of other insects, frequently those of scale insects and their relatives (Hemiptera: Coccoidea) (Harris, 1968).

Where differences in natural enemy abundance were observed within maples in 2016, a native species, A. saccharum, had the lowest abundance of predators and parasitoid wasps. The native species A. rubrum, which often has severe infestations of gloomy scales (Melanaspis tenebricosa) in cities (Dale & Frank, 2014a, 2014b; Metcalf, 1912; Youngsteadt et al., 2015), had significantly higher abundance of Signiphoridae wasps which parasitize scales, mealybugs, or psyllids (Gibson, Huber & Woolley, 1997). Signiphora spp. (Signiphoridae), Encarsia spp. (Aphelinidae), Ablerus spp. (Aphelinidae), and Coccidoctonus (Encyrtidae) have been reared from gloomy scales (Dale & Frank, 2014b). Acer palmatum, which had very low scale insect density, had significantly more Aphelinidae parasitoids than the other Acer species. Members of Aphelinidae, primarily parasitoids of aphids, scales, whiteflies, and other
hemipterans, could have been attracted to *A. palmatum* by aphids or other herbivores we did not sample (Frank et al., 2013).

Many other arthropods are present within oak and maple canopies (Johnson & Lyon, 1976; Southwood, Moran & Kennedy, 1982). For example, 537 and 297 lepidopteran species are associated with the genera *Quercus* and *Acer* respectively (Tallamy & Shropshire, 2009). Thus, many parasitoids and predators we captured may interact with herbivores other than scales or with each other as higher-order natural enemies. In addition, sticky cards are a passive sampling technique that is biased toward flying taxa and can capture “tourists” in addition to species that have close associations with tree species or its herbivores. For example, few North American carabid species are arboreal so some of the carabids we captured could have been incidental or tourists in our study trees. However, arthropods collected from *Q. phellos* and *A. rubrum* foliage with sweep nets in previous research included many of the same taxa as collected on sticky cards in addition to predatory mites (Phytositiidae), lacewings (Neuroptera: Coniopterygidae, Chrysopidae), ants (Hymenoptera: Formicidae), 17 families of spiders, and many others (McCluney, George & Frank, 2018; Meineke et al., 2017).

Low scale density on *A. palmatum* and other exotic species could have resulted from the combined influence of high natural enemy abundance and low susceptibility to many scale species. Generalist predators in the families Anthocoridae and Coccinellidae, which feed on scales and other Hemipterans, were captured in similar numbers in native and exotic trees. Spiders, which are common in urban trees and feed on many taxa, were also of similar abundance in native and exotic trees (McCluney, George & Frank, 2018; Meineke et al., 2017). Other researchers have also found similar densities of arthropod natural enemies on native and exotic trees even though the exotic species had lower herbivore densities (Hartley, Rogers & Siemann, 2010; Proches et al., 2008; Southwood, Moran & Kennedy, 1982). Natural enemies frequently visit and remain in habitats due to the vegetation structure, microclimates, or other resources that may be similar for native and exotic tree species. Our results corroborate these findings but this pattern requires further research to understand the factors, other than herbivores, that define the conservation value of exotic trees.

There is growing evidence that some insect taxa, or even insects in general, are declining due to land use change, climate change, exotic plants, insecticides, and other factors (Conrad et al., 2006; Hallmann et al., 2017; Potts et al., 2010). All these issues converge when managing urban trees to conserve arthropods and minimize pests. Urban forest design and planting recommendations generally include increasing tree diversity at multiple taxonomic levels using a mixture of native and non-native species (Raupp, Cumming & Raupp, 2006; Elevitch & Wilkinson, 2001). The primary goal of increasing urban tree diversity has been to reduce catastrophic damage caused by exotic pests such as emerald ash borer and Dutch elm disease. Although we only studied three exotic maples and one exotic oak they are among the most commonly planted species in our region. Our results suggest that planting these exotic tree species is also a valuable contribution to conserving arthropod communities (Chalker-Scott, 2015; Hitchmough, 2011). Since these exotic species are also less susceptible to scales, and potentially
other pests, they may not require insecticide applications that harm non-target organisms and thus reverse conservation goals (Goulson, 2013; Luck & Dahlstein, 1975; Raupp et al., 2001; Woodcock et al., 2016).

The exotic species we studied conserved similar arthropod natural enemy abundance and community structure at the family level as their native congers. There are likely differences in natural enemy communities at lower taxonomic levels particularly among specialists that require a particular herbivore species on which to feed. Native trees, such as oaks that host hundreds of herbivorous species (Southwood, 1961), may have richer specialist herbivore diversity and a different array of natural enemy species than exotic trees (Burghardt et al., 2010; Keane & Crawley, 2002). However, the extent of these differences may vary with arthropod, life stage, feeding guild, taxonomic isolation of the tree species, and other factors we could not assess (Burghardt & Tallamy, 2013, 2015). In addition, arthropod communities on distantly related tree species or those with no native relatives such as ginkos (Ginkgo biloba) or crape myrtle (Lagerstroemia spp.) are likely more distinct than comparisons between congers (Burghardt & Tallamy, 2013, 2015). However, we hypothesize that herbivory and the biodiversity supported by a tree depends as much on urban variables such as habitat fragmentation, impervious surface cover, and temperature as it does on geographic origin of the tree species (Frank, 2014; Le Roux et al., 2018; Long, D’Amico & Frank, 2018; McCluney, George & Frank, 2018; Meineke et al., 2017). Thus, even a native urban tree will likely support a different arthropod community than the same tree species in a natural habitat and have different conservation value (Herrmann, Pearse & Baty, 2012; Manning, Fischer & Lindenmayer, 2006; Turrini & Knop, 2015). Our results support mixing native and exotic trees to achieve conservation and pest management goals.

CONCLUSIONS

Conservation of arthropods, for their own sake, and to support birds are commonly cited reasons to plant native instead of exotic trees in urban spaces (Goddard, Dougill & Benton, 2010; Tallamy, 2004). Our analyses of the scale insect and natural enemy communities in some native and exotic maple and oak species does not fully support this perspective. The native tree species in our research did not always host more herbivorous scale insects than the exotic species and we found similar natural enemy communities within the native and exotic species. Moreover, high densities of scale insects in native A. rubrum and Q. phellos have been found to reduce tree condition and growth in previous research (Dale & Frank, 2014a; Meineke et al., 2016; Meineke et al., 2018). We conclude that the exotic oak and maple species we studied could be as valuable as the native species for conserving arthropod natural enemies. The pest susceptibility of native tree species must be balanced against potential conservation benefits when selecting trees for urban planting.

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**Competing Interests**
The authors declare no competing interests.

**Author Contributions**
- Steven D. Frank conceived and designed the experiments, performed the experiments, analyzed the data, contributed reagents/materials/analysis tools, prepared figures and/or tables, authored or reviewed drafts of the paper, approved the final draft.
- Kristi M. Backe conceived and designed the experiments, performed the experiments, analyzed the data, prepared figures and/or tables, authored or reviewed drafts of the paper, approved the final draft.
- Casey McDaniel performed the experiments, approved the final draft.
- Matthew Green performed the experiments, approved the final draft.
- Sarah Widney performed the experiments, approved the final draft.
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REFERENCES
Alvey AA. 2006. Promoting and preserving biodiversity in the urban forest. Urban Forestry & Urban Greening 5(4):195–201 DOI 10.1016/j.ufug.2006.09.003.

Aronson MFJ, Handel SN, La Puma IP, Clements SE. 2015. Urbanization promotes non-native woody species and diverse plant assemblages in the New York metropolitan region. Urban Ecosystems 18(1):31–45 DOI 10.1007/s11252-014-0382-z.

Benjamini Y, Hochberg Y. 1995. Controlling the false discovery rate: a practical and powerful approach to multiple testing. Journal of the Royal Statistical Society: Series B (Methodological) 57(1):289–300 DOI 10.1111/j.2517-6161.1995.tb02031.x.

Brennan LA, Morrison MI, Dahlsten DL. 2000. Comparative foraging dynamics of chestnut-backed and mountain chickadees in the western Sierra Nevada. Northwestern Naturalist 81(3):129–147 DOI 10.2307/3536824.

Bruce C. 2013. From metacommunity dynamics to rapid biodiversity assessment: DNA-based approaches expand horizons in both fundamental and applied ecology. Doctoral dissertation, University of East Anglia.

Burghardt KT, Tallamy DW. 2013. Plant origin asymmetrically impacts feeding guilds and life stages driving community structure of herbivorous arthropods. Diversity and Distributions 19(12):1553–1565 DOI 10.1111/ddi.12122.

Burghardt KT, Tallamy DW. 2015. Not all non-natives are equally unequal: reductions in herbivore β-diversity depend on phylogenetic similarity to native plant community. Ecology Letters 18(10):1087–1098 DOI 10.1111/ele.12492.

Burghardt KT, Tallamy DW, Gregory Shriver W. 2009. Impact of native plants on bird and butterfly biodiversity in suburban landscapes. Conservation Biology 23(1):219–224 DOI 10.1111/j.1523-1739.2008.01076.x.

Burghardt KT, Tallamy DW, Philips C, Shropshire KJ. 2010. Non-native plants reduce abundance, richness, and host specialization in lepidopteran communities. Ecosphere 1(5):art11 DOI 10.1890/es10-00032.1.

Chalker-Scott L. 2015. Nonnative, noninvasive woody species can enhance urban landscape biodiversity. Arboriculture & Urban Forestry 41:173–186.

Clark JR, Matheny NP, Cross G, Wake V. 1997. A model of urban forest sustainability. Journal of Arboriculture 23(1):17–30.

Clout M, Hay J. 1989. The importance of birds as browsers, pollinators and seed dispersers in New Zealand forests. New Zealand Journal of Ecology 12(supplement):27–33.

Cockfield SD, Potter DA. 1990. Euonymus scale (Homoptera: Diaspididae) effects on plant growth and leaf abscission and implications for differential site selection by male and female scales. Journal of Economic Entomology 83(3):995–1001 DOI 10.1093/jee/83.3.995.
Cockfield SD, Potter DA, Houtz RL. 1987. Chlorosis and reduced photosynthetic CO2 assimilation of Euonymus fortunei infested with euonymus scale (Homoptera: Diaspididae). *Environmental Entomology* **16**(6):1314–1318 DOI 10.1093/ee/16.6.1314.

Conrad KF, Warren MS, Fox R, Parsons MS, Woiwod IP. 2006. Rapid declines of common, widespread British moths provide evidence of an insect biodiversity crisis. *Biological Conservation* **132**(3):279–291 DOI 10.1016/j.biocon.2006.04.020.

Conway TM, Vander Vecht J. 2015. Growing a diverse urban forest: Species selection decisions by practitioners planting and supplying trees. *Landscape and Urban Planning* **138**:1–10 DOI 10.1016/j.landurbplan.2015.01.007.

Dale AG, Frank SD. 2014a. The effects of urban warming on herbivore abundance and street tree condition. *PLOS ONE* **9**(7):e102996 DOI 10.1371/journal.pone.0102996.

Dale AG, Frank SD. 2014b. Urban warming trumps natural enemy regulation of herbivorous pests. *Ecological Applications* **24**(7):1596–1607 DOI 10.1890/13-1961.1.

Dale AG, Frank SD. 2017. Warming and drought combine to increase pest insect fitness on urban trees. *PLOS ONE* **12**(3):e0173844 DOI 10.1371/journal.pone.0173844.

Dale AG, Frank SD. 2018. Urban plants and climate drive unique arthropod interactions with unpredictable consequences. *Current Opinion in Insect Science* **29**:27–33 DOI 10.1016/j.cois.2018.06.001.

De Mendiburu F. 2016. *agricolae: Statistical procedures for agricultural research*. R package version 1.2–4. Available at https://cran.r-project.org/web/packages/agricolae/index.html.

Dixon A. 1971. The role of aphids in wood formation. I. The effect of the sycamore aphid, Dreopanosiphum platanoides (Schr.)(Aphididae), on the growth of sycamore, *Acer pseudoplatanus* (L.). *Journal of Applied Ecology* **8**(1):165–179 DOI 10.2307/2402135.

Ehrlich PR, Raven PH. 1964. Butterflies and plants: a study in coevolution. *Evolution* **18**(4):586–608 DOI 10.1111/j.1558-5646.1964.tb01674.x.

Elevitch CR, Wilkinson K. 2001. *The overstory book*. Holualoa: Permanent Agriculture Resources.

Evans AE, Towns DR, Beggs JR. 2015. Relative importance of sugar resources to endemic gecko populations in an isolated island ecosystem. *New Zealand Journal of Ecology* **39**(2):262–272.

Farrell BD, Mitter C, Futuyma DJ. 1992. Diversification at the insect-plant interface. *BioScience* **42**(1):34–42 DOI 10.2307/1311626.

Frank SD. 2014. Bad neighbors: urban habitats increase cankerworm damage to non-host understory plants. *Urban Ecosystems* **17**(4):1135–1145 DOI 10.1007/s11252-014-0368-x.

Frank SD, Klingeman WE, White SA, Fulcher A. 2013. Biology, Injury, and Management of Maple Tree Pests in Nurseries and Urban Landscapes. *Journal of Integrated Pest Management* **4**(1):1–14 DOI 10.1603/ipm12007.

Gibson GA, Huber JT, Woolley JB. 1997. *Annotated keys to the genera of nearctic chalcidoidea* (Hymenoptera). Ottawa: NRC Research Press.

Goulson D. 2013. An overview of the environmental risks posed by neonicotinoid insecticides. *Journal of Applied Ecology* **50**(4):977–987 DOI 10.1111/1365-2664.12111.
Grimm NB, Faeth SH, Golubiewski NE, Redman CL, Wu J, Bai X, Briggs JM. 2008. Global change and the ecology of cities. *Science* **319**(5864):756–760 DOI 10.1126/science.1150195.

Hagen KS, Mills NJ, Gordh G, McMurtry JA. 1999. Terrestrial arthropod predators of insect and mite pests. In: Bellows TS, Fisher TW, eds. *Handbook of Biological Control*. New York: Academic Press, 383–503.

Hallmann CA, Sorg M, Jongejans E, Siepel H, Hofland N, Schwan H, Stenmans W, Müller A, Sumser H, Hörren T, Goulson D, De Kroon H. 2017. More than 75 percent decline over 27 years in total flying insect biomass in protected areas. *PLOS ONE* **12**(10):e0185809 DOI 10.1371/journal.pone.0185809.

Hanks LM, Denno RF. 1993. Natural enemies and plant water relations influence the distribution of an armored scale insect. *Ecology* **74**(4):1081–1091 DOI 10.2307/1940478.

Harris KM. 1968. A systematic revision and biological review of the cecidomyiid predators (Diptera: Cecidomyiidae) on world Coccoidea (Hemiptera-Homoptera). *Transactions of the Royal Entomological Society of London* **119**(13):401–488 DOI 10.1111/j.1365-2311.1968.tb00504.x.

Hartley MK, Rogers WE, Siemann E. 2010. Comparisons of arthropod assemblages on an invasive and native trees: abundance, diversity and damage. *Arthropod-Plant Interactions* **4**(4):237–245 DOI 10.1007/s11829-010-9105-4.

Herrmann DL, Pearse IS, Baty JH. 2012. Drivers of specialist herbivore diversity across 10 cities. *Landscape and Urban Planning* **108**(2–4):123–130 DOI 10.1016/j.landurbplan.2012.08.007.

Hitchmough J. 2011. Exotic plants and plantings in the sustainable, designed urban landscape. *Landscape and Urban Planning* **100**(4):380–382 DOI 10.1016/j.landurbplan.2011.02.017.

Hokkanen HM, Pimentel D. 1989. New associations in biological control: theory and practice. *The Canadian Entomologist* **121**(10):829–840.

Isaacs R, Tuell J, Fiedler A, Gardiner M, Landis D. 2009. Maximizing arthropod-mediated ecosystem services in agricultural landscapes: the role of native plants. *Frontiers in Ecology and the Environment* **7**(4):196–203 DOI 10.1890/080035.

Ji Y, Ashton L, Pedley SM, Edwards DP, Tang Y, Nakamura A, Kitching R, Dolman PM, Woodcock P, Edwards FA, Larsen TH, Hsu WW, Benedick S, Hamer KC, Wilcove DS, Bruce C, Wang X, Levi T, Lott M, Emerson BC, Yu DW. 2013. Reliable, verifiable and efficient monitoring of biodiversity via metabarcoding. *Ecology Letters* **16**(10):1245–1257 DOI 10.1111/ele.12162.

Johnson WT, Lyon HH. 1976. *Insects that feed on trees and shrubs*. Ithaca: Cornell University Press, 560.

Just MG, Frank SD, Dale AG. 2018. Impervious surface thresholds for urban tree site selection. *Urban Forestry & Urban Greening* **34**:141–146 DOI 10.1016/j.ufug.2018.06.008.

Keane RM, Crawley MJ. 2002. Exotic plant invasions and the enemy release hypothesis. *Trends in Ecology & Evolution* **17**(4):164–170 DOI 10.1016/s0169-5347(02)02499-0.

Klejdysz T, Klukowski Z, Pruszyński G, Kubasik W. 2018. New data and a checklist of Dryinidae (Hymenoptera) from Poland, and their role in controlling leafhopper and planthopper crop pests (Hemiptera: Cicadomorpha, Fulgoromorpha). *Polish Journal of Entomology* **87**(1):41–55 DOI 10.2478/pjen-2018-0003.

Kosztarab M. 1996. *Scale insects of northeastern North America: identification, biology, and distribution*. Martinsville: Virginia Museum of Natural History.
Le Roux DS, Ikin K, Lindenmayer DB, Manning AD, Gibbons P. 2018. The value of scattered trees for wildlife: Contrasting effects of landscape context and tree size. *Diversity and Distributions* **24**(1):69–81 DOI 10.1111/ddi.12658.

Long LC, D’Amico V, Frank SD. 2018. Urban forest fragments buffer trees from warming and pests. *Science of the Total Environment* **658**:1523–1530 DOI 10.1016/j.scitotenv.2018.12.293.

Luck RF, Dahlstein DL. 1975. Natural decline of a pine needle scale (Chionaspis pinifoliae [Fitch]), outbreak at South Lake Tahoe, California following cessation of adult mosquito control with malathion. *Ecology* **56**(4):893–904 DOI 10.2307/1936299.

Manning AD, Fischer J, Lindenmayer DB. 2006. Scattered trees are keystone structures—implications for conservation. *Biological Conservation* **132**(3):311–321 DOI 10.1016/j.biocon.2006.04.023.

McCluney KE, George T, Frank SD. 2018. Water availability influences arthropod water demand, hydration and community composition on urban trees. *Journal of Urban Ecology* **4**(1):juy003 DOI 10.1093/jue/juy003.

McClure MS. 1977. Resurgence of scale, fiorinia-externa (homoptera-diaspididae), on hemlock following insecticide application. *Environmental Entomology* **6**(3):480–484 DOI 10.1093/ee/6.3.480.

McKinney ML. 2002. Urbanization, biodiversity, and conservation. *BioScience* **52**(10):883–890 DOI 10.1641/0006-3568(2002)052[0883:Ubac]2.0.co;2.

McKinney ML. 2006. Urbanization as a major cause of biotic homogenization. *Biological Conservation* **127**(3):247–260 DOI 10.1016/j.biocon.2005.09.005.

Meineke EK, Dunn RR, Frank SD. 2014. Early pest development and loss of biological control are associated with urban warming. *Biology Letters* **10**(11):20140586 DOI 10.1098/rsbl.2014.0586.

Meineke EK, Dunn RR, Sexton JO, Frank SD. 2013. Urban warming drives insect pest abundance on street trees. *PLOS ONE* **8**(3):e59687 DOI 10.1371/journal.pone.0059687.

Meineke EK, Frank SD. 2018. Water availability drives urban tree growth responses to herbivory and warming. *Journal of Applied Ecology* **55**(4):1701–1713 DOI 10.1111/1365-2664.13130.

Meineke EK, Holmquist AJ, Wimp GM, Frank SD. 2017. Changes in spider community composition are associated with urban temperature, not herbivore abundance. *Journal of Urban Ecology* **3**(1):juw010 DOI 10.1093/jue/juw010.

Meineke E, Youngsteadt E, Dunn RR, Frank SD. 2016. Urban warming reduces aboveground carbon storage. *Proceedings of the Royal Society B: Biological Sciences* **283**(1840):20161574 DOI 10.1098/rspb.2016.1574.

Metcalf ZP. 1912. The gloomy scale, an important enemy of shade trees in North Carolina. *Journal of the Elisha Mitchell Scientific Society* **28**:88–91.

Moed A, Fitzgerald BM. 1982. Foods of insectivorous birds in forest of the Orongorongo Valley, Wellington, New Zealand. *New Zealand Journal of Zoology* **9**(3):391–403 DOI 10.1080/03014223.1982.10423869.

Morse DH. 1971. The insectivorous bird as an adaptive strategy. *Annual Review of Ecology and Systematics* **2**(1):177–200 DOI 10.1146/annurev.es.02.110171.001141.

Oksanen J, Blanchet FG, Kindt R, Legendre P, O’hara R, Simpson GL, Solymos P, Stevens MHH, Wagner H. 2010. vegan: community ecology package. R package version 1.17-2. Available at [http://cran r-project org](http://cran r-project.org) (accessed 23 January 2010).
Parker JD, Hay ME. 2005. Biotic resistance to plant invasions? Native herbivores prefer non-native plants. *Ecology Letters* 8(9):959–967.

Potts SG, Biesmeijer JC, Kremen C, Neumann P, Schweiger O, Kunin WE. 2010. Global pollinator declines: trends, impacts and drivers. *Trends in Ecology & Evolution* 25(6):345–353 DOI 10.1016/j.tree.2010.01.007.

Procheş Ş, Wilson JRU, Richardson DM, Chown SL. 2008. Herbivores, but not other insects, are scarce on alien plants. *Austral Ecology* 33(5):691–700 DOI 10.1111/j.1442-9993.2008.01836.x.

R Core Team. 2016. *R: A language and Environment for Statistical Computing*. Vienna: R Foundation for Statistical Computing. Available at [https://www.R-project.org/](https://www.R-project.org/).

Raupp MJ, Cumming AB, Raupp EC. 2006. Street tree diversity in eastern North America and its potential for tree loss to exotic borers. *Arboriculture & Urban Forestry* 32:297–304.

Raupp MJ, Holmes JJ, Sadof C, Shrewsbury PM, Davidson JA. 2001. Effects of cover sprays and residual pesticides on scale insects and natural enemies in urban forests. *Journal of Arboriculture* 27(4):203–214.

Raupp MJ, Shrewsbury PM, Herms DA. 2010. Ecology of herbivorous arthropods in urban landscapes. *Annual Review Entomology* 55(1):19–38 DOI 10.1146/annurev-ento-112408-085351.

Riley CB, Herms DA, Gardiner MM. 2018. Exotic trees contribute to urban forest diversity and ecosystem services in inner-city Cleveland, OH. *Urban Forestry & Urban Greening* 29:367–376 DOI 10.1016/j.ufug.2017.01.004.

Robayo Camacho E, Chong J-H, Braman SK, Frank SD, Schultz PB. 2018. Natural Enemy Communities and Biological Control of *Parthenolecanium* spp. (Hemiptera: Coccidae) in the Southeastern United States. *Journal of Economic Entomology* 111(4):1558–1568 DOI 10.1093/jee/toy102.

Shochat E, Warren P, Faeth S, McIntyre NE, Hope D. 2006. From patterns to emerging processes in mechanistic urban ecology. *Trends in Ecology & Evolution* 21(4):186–191 DOI 10.1016/j.tree.2005.11.019.

Smith RM, Gaston KJ, Warren PH, Thompson K. 2006a. Urban domestic gardens (VIII): environmental correlates of invertebrate abundance. *Biodiversity and Conservation* 15(8):2515–2545 DOI 10.1007/s10531-005-2784-y.

Smith RM, Warren PH, Thompson K, Gaston KJ. 2006b. Urban domestic gardens (VI): environmental correlates of invertebrate species richness. *Biodiversity & Conservation* 15(8):2415–2438 DOI 10.1007/s10531-004-5014-0.

Southwood TRE. 1961. The number of species of insect associated with various trees. *Journal of Animal Ecology* 30(1):1–8 DOI 10.2307/2109.

Southwood TRE, Moran VC, Kennedy CEJ. 1982. The richness, abundance and biomass of the arthropod communities on trees. *Journal of Animal Ecology* 51(2):635–649 DOI 10.2307/3988.

Southwood TRE, Wint GRW, Kennedy CEJ, Greenwood SR. 2004. Seasonality, abundance, species richness and specificity of the phytophagous guild of insects on oak (*Quercus*) canopies. *European Journal of Entomology* 101(1):43–50 DOI 10.14411/eje.2004.011.

Southwood TRE, Wint GRW, Kennedy CEJ, Greenwood SR. 2005. The composition of the arthropod fauna of the canopies of some species of oak (*Quercus*). *European Journal of Entomology* 102(1):65–72 DOI 10.14411/eje.2005.009.

Speight MR. 1991. The impact of leaf-feeding by nymphs of the horse chestnut scale Pulvinaria regalis Canard (Hem., Coccidae), on young host trees. *Journal of Applied Entomology* 112(1–5):389–399 DOI 10.1111/j.1439-0418.1991.tb01072.x.
Speight MR, Hails RS, Gilbert M, Foggo A. 1998. Horse Chestnut Scale (Pulvinaria regalis) (Homoptera: Coccidae) and urban host tree environment. *Ecology* 79(5):1503–1513 DOI 10.1890/0012-9658(1998)079[1503:hcsprh]2.0.co;2.

Sperry CE, Chaney WR, Guofan S, Sadof CS. 2001. Effects of tree density, tree species diversity, and percentage of hardscape on three insect pests of honeylocust. *Journal of Arboriculture* 27:263–271.

Stagoll K, Lindenmayer DB, Knight E, Fischer J, Manning AD. 2012. Large trees are keystone structures in urban parks. *Conservation Letters* 5(2):115–122 DOI 10.1111/j.1755-263x.2011.00216.x.

Tallamy DW. 2004. Do alien plants reduce insect biomass? *Conservation Biology* 18(6):1689–1692 DOI 10.1111/j.1523-1739.2004.00512.x.

Tallamy DW, Shropshire KJ. 2009. Ranking lepidopteran use of native versus introduced plants. *Conservation Biology* 23(4):941–947 DOI 10.1111/j.1523-1739.2009.01202.x.

Tooker JF, Hanks LM. 2000. Influence of Plant Community Structure on Natural Enemies of Pine Needle Scale (Homoptera: Diaspididae) in Urban Landscapes. *Environmental Entomology* 29(6):1305–1311 DOI 10.1603/0046-225x-29.6.1305.

Turrini T, Knop E. 2015. A landscape ecology approach identifies important drivers of urban biodiversity. *Global Change Biology* 21(4):1652–1667 DOI 10.1111/gcb.12825.

United States Department of Agriculture (USDA). 2018. *The PLANTS database*. Greensboro: National Plant Data Team. Available at http://plants.usda.gov (accessed 20 December 2018).

Viggiani G. 1984. Bionomics of the aphelinidae. *Annual Review of Entomology* 29(1):257–276 DOI 10.1146/annurev.ento.29.1.257.

Vranjic JA, Ash JE. 1997. Scale insects consistently affect roots more than shoots: The impact of infestation size on growth of Eucalypt seedlings. *Journal of Ecology* 85(2):143–149 DOI 10.2307/2960646.

Wang Y, Naumann U, Wright S, Eddelbuettel D, Warton D. 2014. *mvabund: statistical methods for analysing multivariate abundance data*. R package version 3. Available at https://cran.r-project.org/web/packages/mvabund/index.html.

Warton DI, Foster SD, De’ath G, Stoklosa J, Dunstan PK. 2015. Model-based thinking for community ecology. *Plant Ecology* 216(5):669–682 DOI 10.1007/s11258-014-0366-3.

Warton DI, Wright ST, Wang Y. 2012. Distance-based multivariate analyses confound location and dispersion effects. *Methods in Ecology and Evolution* 3(1):89–101 DOI 10.1111/j.2041-210x.2011.00127.x.

Witmer MC. 1996. Annual diet of cedar waxwings based on U.S. biological survey records (1885–1950) compared to diet of American Robins: contrasts in dietary patterns and natural history. *Auk* 113(2):414–430 DOI 10.2307/4088908.

Woodcock BA, Isaac NJB, Bullock JM, Roy DB, Garthwaite DG, Crowe A, Pywell RF. 2016. Impacts of neonicotinoid use on long-term population changes in wild bees in England. *Nature Communications* 7(1):12459 DOI 10.1038/ncomms12459.

Wu Z, Jamieson S, Kielbaso J. 1991. Urban forest pest management. *Journal of Arboriculture* 17:150–158.

Youngsteadt E, Dale AG, Terando AJ, Dunn RR, Frank SD. 2015. Do cities simulate climate change? A comparison of herbivore response to urban and global warming. *Global Change Biology* 21(1):97–105 DOI 10.1111/gcb.12692.
Zueflé ME, Brown WP, Tallamy DW. 2007. Effects of non-native plants on the native insect community of Delaware. *Biological Invasions* 10(7):1159–1169. DOI 10.1007/s10530-007-9193-y.

Zueflé ME, Brown WP, Tallamy DW. 2008. Effects of non-native plants on the native insect community of Delaware. *Biological Invasions* 10(7):1159.

Zvereva EL, Lanta V, Kozlov MV. 2010. Effects of sap-feeding insect herbivores on growth and reproduction of woody plants: a meta-analysis of experimental studies. *Oecologia* 163(4):949–960. DOI 10.1007/s00442-010-1633-1.