Bad neighbors: urban habitats increase cankerworm damage to non-host understory plants

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Abstract Plants growing in vegetationally diverse habitats or near taxonomically distinct neighbors often experience less herbivory than plants in more simple habitats. When plants experience more herbivory in these situations it is called associational susceptibility and is most common when herbivores spill from their preferred plant host onto neighboring plants. Cankerworms are common pests of urban trees that have been shown in forests to disperse from preferred to less preferred hosts. I found that two common characteristics of urban habitats, low vegetational diversity and exotic plants, affect cankerworm herbivory of non-host understory plants. In an urban landscape I measured cankerworm herbivory on native dogwood trees growing in the open and below cankerworm host and non-host trees. Herbivory of native dogwoods was ten times greater below cankerworm hosts than on trees below non-hosts or in the open. At an arboretum I measured herbivory of native and exotic plants growing below cankerworm hosts in simple landscape plantings and in natural forests. Associational susceptibility of native dogwoods and *Rhododendron* spp. disappeared when they were growing in complex natural forests even though cankerworm hosts were more abundant. Cankerworms consistently preferred native plant species more than exotic congeners in laboratory experiments. As such, exotic plants experienced very little herbivory regardless of habitat. Herbivorous pests are often more abundant on urban plants than plants in natural habitats. My research shows that, although some plants experience more herbivory when growing near cankerworm hosts, increasing urban habitat complexity could reduce pest damage overall.

Keywords Plant diversity · Associational resistance · Associational susceptibility · Vegetational diversity · Enemies hypothesis · Exotic plants

Vegetational diversity—the kinds, spatial array, and temporal overlap of plants in a habitat (sensu Andow 1991)—affects the herbivory experienced by plants in that habitat (Atsatt and O'Dowd 1976; Andow 1991; Barbosa et al. 2009). Plants in vegetationally diverse habitats often experience less herbivory than plants in simple habitats (Andow 1991). This phenomenon is called associational resistance and has been documented in agricultural (Pimentel 1961; Root 1973), urban (Hanks and Denno 1993; Shrewsbury and Raupp 2000; Tooker and

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Hanks 2000), and natural ecosystems (Kareiva 1983). Although associational resistance is the most common outcome, sometimes herbivory increases on plants growing with taxonomically distinct neighbors (Andow 1991; Barbosa et al. 2009). This is called associational susceptibility and occurs when herbivores spill from their preferred plant on to neighboring less preferred plants (White and Whitham 2000; Barbosa et al. 2009).

Associational susceptibility could be less common in urban than natural habitats since plant and herbivore diversity are often low (Raupp et al. 2001; McKinney 2002; Walker et al. 2009). This reduces the probability that plants will share the same herbivores since most landscape pests and other herbivores eat relatively few plant taxa (Raupp and Noland 1984; Bernays and Chapman 1994). In addition, urban habitats have a high proportion of exotic plants that are not hosts for native herbivores (Keane and Crawley 2002; Tallamy 2004). This too could reduce the likelihood of herbivores spilling from one plant species to another. Alternatively, some urban plants could experience associational susceptibility more frequently because herbivore abundance tends to be high in urban habitats (Raupp et al. 2010; Meineke et al. 2013) and associational susceptibility is most common when herbivores reach high densities (White and Whitham 2000; Barbosa et al. 2009). Urban plants could also experience associational susceptibility since plant density and diversity are lower in urban than natural habitats (McKinney 2002; Walker et al. 2009). Thus, herbivores leaving their preferred host may be concentrated on fewer palatable plants.

Spring cankerworms (*Paleacrita vernata* Peck) and fall cankerworms (*Alsophila pometaria* Harr., Lepidoptera: Geometridae) are generalist, native lepidopterans that feed on many deciduous tree species in urban and natural forests (Riley et al. 1883; Baker 1972). Associational susceptibility has been documented when fall cankerworms (Futuyma and Wasserman 1980; White and Whitham 2000) and other forest caterpillars (Cuming 1961; Vehviläinen et al. 2007) feed on less preferred or non-host plants growing in close proximity to their primary hosts. For example, cottonwoods (*Populus* spp.) growing beneath the cankerworm host, box elder (*Acer negundo*), experienced greater herbivory during a fall cankerworm outbreak than cottonwoods that were not growing near box elder (White and Whitham 2000).

In this study, I examined the effect of vegetational diversity on the strength of associational susceptibility experienced by native and exotic plants growing beneath the canopy of cankerworm hosts. The objectives of this study were to determine if 1) understory dogwood trees experienced associational susceptibility to cankerworm herbivory in an urban landscape; 2) associational susceptibility is greater in simple than complex habitats; 3) associational susceptibility is greater for native than exotic plant species. I predicted that, during cankerworm outbreaks, herbivory would be greater on plants growing beneath cankerworm hosts than the same plants growing below non-host trees and that associational susceptibility would increase as cankerworm density and herbivory in the host tree increased. In addition, I predicted that low vegetational diversity would increase the severity of associational susceptibility on native but not exotic plants compared to natural habitats. This research will increase understanding of how plant associations affect herbivory in urban landscapes and contribute to urban plant management.

Methods

Study system Fall and spring cankerworms are univoltine. They lay eggs in tree branches between late fall (fall cankerworms) and early spring (spring cankerworms). Larvae hatch in synchrony with bud break of their host tree and feed on young leaves for 4–6 weeks before dropping to the ground to pupate (Baker 1972). In spring 2012 and 2013, many North Carolina cities including Raleigh and Charlotte had higher cankerworm abundance and defoliation than

had occurred in at least 4 years (S.D. Frank personal observation). Cankerworm larvae can feed on many deciduous plant species though at my research sites oak trees hosted more cankerworms than other tree species (S.D. Frank personal observation). Oak trees were also the most common over story trees at my research sites.

Shrewsbury and Raupp (2000) defined habitat complexity by the number of habitat strata (ground cover/turf, herbaceous vegetation, shrubs, understory trees, over story trees) that contained vegetation. In this research, simple habitats had plants in just two habitat strata: understory trees or shrubs, which were the study plants and over story trees, which were the cankerworm hosts. Complex habitats were natural forests that contained plants in all layers.

Associational susceptibility in an urban landscape This research was conducted in Raleigh, North Carolina on North Carolina State University campus. On campus, cankerworm larvae fed primarily on willow oaks (*Quercus phellos*) some of which were over 50 % defoliated (Chanthammavong et al. 2014). To assess the associational susceptibility experienced by urban landscape plants I recorded cankerworm herbivory on flowering dogwood trees (*Cornus florida*) in three settings following the design of White and Whitham (2000). I measured cankerworm herbivory on *C. florida* below the canopy of willow oak trees (cankerworm host), below the canopy of non-host trees (*Pinus* spp., *Lagerstroemia* spp., *Palonia* spp. and *Fagus* spp.) and on *C. florida* growing in the open to control for tree canopy effects. I selected *C. florida* because they were common enough on campus that to find replicated trees in each setting separated by at least 100 m. In addition, *C. florida* are not a preferred host for cankerworms and have been reported as a non-host (Schneider 1980). I searched each study tree for 2 min and did not find any cankerworm egg cases indicating that adult cankerworms did not oviposit on *C. florida*.

On 6 April 2012, I recorded the percent leaf area missing from ten randomly selected leaves per tree. I also recorded percent area missing from ten randomly selected clusters of white bracts (four bracts per cluster). Percent leaf or bract area missing was estimated visually and recorded to the nearest 10 %. I recorded 1 % if herbivory was present but was closer to 0 % than 10 %. I collected data when cankerworm feeding was almost finished and very few caterpillars were present. Therefore, the herbivory estimates represent the accumulation of herbivory over the entire larval feeding period.

Percent missing leaf area on leaves and bracts on *C. florida* in each treatment were divided by 100 to get proportion leaf area missing. Proportions were (arcsin√x) transformed and compared with one-way ANOVA followed by Fisher's Protected LSD means comparisons. The number of berries per flower (total berries per tree/10) was analyzed with one-way ANOVA followed by Fisher's Protected LSD means comparisons in the MIXED Procedure of SAS v. 9.3 (SAS 2012).

In spring 2013, I tested the hypothesis that associational susceptibility will increase as cankerworm abundance and herbivory of the host tree increases. On 12 April, approximately 1 week after cankerworm feeding began, I placed potted *C. florida* trees (1 m tall in 11.4 l pots) beneath the canopies of 13 willow oak trees. Potted trees were watered daily. I sampled larval abundance in the oak trees by placing a 30×60 cm black tray filled with 3–5 cm of soapy water on the ground below each tree to capture larvae as the dropped from the canopy. I deployed the trays nine times between 18 and 30 April 2013 and counted the larvae after 12–24 h each time. All counts were converted to larvae per 12 h for analyses. On May 7, 2013, two observers examined each oak tree from two points of view, 180° apart, to estimate the percent of leaf area missing from the canopies. I used the mean of the four observations (two observations from two observers) as the data for analysis. On 3 May, I visually estimated the percent area missing on 20 randomly selected leaves (about half of all the leaves) on each potted *C. florida*. I tested the correlation between mean percent leaf area missing (arcsin√x transformed) on the

C. florida and cankerworm abundance (log(x+1) transformed) and the correlation between percent leaf area missing (arcsin√x transformed) on the *C. florida* and percent oak defoliation of oak tree canopies in the CORR Procedure of SAS v. 9.3 (SAS 2012).

On 17 April 2013 I conducted laboratory experiments to test cankerworm preference for willow oak and *C. florida* leaves. I collected leaves from five plants of each species. I mixed the leaves from the five trees in a bag and randomly drew one leaf of each species for each experimental replicate. I trimmed the leaves with scissors to fit in a 10 cm petri dish and to be similar dimensions. I placed one leaf of each species in 10 cm petri dishes lined with moist filter paper. I placed a fall cankerworm (approximately 2 cm) in each dish and recorded percent leaf area of each leaf consumed after 17 h.

Effect of vegetational diversity on associational susceptibility of native and exotic plants I assessed the effects of vegetational diversity on susceptibility of native and exotic understory plants at the Bartlett Tree Research Laboratories and Experimental Grounds and Arboretum in Charlotte, NC. This facility has plant beds surrounded by turf that contain shrubs and understory trees below large deciduous over-story trees. I found seven beds that contained an infested cankerworm host tree with several species of understory trees and shrubs growing beneath. All the beds contained shredded hardwood mulch but no ground cover plants and no plants other than the understory layer and canopy layer. None of the understory plants within a bed were touching and all were completely within the canopy drip line. With these beds, I was able to test the effects of low vegetational diversity, similar to the urban sites with only a canopy layer and an understory layer, but without other urban features such as buildings and impervious surfaces. In each bed, I estimated the percent leaf area missing from ten random leaves on native and exotic congeners (Table 1).

Another part of this facility is a forest with native and exotic *Rhododendron* spp. and native *C. florida* planted in the understory. The forest contained many plants and plant species in the ground cover, shrub, understory tree, and canopy tree layers. The ground was covered with leaf litter. This area allowed me to evaluate associational susceptibility in a vegetationally complex habitat on *C. florida* and the same *Rhododendron* species that I measured in the simple arboretum habitat. I estimated the percent leaf area missing from ten randomly selected leaves per plant. I only estimated bract herbivory on *C. florida* in both habitats since exotic *Cornus* spp. were not flowering yet.

Table 1 The species of native and exotic congeners from which leaf area missing was recorded in simple habitats under cankerworm hosts

Genus	Native species	Exotic species
Cercis	*canadensis*	*gigantea*
		griffithii
Cornus	*florida*	*mas*
		kousa
		bret
		porlock
		officinalis
Hamamelis	*vernalis*	*intermedia*
Rhododendron	*canescens*	*indicum*
	austrinum	
	atlanticum	
	alabamense	

Native and exotic *Cercis* spp. (Redbud) and *Hamamelis* spp. (witch hazel) were present in some of the simple arboretum sites. I estimated the percent leaf area missing from ten leaves from three native and three exotic *Cercis* plants (Table 1) and three native and three exotic *Hamamelis* plants (Table 1).

Estimates of proportion missing leaf area (percent/100) were (arcsin√x) transformed to normalize their distribution. I analyzed data from *Rhododendron* spp. using 2-way ANOVA with two levels of vegetational diversity (low and high) and two plant origin treatments (native and exotic). Exotic *Cornus* spp. only occurred in simple arboretum habitat simple but *C. florida* occurred in both habitats. Therefore, I analyzed these data using a one-way ANOVA with three treatments: *C. florida* in complex habitats, *C. florida* in simple habitats, and exotic *Cornus* spp. in simple habitats. I tested the hypothesis that native *C. florida* in simple habitats would experience more herbivory (associational suscepti-bility) than exotic *Cornus* spp. in simple habitats or *C. florida* in complex habitats. I compared the proportion leaf area missing from native and exotic *Cercis* spp. and native and exotic *Hammamelis* spp. using Kruskal–Wallace tests in the NPAR1WAY procedure of SAS v. 9.3 (SAS 2012) since data did not meet the assumptions of ANOVA after transformations.

On 17 April 2013 I conducted laboratory experiments to further compare herbivory of native and exotic congeners. I collected leaves from native and exotic species of *Acer*, *Cercis*, and *Rhododendron* from the J.C. Raulston Arboretum in Raleigh, NC (Table 2). Within 1 h of collection, I placed a pair of similar sized leaves, one native and one exotic, in 10 cm petri dishes lined with moist filter paper. I placed a fall cankerworm (approximately 2 cm) in each dish and recorded percent leaf area of each leaf consumed after 17 h. Ten petri dishes (replicates) were set up in this manner for each genus. I compared the proportion leaf area missing from native and exotic species using Kruskal–Wallace tests in the NPAR1WAY procedure of SAS v. 9.3 (SAS 2012).

Results

Associational susceptibility in an urban landscape Cornus florida growing beneath canker-worm infested willow oaks experience significantly more herbivory on leaves ($F_{2, 16}=26.07$;

Table 2 The species offered, proportion of leaf area missing, and statistical results of 17 h petri dish choice experiments comparing cankerworm preference for native or exotic congeners

Genus	Native species	Exotic species	Test statistic; P
Acer	*rubrum*	*palmatum*	
Mean ± SEM	0.72±0.07	0.08±0.02	$\chi^2=14.97$; $P<0.0001$
Cercis	*canadensis*	*chinensis*	
		griffithii	
Mean ± SEM	0.00±0.00	0.00±0.00	No test
Cornus	*florida*	*kousa*	
Mean ± SEM	0.37±0.08	0.16±0.05	$\chi^2=3.69$; $P=0.0545$
Rhododendron	*canescens*	*indicum*	
	alabamense		
Mean ± SEM	0.59±0.10	0.00±0.00	$\chi^2=13.89$; $P=0.0002$

$P<0.0001$; Fig. 1) and bracts ($F_{2, 10}=14.13$; $P=0.001$; Fig. 1) than trees beneath non-host trees and trees in the open. This result confirms that associational susceptibility occurs in simple, urban habitats when cankerworms are abundant.

Percent leaf area consumed on potted *C. florida* was positively correlated with the number of cankerworms captured in trays ($r=0.749$; $n=13$; $P=0.003$; Fig. 2) and with defoliation of over-story oak trees ($r=0.538$; $n=13$; $P=0.058$; Fig. 2).

In the petri dish experiment, cankerworms showed a preference for willow oaks by consuming a greater proportion of willow oak (0.97 ± 0.03) leaves than *C. florida* leaves (0.35 ± 0.1).

Effect of vegetational diversity on associational susceptibility of native and exotic plants Native *Rhododendron* species experienced three times more herbivory than exotic species ($F_{1, 12}=8.65$; $P=0.0123$; Fig. 3). Both native and exotic species experienced more herbivory in simple habitats than in complex habitats ($F_{1, 12}=17.10$; $P<0.0014$; Fig. 3). There was no interactive effect of plant origin and vegetational diversity on herbivory ($F_{1, 12}=0.01$; $P=0.9612$; Fig. 3).

Plant origin and vegetational diversity both affected leaf herbivory on dogwoods. Native dogwoods (*C. florida*) in simple habitats experienced four times more leaf herbivory than native dogwoods in complex habitats or exotic dogwoods in simple habitats ($F_{2, 13}=4.08$;

Fig. 1 Mean (±SEM) proportion of **a** leaf area and **b** bract area missing from native dogwoods, *C. florida*, growing below canker-worm host trees, non-host trees, or no tree. *Bars with different letters are significantly different at* $P<0.05$ level
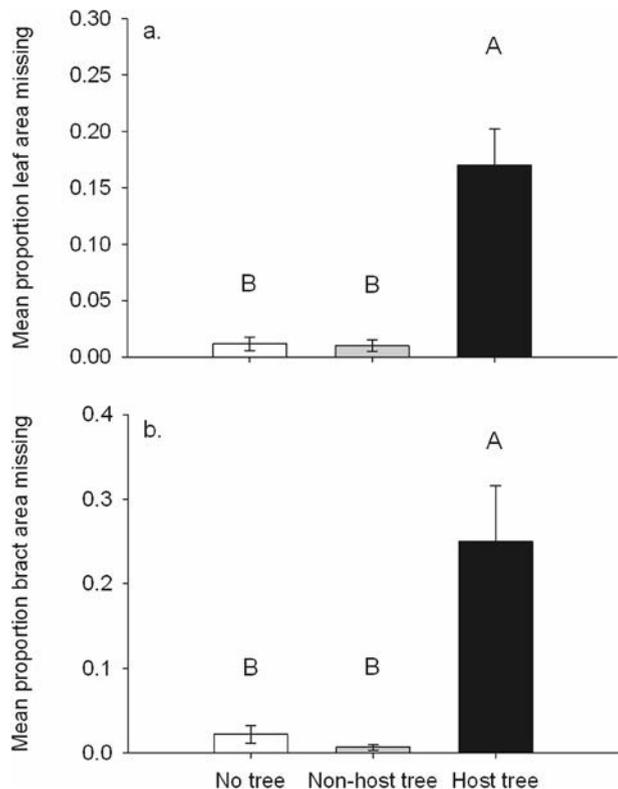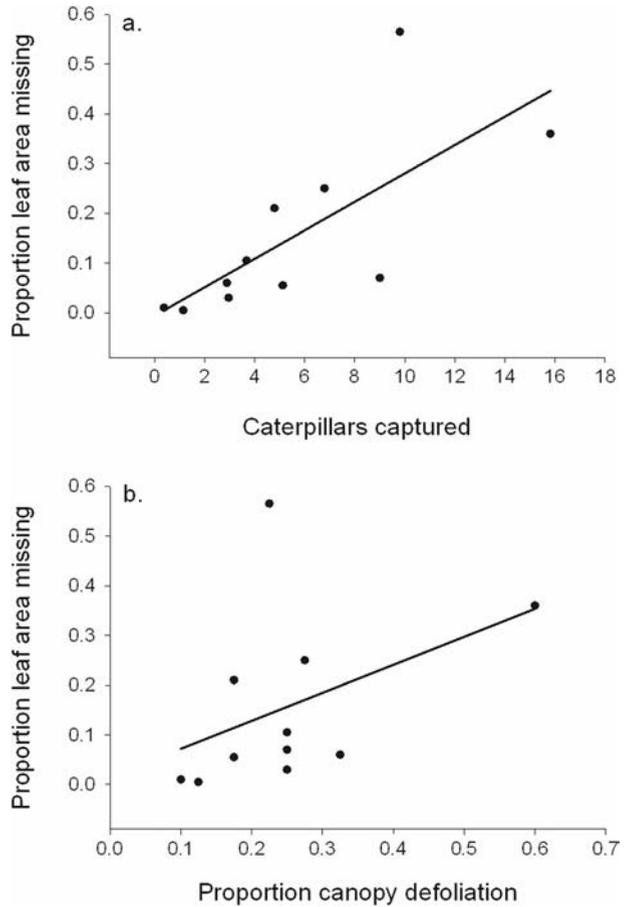
Fig. 2 Correlation between percent leaf area consumed on potted dogwood trees positioned below cankerworm-infested willow oaks and **a** the number of cankerworms that fell from the willow oak into collecting trays and **b** percent herbivory of the willow oak canopy

$P=0.0421$; Fig. 4). Bract herbivory was nearly eight times greater on native dogwoods in simple than complex habitats ($T_7=3.16$; $P=0.016$; Fig. 4).

Herbivory (mean ± SEM) was over 12 times greater on native *Cercis canadensis* (0.063 ± 0.028) than on exotic *Cercis* species (0.01 ± 0.01; $\chi^2=3.97$; df=1; $P=0.0463$) but

Fig. 3 Mean (±SEM) proportion leaf area missing from native and exotic *Rhododendron* spp. in simple and complex habitats. ANOVA found significant ($P<0.05$) main effects of habitat type and plant status as native or exotic
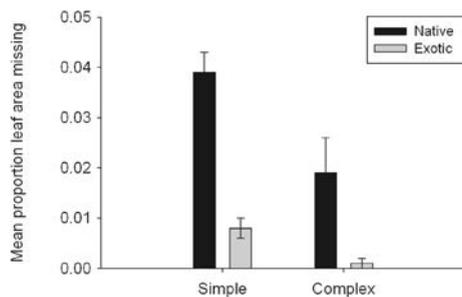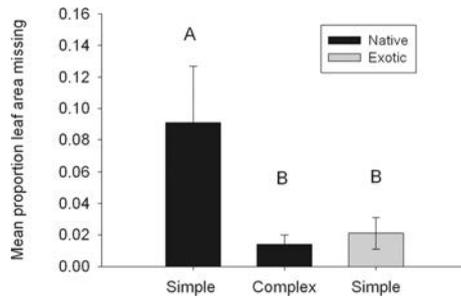
Fig. 4 Leaf area missing from native dogwood in simple and complex habitats and exotic dogwoods in simple habitats

did not differ between native (0.12±0.05) and exotic *Hammamelis* species (0.06±0.01; $\chi^2=0.51$; df=1; $P=0.467$).

After 17 h cankerworms consumed greater proportion leaf area of native than exotic *Acer* spp. and *Rhododendron* spp. when offered together in petri dishes but greater proportion of exotic *Cornus* spp. (Table 2). Cankerworms did not eat any native or exotic *Cercis* spp. leaves.

Discussion

Herbivore abundance and damage are often greater on urban plants than plants in natural habitats (Raupp et al. 2010). Increasing vegetational diversity, in terms of plant species diversity or structural complexity, can reduce herbivory—associational resistance—on urban plants (Hanks and Denno 1993; Tooker and Hanks 2000; Shrewsbury and Raupp 2000; Raupp et al. 2010). During cankerworm outbreaks, I found that urban landscape plants experience more herbivory—associational susceptibility—when growing below cankerworm host trees. Thus, contrary to other research on urban plant pests, plants in more vegetationally diverse habitats, with two plant species and two vegetation strata, could experience more herbivory than plants in less diverse habitats with one plant species and one vegetation strata. However, when vegetational diversity was even higher in a forest habitat cankerworm herbivory of my focal plants was minimal despite the abundance of over-story cankerworm hosts. This difference suggests associational resistance and associational susceptibility occur on a continuum affected by the specifics of vegetational complexity and herbivore characteristics.

Herbivore diet breadth and preference affect whether plants experience associational resistance or associational susceptibility in vegetationally diverse habitats (Barbosa et al. 2009). Theory predicts that associational susceptibility is more likely to occur in diverse plant communities when polyphagus herbivores, like cankerworms, are present than when specialist herbivores are present (Andow 1991; Barbosa et al. 2009). In my study, as theory predicts, cankerworms that left their host tree fed on *Cornus* spp., *Rhododendron* spp., *Cercis* spp., and *Hamellis* spp. growing below. In contrast, Shrewsbury and Raupp (2000) found that azalea plants in vegetationally diverse urban yards experienced associational resistance to azalea lacebugs compared to azaleas in simple yards. In this case, and others (e.g. Tooker and Hanks 2000), the focal herbivore was oligophagus so other plants in the landscape were not susceptible to feeding.

The preference of polyphagus herbivores also affects whether plants experience associational susceptibility. Less preferred plants are more likely to experience associational susceptibility when they grow near a plant preferred by the herbivore. White and Whitham (2000) found that cottonwood trees experienced associational susceptibility when growing beneath

cankerworms' preferred host, box elder, than when growing beneath other cottonwoods where cankerworm density was low. Similarly, dogwoods growing beneath less preferred trees in my study had herbivory comparable to trees growing in the open. Dogwood trees in my experiment and cottonwood trees in experiments by White and Whitham (2000) were less preferred but still acceptable hosts to cankerworms. In my laboratory feeding experiment, exotic plants were less preferred by cankerworms than native congeners and in some cases were not eaten at all. This corroborates my field observations that some exotic plants experienced less herbivory than natives.

My arboretum and campus study sites typified urban plant beds that contain one or a few shrubs, an over-story tree, and mulch ground cover. Forest sites had a continuous canopy of cankerworm host trees the majority of which were oak (*Quercus* spp.) but also hickory (*Carya* spp.), maple (*Acer* spp.), and beech (*Fagus* spp.). The difference in herbivory between urban and forest sites suggests that there can be a general benefit of increasing vegetational diversity despite herbivore diet breadth and preference. Several aspects of the complex forest habitat could have reduced the associational susceptibility of the understory plants. First, although cankerworm hosts were abundant in the forest site cankerworm density could have been less. Cankerworms and other caterpillars disperse from host trees when density is high or food becomes scarce and they are willing to accept less preferred hosts (White and Whitham 2000). Thus, cankerworm herbivory of dogwoods was correlated with cankerworm abundance in trays and with herbivory of the willow oak host trees. With more available food in the forest canopy cankerworms may have never reached a density at which dispersal was great.

Greater amount and complexity of understory vegetation in the forest habitat could have reduced the apparency of my study plants and the likelihood that cankerworms would encounter them (Root 1973; Feeny 1976). When cankerworms dropped from the canopy in urban habitats they had one or a few plants to land on or crawl to if they landed on the ground. Thus, herbivory would be concentrated on these isolated plants. In the forest, cankerworms could have landed and climbed many different host and non-host plants. Cankerworms that landed on the ground would have to negotiate leaf litter and other debris before finding a plant to climb.

Finally, vegetational complexity can reduce herbivory by increasing biological control by natural enemies (Root 1973). Several parasitoid species attack cankerworm eggs and larvae (Riley et al. 1883; Fedde et al. 1973). Larvae are also susceptible to many generalist arthropod predators, such as spiders, ground beetles, and wasps, on the ground and in tree canopies that could be more abundant in forest than urban habitats (Riley et al. 1883). Birds consume caterpillars, particularly in spring when rearing chicks (Riley et al. 1883) and forests tend to have more arthropod-feeding bird species than cities which tend to have more granivorous species (Chase and Walsh 2006).

Urban landscapes contain assemblages of plants selected by people. The extent to which ecological theory developed in other ecosystems applies to urban ecosystems is unclear (McDonnell and Pickett 1990; Grimm et al. 2008). I found that two common components of urban landscapes, low vegetational diversity and exotic plants, can affect damage by a generalist herbivore. In support of established theories herbivory was less on plants in vegetationally diverse habitats (Root 1973) and on exotic plants to which the native herbivores may not be adapted (Keane and Crawley 2002; Tallamy 2004). Cankerworm outbreaks are common in many urban areas where they damage host trees, become a nuisance to pedestrians and, I show, damage other landscape plants. Some municipalities have programs to reduce cankerworm abundance (Eirich 2008), which should have dual benefit since damage to trees, and landscape plants increases with cankerworm density (Chanthammavong et al. 2014). These programs combined with diversifying urban landscape plantings could help reduce damage by cankerworms and other plant pests.

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