Ecology of Herbivorous Arthropods in Urban Landscapes

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Abstract

Urbanization affects communities of herbivorous arthropods and provides opportunities for dramatic changes in their abundance and richness. Underlying these changes are creation of impervious surfaces; variation in the density, diversity, and complexity of vegetation; and maintenance practices including pulsed inputs of fertilizers, water, and pesticides. A rich body of knowledge provides theoretical underpinnings for predicting and understanding impacts of urbanization on arthropods. However, relatively few studies have elucidated mechanisms that explain patterns of insect and mite abundance and diversity across urbanization gradients. Published accounts suggest that responses to urbanization are often taxon specific, highly variable, and linked to properties of urbanization that weaken top-down and/or bottom-up processes, thereby destabilizing populations of herbivores and their natural enemies. In addition to revealing patterns in diversity and abundance of herbivores across urbanization gradients, a primary objective of this review is to examine mechanisms underlying these patterns and to identify potential hypotheses for future testing.

INTRODUCTION

Urbanization brings about dramatic changes in land use as croplands, old fields, forests, and natural areas give way to cities and suburbs and their buildings, roads, airports, waterways, gardens, and parks (32, 97). Biotic elements shift from communities of plants and animals at various stages of succession to communities associated with ornamental plants and remnants of natural habitats (32, 97). Urbanization creates a unique ecological gradient along which patterns of richness, abundance, and ecosystem processes can be studied in a context of human culture, economics, and politics (27, 37, 97, 98, 123).

Dramatically elevated densities have been documented frequently in urban forests by herbivorous arthropods that rarely, if ever, reach high densities in natural forests (27, 37, 50, 141, 149, 151). For example, the abundance of tetranychid mites generally increased, often dramatically, with increasing levels of urbanization (6, 30, 78, 132, 140). Economically important infestations of scale insects have been documented more frequently in urbanized areas than in natural areas (28, 50, 141, 149, 151). By contrast, urbanization can also lead to decreased abundance and diversity of phytophagous arthropods. For example, destruction and deterioration of habitats associated with urbanization led to the disappearance of almost half of the indigenous species of butterflies in the San Francisco Bay Area, and local extinctions are common as buildings and roads replaced forests and grasslands (46, 112).

In some cases, but not all, elevated densities of herbivores were called outbreaks. We consider outbreaks to be dramatic increases in the abundance of arthropods that occur in relatively short periods (9) and are often associated with feeding injury to plants that exceeds economic or aesthetic thresholds. In many cases, herbivores were associated with plants of economic or aesthetic value and hence were considered pests. Herbivore outbreaks in urban environments have been linked to improved host quality resulting from environmental stress

associated with impervious surfaces and elevated temperatures, as well as escape from natural enemies. In most cases, however, the data are insufficient to establish a mechanistic basis for the observed patterns, and the population dynamics of arthropods in urban environments remains poorly understood (27, 32, 37, 97, 98, 123).

Several previous reviews provided conceptual frameworks for understanding the ecology of urban biota in general (97, 127) and insects in particular (27, 32, 37, 98, 130). This review examines how features of urban landscapes generate properties that affect arthropod richness and abundance and predispose plants to attack by herbivorous arthropods. In some studies, the urbanization gradient was clear, ranging from natural areas and parks to residential areas and finally to cities. Other studies measured patterns of herbivore abundance along key features that vary across urban gradients such as plant density, abundance, diversity, vegetational complexity, relative frequency of native and exotic plants, patterns of land use, proportion of impervious surface, and frequency and intensity of common maintenance practices such as pulsed inputs of fertilizers, water, and pesticides. Properties of urban environments that create opportunities for insects and mites to increase include changes in host quality and accessibility (bottom-up factors), natural enemy abundance and diversity (top-down factors), microhabitats including creation of heat islands, and matrixes that disrupt movement and colonization of herbivores and natural enemies (58, 71, 137, 147).

We focus on assemblages of arthropods associated with shade trees and woody ornamental plants rather than arthropods of turfgrass (reviewed in Reference 109), structures, or those deemed as medically important (reviewed in Reference 37). We found that most published accounts of arthropods in urban settings dealt with species associated with woody rather than herbaceous plants. We review empirical studies on the diversity and abundance of herbivores and their natural enemies along urban gradients and explore how features and properties

Urbanization gradient: an environmental gradient with less developed natural or agricultural areas at one extreme and highly developed areas dominated by anthropogenic structures and inputs at the other extreme

Bottom-up: when host plants regulate the structure and population dynamics of herbivores and other organisms at higher trophic levels

Top-down: when natural enemies and organisms at higher trophic levels regulate the structure and population dynamics of organisms at lower levels

Heat islands: elevated air temperatures in middle and high latitudinal cities compared with those in nearby rural areas related to impervious surfaces and other anthropogenic effects

of urbanization affect arthropod abundance and diversity, and ecosystem processes in general, as they relate to herbivore populations.

Many studies speculated about causes of variation in abundance, but most did not examine features of urbanization independently and variables were often confounded. In very few studies were mechanisms underlying patterns convincingly documented. Generally, it is difficult or impossible to separate processes associated with urbanization, such as deterioration in habitat quality, from those associated with habitat loss, fragmentation, and isolation (105, 123). A primary objective of this review is to propose mechanistic explanations as hypotheses for testing. In doing so, we hope to advance the study of arthropod ecology in urban environments.

IMPACT OF URBANIZATION ON ARTHROPOD DIVERSITY AND ABUNDANCE

Vegetational Texture Along the Urbanization Gradient

Vegetational texture has been defined in terms of plant density, diversity, patch size, and structural complexity (25, 69, 136). Other components linked to vegetational texture include evenness, richness, growth form, volatile plant compounds (84), and proportion of native and exotic plants (97, 98, 145). Differences in vegetational texture result in variation in temperature, light exposure, and other microhabitat regimes (4, 69).

Patterns in vegetational texture. Components of vegetational texture vary along urbanization gradients (98, 118, 136). Many areas once forested and subsequently cleared for agriculture followed by urban development are now characterized by habitat fragmentation and degradation (32, 97, 123), which can decrease plant density and host patch size, plant diversity including proportion of native plants, and vegetational complexity (97, 98). Furthermore, urban sites formerly in agricultural production

may have fewer plant genera than sites never farmed, suggesting that legacy effects of agriculture on plant diversity can be long-lasting. Plant diversity was inversely related to the age of housing in urban sites, with newly established urban plantings more diverse than older ones (62). Studies in metropolitan New York City (3) and Washington, DC (39, 61) documented dramatic reductions in tree diversity and density with increasing levels of urbanization. For example, 30 species of trees lined streets in a city in Maryland at a density of approximately 48 trees km^{-2}, whereas nearby residential landscapes supported more than 100 species of woody plants at a density of about 69,000 plants km^{-2} (39, 61).

Urbanization does not always correlate with a reduction in floristic diversity (27, 107, 112). Extensive tree planting and landscaping, such as occurs in urban areas that lacked trees prior to development (e.g., cities built in deserts and prairies) and those with rich horticultural traditions, enjoy increased floristic richness and associated biodiversity (27, 32, 62, 107). A garden in Leicester, United Kingdom, contained more than 143 native and 175 alien species of plants, far more species than occupied nearby natural and agricultural lands (107). Generic diversity of perennial plants in metropolitan Phoenix, Arizona, was substantially greater in urban sites relative to desert, agricultural sites, or transportation corridors (62).

Community structure and herbivore diversity. Variation in vegetational texture can shape communities of herbivorous arthropods through effects on abundance, diversity, and distribution of their host plants and natural enemies (44, 69, 125, 137). Across urbanization gradients, herbivore richness may be directly related to plant density, richness, diversity, and origin. Within suburban residential landscapes there were direct monotonic correlations between the richness of arthropod pests and total plant abundance and plant species richness (117, 118). Plant diversity showed significant positive correlation with pest species richness. The relationship between plant richness and

Vegetational texture: attributes of plant communities that influence the distribution and abundance of arthropods

Deep urban site:
locations such as city streets with a high degree of impervious surface and low plant density, where plants are isolated and inhospitable matrices may reduce survival, movement, and interactions among members of food webs

Suburban adapters:
herbivores that attain greatest abundance at intermediate points across urbanization gradients

pest richness was also positive, but far less than 1:1, reflecting the fact that many arthropod pests such as cankerworms, Japanese beetles, and bagworms are generalized feeders and that many plants receive no important damage.

Increased fragmentation of habitats and reductions in patch size are often linked with urbanization (97) and can have important effects on herbivore communities. Lepidoptera respond to destruction and deterioration of habitats associated with urbanization, and local extinctions are common. In the San Francisco Bay Area, almost half of the indigenous species of butterflies disappeared as buildings and roads replaced forests and grasslands (46, 112). Distribution and abundance of butterflies along an urbanization gradient near Palo Alto, California, revealed peaks in species richness and diversity at intermediate levels of urbanization, while relative abundance generally declined from less developed to more urbanized sites. Many original resident species were absent from office parks and business centers, and no species attained maximum abundance in deep urban sites. Elevated levels of lepidopteran diversity at intermediate levels of development (107, 112) are consistent with hypotheses suggesting that intermediate levels of disturbance or development correlate with peak levels of biotic diversity and richness (10). Unlike externally feeding butterflies, species richness of leafminers associated with remnant patches of *Quercus agrifolia* in the San Francisco Bay Area did not change along an urbanization gradient. Moreover, only 3 of 13 species varied in abundance, with 2 increasing and 1 decreasing as urbanization increased (123). In addition, richness and abundance of these leaf-mining moths were positively correlated with patch size rather than variables associated with urbanization and land use per se (123). Patch size had a significant, but weak, positive effect on the abundance of lace bugs in residential landscapes (136). Nonhost plants in diverse communities may interfere with the ability of herbivores to find and colonize hosts, for example, by obscuring visual cues or producing volatile chemicals that mask host odors (associational resistance) (144). However,

nonhost effects on host finding and movement did not explain patterns of abundance of lace bugs on azaleas in residential landscapes (137).

Host density appears to be less important than richness. In examining relationships of trees and shrubs in residential landscapes, no correlation between the relative commonness of a plant taxon in a landscape and the frequency with which it was attacked by herbivores was found (117, 118). However, regardless of their relative abundance in the landscape, plants in the family Rosaceae were significantly more likely to have arthropod pests than plants in other families. Although the mechanism underlying this association is unknown, perhaps a long history of cultivation for the production of edible fruit or ornamental traits has reduced naturally occurring resistance in rosaceous plants. Genetic domestication of crop plants has been associated with loss of pest resistance due to allocation trade-offs resulting from artificial selection for increased growth and yield (75, 126). It is noteworthy, however, that the great majority of plants, native and alien, receive little or no herbivory during a growing season (114, 117). The complex responses of herbivores to patch size, as well as host density, diversity, and richness, suggest multiple mechanisms are at play.

In some cases, diversity of plants may be greater in urban areas than in adjacent natural areas, thereby enhancing opportunities for colonization by exotic and endemic herbivores (10, 98, 107, 112, 145). For example, in a Mediterranean habitat, residential landscapes, golf courses, and open recreation areas provided unique opportunities for colonization by butterflies called suburban adapters by providing larval host plants such as grasses, forbs, and garden plants and prolonged periods of host availability extended by irrigation (10). As native genera such as *Celtis* and *Gleditsia* gained popularity as shade and ornamental trees, the abundance of many herbivorous arthropods increased with increasing levels of urbanization (112, 152). This also appears to be the case for the nymphalid *Brassolis sophorae* in São Paulo, Brazil, where the use of palm trees in urban

areas provided hosts for caterpillars and man-made structures like garages provided partial refuge from parasitoids (128). In Pennsylvania, the abundance of lepidopteran larvae was four times greater in residential landscapes where plant species richness was greater, and the proportion of native plants exceeded that of alien plants (14).

Alien species and herbivore diversity and abundance. In general, the proportion of alien plants in a landscape increases with increasing levels of urbanization (97, 98, 107), which may negatively affect the diversity and abundance of herbivores in urban settings (14, 145). The Enemy Release Hypothesis has been invoked to explain the successful invasion of natural systems by alien plants, predicting that exotic plants should support fewer herbivores than native plants (70, 145). In addition, some exotic plants used in urban landscapes have been selected specifically for their resistance to key pests (57, 116, 145). This may further reduce richness and abundance of herbivores. One striking example of how an exotic plant threatens native herbivores has been documented in Australia, where the ornamental vine Dutchman's pipe, *Aristolochia elegans*, has been planted and become invasive. The Richmond birdwing butterfly, *Ornithoptera richmondia*, readily oviposits on Dutchman's pipe, but the foliage is lethal to larvae (129).

Countering this trend for reduced herbivore richness and abundance on exotic plants are specialists that switch from indigenous congeners to alien plants, as well as native generalists that incorporate introduced plants into their diet (2, 70, 107, 145). Moreover, specialist herbivores from the endemic range of exotic plants have often been cointroduced with their host into new regions and have become key pests. The azalea lace bug, *Stephanitis pyrioides*, and the euonymus scale, *Unaspis euonymi*, are prominent examples. Invasion of North American cites by the alien tree *Ailanthus altissima* has allowed its coevolved specialist moth, *Samia cynthia*, to persist in deep urban environments (111). When their natural enemies are lacking,

alien herbivores of exotic plants may be more prone to outbreaks, as they exist in enemy-free space (145).

Empirical studies in urban systems provide mixed support for these hypotheses. Herbivory does not always vary across gradients of urbanization, especially when herbivore populations are at low background levels (105). In Phoenix, host plant quality was higher in urban environments than in the surrounding desert, but herbivore populations did not increase because bird predation was also greater (32). In Sydney, Australia, endemic trees received twice the defoliation in small forested remnants compared with large habitat patches in nearby parks. However, herbivory by some feeding guilds did not vary across the gradient (17). The richness and abundance of butterflies in suburban landscapes dominated by species of native plants were three and four times greater, respectively, than the richness and abundance in similar landscapes dominated by alien plants (14). However, other studies documented expansion of host range of endemic herbivores to include alien plants (20, 107, 112). Species richness of phytophagous and predatory mites on trees lining avenues and populating parks was greater than richness on trees in wooded suburbs of Como, Italy, where a diverse combination of resident native trees and exotic trees elevated arthropod diversity at two trophic levels (124). It is not yet clear whether increased diversity of alien plants in urban environments positively or negatively affects herbivore richness or abundance.

Coevolution and defense free space. Although many herbivores are restricted to coevolved hosts (64), there are numerous notable exceptions. During the last two centuries, the number of alien arthropods that have established on woody plants in North America has increased exponentially (85). Consequently, plants and insects in urban environments interact in a complex matrix that includes alien arthropods utilizing endemic hosts and endemic arthropods utilizing alien hosts. Escape from natural enemies is often a key factor

Enemy Release Hypothesis: decreased regulation by herbivores and other enemies that allow exotic plants to increase in distribution and abundance, thereby enhancing invasiveness

Defense free space:
indigenous host plants lacking coevolutionary history with exotic pests may lack effective defenses, thereby releasing pests from bottom-up regulation and contributing to persistence and eruptive population dynamics

facilitating the success of invasive species (85). However, if indigenous host plants are not well defended from alien herbivores owing to lack of a coevolutionary history with the invader, then release from bottom-up regulation may be just as important in the population dynamics of some invasive pests of urban and natural forests as they proliferate in defense free space (40). For example, fecundity and survival of the pine needle scale, which is endemic to North America, was much lower on its coevolved hosts than on Eurasian *Pinus mugo* and *P. sylvestris* (41, 102). Although high pine needle scale densities on exotic pines have been attributed to low diversity and abundance of natural enemies in the urban landscapes, nurseries, and Christmas tree plantations, where they are generally planted (31, 149), further research is needed to elucidate the relative strength of top-down and bottom-up factors.

Experimental evidence also documents increased susceptibility of naïve hosts relative to coevolved congeneric hosts to key herbivores in the cases of hemlock woolly adelgid and eastern North American hemlocks (54), balsam wooly adelgid and North American firs (155), beech bark scale and North American beeches (44), bronze birch borer and Eurasian birches (57, 101), and emerald ash borer and North American ashes (121). The pattern, however, is not universal, as the fecundity of two species of Asian diaspidid scales was higher on their coevolved hemlock hosts than on naïve North American hemlocks (95).

Urbanization and Top-Down Effects on Herbivore Populations

Several studies have documented or inferred that urban habitats with greater vegetational diversity or complexity supported greater abundance (35, 50, 135) or richness (149) of natural enemies, especially predators with broad dietary breadth. For example, spider abundance, particularly lycosids and linyphiids, increased in productive habitats such as agricultural fields and mesic gardens compared

with desert parks, urban desert remnants, and industrial sites (134). However, their dominance decreased overall spider diversity (134).

Increased vegetational diversity and structural complexity may provide more favorable microhabitats and refuge from predators, as well as alternative food sources, such as pollen and nectar, and diverse alternative prey for generalist predators (80, 81, 137). Diverse and complex habitats stabilized availability of food for generalist predators in urban environments (50, 35, 135, 137, 149) and provided a refuge for parasitoids (38). Greater abundance of resident predators provided a mechanism for dampening herbivore outbreaks in diverse and complex habitats (81, 137). Alternatively, general reductions in vegetational diversity and complexity, and the shrinking proportion of native plants associated with urbanization, may contribute to important reductions in the abundance and richness of natural enemies and services they provide. *Tilia* spp. lining broad city streets in Berlin housed dramatically, often 10-fold-greater numbers of *Eotetranychus tiliarium* and other spider mites than *Tilia* residing on narrower side streets amid gardens or in parks or natural areas where vegetational complexity was greater (6, 132). Elevated spider mite abundance was attributed to the relative rarity of predators in trees along hot, wide boulevards (6, 132). Abundance of the native holly leafminer, *Phytomyza ilicicola*, was 10 times greater in urban landscapes than in forests (67), possibly because of lower rates of parasitism and predation in urban sites (68).

Planting trees at urban sites may remove herbivores from the ambit of their natural enemies, thereby uncoupling predator-prey and host-parasitoid interactions. Spindle galls produced by the midge *Pinyonia edulicola* were rare in natural settings, but extremely abundant in some urban sites. Gall midges were thought to colonize urban sites in advance of their natural enemies, which likely created temporal windows of relaxed top-down regulation enabling gall midge populations to increase

temporarily in urban settings (36). A cynipid gall wasp, *Disholcaspis cinerosa*, attained much higher densities in urban sites than in natural areas. Newly transplanted trees were the most heavily attacked, with increased host quality and temporal escape from parasitoids implicated as contributing factors (38). In tests of mechanisms underlying these patterns, Shrewsbury & Raupp (137) found that vegetationally complex residential landscapes had greater abundance and retention of generalist predators, notably the hunting spider *Anyphaena celer*, than did landscapes with reduced complexity. Greater abundance of predators was attributed to more abundant alternative prey and resulted in enhanced top-down pressure and lowered abundance of a key pest, the azalea lace bug, *S. pyrioides*. Elevated populations of lace bugs were observed only in landscapes with low levels of complexity despite the fact that host quality was lower, which suggests release from top-down regulation in simple communities. Rates of immigration and emigration were not affected by level of complexity (137). Similarly, densities of the armored scale, *Pseudaulacaspis pentagona*, on mulberry were three orders of magnitude greater in mesic open landscapes than in dry landscapes or forests (50). Reduced survival of immatures due to moisture stress in dry urban sites and abundant natural enemies in forested sites enabled *P. pentagona* to persist at high densities only in mesic sites depauperate in natural enemies.

A comparison of epigeal arthropods across four common urban land use types, residential, industrial, agricultural, and desert remnant, revealed great variation in trophic dynamics. Predators, herbivores, and detritivores were most abundant in agricultural sites, while omnivores were equally abundant in all land use types (99). In urban habitat fragments that varied in age and size, spiders and carabids were more abundant in smaller and older fragments than in larger and younger fragments (12). In general, predators appear to be more influenced by local effects of habitat diversity and complexity than by broadscale effects of urbanization.

Impervious Surfaces, Solar Radiation, Heat Islands, and Ecosystem Processes

Domination of surface area by man-made structures is a hallmark of urbanization. Impervious surfaces, also known as hardscapes, include buildings and infrastructure associated with transit, parking areas, and sidewalks. The proportion of impervious surfaces, which vary dramatically across urban gradients, fragments habitats, affects plant density, alters thermal regimes and plant-water relations, and inhibits movement of herbivores and their natural enemies (5, 97, 98, 123, 106, 139, 140).

Impervious surfaces largely displace vegetation including trees, shrubs, and ground covers (103, 143), all of which reduce the amount of solar radiation reaching the ground and buildings, where it is absorbed and reradiated as heat (106). Trees can reduce incoming solar radiation by 90% and vegetation further cools urban areas through evapotranspiration (103, 106, 143). Furthermore, rapid runoff from impervious surfaces reduces water available for transpiration (143). Collectively, these factors can result in heat islands and cities can be 10°C warmer than surrounding suburban and natural areas (5, 71, 106).

The amount of impervious surface beneath the canopy of its host was the best predictor of abundance of the horse chestnut scale, *Pulvinaria regalis*. Distance to the nearest building also correlated with increased scale abundance on vigorous trees. Natural enemies were unimportant in establishing these patterns, but bottom-up effects related to plant stress were implicated (139). The abundance of *Platytetranychus multidigituli* on honeylocust was directly related to the amount of hardscape immediately surrounding its host and linked to increasing levels of plant stress (140). Abundance of the mimosa webworm, *Homaduala anisocentra*, varied at different spatial scales along three gradients of hardscape, host density, and tree diversity with little pattern except in the immediate vicinity of the host tree, where webworm abundance was positively associated with the amount of hardscape (140). Buildings near host trees provided a thermal

refuge for overwintering webworm pupae (53). However, abundance of honeylocust plant bug, *Diaphnocoris chlorionis*, was not affected by the amount of hardscape, suggesting other factors related to vegetational texture affected plant bug abundance (140).

It is not surprising that elevated temperatures have been implicated as favoring increased populations of multivoltine arthropods in urban habitats. Abundance of the mite *E. tiliarium* on lindens on the sunny side of a street was four times greater and lifetime fecundity three times higher than on the shaded side of the street, where temperatures were cooler (132). Elevated temperatures also dramatically increased the net reproductive rate of *E. tiliarium* on lindens in Warsaw, Poland (78). In addition to increasing developmental rates, buildings may provide thermal refuges for overwintering stages of insects (53).

Higher temperatures in urbanized habitats may also indirectly reduce herbivore mortality by natural enemies. The Slow Growth— High Mortality Hypothesis proposes that host-quality traits that influence the development rate of insects in turn may influence the duration herbivores are vulnerable or exposed to natural enemies (7). Many insects have specific windows of vulnerability that leave them susceptible to attack. For example, susceptibility of five instars of *Agrotis ipsilon* to 12 predators (carabids, staphylinids, spiders) of varying sizes was examined (34). In general, smaller predators were unable to eat larger instars, but larger predators consumed larvae of most stages, demonstrating that once prey obtained a certain size they were no longer accessible to specific predators (34). Early instars of *S. pyrioides* were more susceptible to predation by larvae of *Chrysoperla carnea* than were older, more active nymphs and adults, which have behavioral defenses (83). Moreover, lace bugs attained their less vulnerable adult stage three days faster in sunny habitats than in shady ones. In simple urban habitats where herbivores may be exposed to elevated temperature, the combination of faster development and decreased predation should favor greater abundance of herbivores.

Bottom-Up Effects, Urban Stress, and Anthropogenic Inputs

Stress has been defined as an external constraint that limits resource acquisition, growth, and/or reproduction of plants (45). Relative to natural forests, trees in urban sites experience more frequent and intense stress, including water deficits, compacted soil deficient in nutrients and organic matter, air pollution, de-icing chemicals, and increased incidence of mechanical injury (8, 131, 154). Consequently, attempts to establish, grow, and protect landscape plants from pests in urban landscapes commonly lead to the addition of pulsed management inputs including water, fertilizer, and pesticides (58, 116), all of which can affect herbivorous arthropods through complex bottom-up effects on nutritional quality and chemical defenses of their host plants (63, 73, 82). When anthropogenic inputs are combined with management practices such as pruning, host plant quality may improve to the benefit of herbivores. For example, *Aphis nerii* attained densities that were two times greater in urban compared to rural landscapes, as cultural practices such as irrigation and pruning promoted the production of vigorous, succulent growth of *Nerium oleander* (49).

Nutrient availability and host quality. Ornamental landscapes are commonly fertilized (13), based in part on the rationale that it enhances host plant resistance (15, 138). However, numerous studies show that fertilization generally decreases the resistance of woody plants to sucking arthropods including aphids, adelgids, scales, psyllids, plant bugs, and spider mites; folivores including caterpillars, sawflies, and leaf beetles; as well as subcortical feeding shoot and stem borers (56, 79). Elevated levels of fertilization have been implicated in outbreaks of spider mites in urban sites such as shopping malls (30). Thus, fertilization has the potential to increase herbivore populations, especially those species such as mites, scales, and adelgids that complete multiple generations on the same plant (56).

Positive effects of fertilization on host quality have been attributed to the effects of nitrogen on enhanced nutritional quality and decreased secondary metabolite concentrations (56, 79). Nitrogen is the nutrient most often limiting to trees in urban soils (52), and phosphorus fertilization has little effect on secondary metabolism of woody plants (74). The growth and reproduction of phytophagous insects generally increase with the nitrogen concentration of their host (92), which is a nearly universal response of woody plants to nitrogen fertilization (74). The Growth-Differentiation Balance Hypothesis (GDBH) attributes fertilizer effects on chemical defense to a physiological trade-off that results in decreased secondary metabolite concentrations as plant growth rate increases (56, 59). Recent tests of GDBH have reinforced the generalization that increased nutrient availability decreases secondary metabolism and insect resistance of woody plants (42, 43, 48, 88).

High secondary metabolite concentrations are maintained in nutrient-deficient plants because photosynthesis per unit leaf area is less sensitive to moderate nutrient limitation than growth is (91), which can increase the availability of carbon to support secondary metabolism when growth is limited (43). In contrast, when nutrient limitation is severe enough to decrease photosynthesis, GDBH predicts that secondary metabolism will also be decreased as all plant functions are carbon-limited, thus resulting in a nonlinear, parabolic pattern of secondary metabolism across a nutrient gradient (59).

Degraded urban soils are often characterized by extreme nutrient limitation (131). Hence, it could be hypothesized that fertilization increases pest resistance in such sites. However, because of physiological buffering mechanisms that include increased root/shoot ratios and nutrient use efficiency (1), even severe nitrogen deficiency rarely induces chlorosis in established trees (52). Rather, chlorosis is induced and photosynthesis decreased in response to nitrogen deficiency only when a plant cannot adjust to sudden changes in its internal nutrient balance. This can occur,

for example, when trees are transplanted from high- to low-nutrient sites to which they will eventually acclimate (52). For example, in two species of willow, secondary metabolism was only decreased temporarily in response to extreme nutrient limitation and increased over time as plants acclimated to nutrient stress (43). In conclusion, theory and empirical studies suggest few situations in which fertilization will increase tree resistance to insects.

Drought stress and host quality. Drought stress may impose bottom-up effects on arthropod populations in urban environments. For instance, a large body of mostly anecdotal evidence has led to the proposition that drought stress can trigger insect outbreaks by enhancing host quality (93). The Stress Hypothesis proposes that water deficits increase the nutritional quality and/or weaken the natural defenses of plants, thereby increasing herbivore fecundity and survival (122, 153). Indeed, stress has been proposed as a key cause of insect outbreaks in urban forests (27, 98). However, reviews of empirical studies challenge this generality, concluding that effects of stress on host quality are highly variable (57, 63, 73, 82).

Only a few studies have actually examined the relationship between urban stress and insect infestation and results vary. Oaks growing in a downtown site experienced more severe stress and associated lace bugs and aphids were generally more numerous than on trees growing on a nearby campus (22). In another study, density of *P. regalis* was highest where water and nutrient infiltration were inhibited by impermeable surfaces, and the authors concluded that stress enhanced host quality (139). The armored scales *Fiorinia externa* and *Nuculaspis tsugae*, which infest two species of hemlocks in Japan, were 50–100% more abundant in cultivated plots than in natural areas. Elevated densities were unrelated to parasitoid activity but attributable to greater survivorship of nymphs and higher fecundity of females on trees at managed sites. Greater fitness of scales on hemlocks under cultivation was hypothesized to result from improved host quality related to elevated levels of stress in

Growth-Differentiation Balance Hypothesis: a physiological trade-off between plant growth and secondary metabolism interacts with effects of resource availability on net photosynthesis and growth rate to predict that gradients of nutrient and water availability will have a parabolic effect on secondary metabolite concentration

cultivated trees compared with those growing in natural areas (96). A similar study of a wax scale, *Ceroplastes rubens*, in Australia revealed elevated densities on trees along roads compared with those in gardens and proposed superior host suitability or elevated colonization as potential underlying mechanisms (89). These results contrast with the general notion that drought stress decreases host quality of woody plants for sucking insects (73). For example, survival of *P. pentagona* on white mulberry, *Morus alba*, was lower on water-stressed trees in urban environments than on trees in forested sites and urban sites that experienced less stress (50).

Effects of drought stress on folivores have been more variable. Water stress decreased folivore performance in some cases, but other studies reached the opposite conclusion or found effects to be minimal (57). Studies with bark beetles have also reached conflicting conclusions (57). It has been proposed that effects of drought stress on secondary metabolism and host plant resistance may be nonlinear, with moderately drought stressed trees more resistant to herbivores than either severely stressed or rapidly growing trees (59, 82, 93), which provides a potential explanation for otherwise contradictory results. Although evidence for the quadratic effects of drought on host quality is limited, there is some (55).

The evidence is stronger that drought-stressed trees are more susceptible to wood borers (57, 63, 82). For example, *Fraxinus pennsylvanica* planted in a downtown urban environment experienced more severe drought stress and suffered higher levels of borer damage than did trees planted on a park-like campus (22). Similarly, *Cornus florida*, an understory species that does not tolerate midday water stress, was much more susceptible to colonization by the dogwood borer, *Synanthedon scitula*, when planted in full sun relative to trees planted in at least partial shade (110). Water stress also increased the susceptibility of eucalyptus to the cerambycid wood borer *Phoracantha semipunctata* (51).

Huberty & Denno (63) suggested that intermittent as opposed to chronic drought stress may have underappreciated effects on host quality for herbivores, especially phloem sap suckers. Their Pulsed Stress Hypothesis proposes that bouts of drought followed by recovery of turgor increase nitrogen content of phloem sap, which favors sucking insects. This hypothesis may have particular relevance to the urban forest because trees and shrubs are often planted in medians, planters, and other confined spaces where they experience more intense water deficits than trees growing in extensive soil profiles (76, 87). The frequency of water deficit may also be increased because, for example, restricted soil volumes dry faster during dry periods and saturate more rapidly when it rains. Attempts to alleviate drought stress by periodic irrigation may further exacerbate this problem and enhance susceptibility of trees in urban sites. If so, then the Pulsed Stress Hypothesis predicts that the effects of host quality on population dynamics of sap-sucking arthropods will differ markedly across the urban-rural gradient.

Pollution and host quality. Ozone is an important stressor in urban forests (11, 146). It has been proposed that ozone stress generally decreases tree resistance to insects (47). Accordingly, a recent meta-analysis found that ozone generally increased host quality for insect herbivores (150). However, the pattern was variable. For example, experimental ozone fumigation increased the host quality of *Populus tremuloides* for four species of outbreak Lepidoptera including gypsy moth (60), but had no effect on the quality of *Acer saccharum* or hybrid poplar as hosts for gypsy moth (86), or on the host quality of *Betula papyrifera* for *Orgyia leucostigma* (72). Similarly, exposure of *Populus deltoides* to ozone had no effect on the aphid *Chaitophorus populicola* (18), but decreased fecundity of *Plagiodera versicolora* (19).

Deposition of atmospheric nitrogen originating from fossil fuel combustion provides a potential mechanism by which nitrogen enrichment may influence the population dynamics of phytophagous insects in urban environments on a wide scale. The magnitude of nitrogen

deposition can be substantial, exceeding 30 kg ha^{-1} in many urban and rural regions of Europe and North America (11, 146). Chronic nitrogen loading alters patterns of nutrient cycling and increases nitrogen uptake in forest ecosystems, with the potential to increase herbivore populations and alter herbivore community structure through effects on host quality (148). In southern California, nitrogen deposition and ozone exposure interacted to increase pine susceptibility to bark beetle infestation during drought (66). Nitrogen deposition associated with vehicle exhaust was also implicated in higher host quality for the lymantriid *Euproctis similis* and resulted in elevated populations of the moth on trees near roadways (108). These studies reveal that several hemipterans attained high densities in urban environments and were associated with reductions in vegetational texture, improved host quality, and reduced function of natural enemies.

De-icing salts are commonly applied in cities where snow accumulates on streets. The use of de-icing salts in European cities has been implicated in improving the quality of hosts for herbivores and contributing to dramatically elevated populations of spider mites along roadways compared with more natural areas such as parks (33, 77).

Pollutants affect the quality of host plants for natural enemies as well as herbivores. Airborne particulates such as dust from roadways can disrupt activities of natural enemies on foliage and may result in elevated populations of herbivores near thoroughfares. Greater abundance of the armored scale *Nuculaspis californica* has been associated with increased levels of dust along roadways compared to natural areas (28).

Further research is necessary before a robust predictive framework emerges regarding the relative importance of bottom-up effects on population dynamics of phytophagous arthropods in urban environments. Clearly, the effects of abiotic stress on host quality are variable and complex and depend on the type, timing, and intensity of stress; the physiological response of the plant; and the behavior, physiology, and life history of the herbivore (65). Few studies have

adequately quantified these variables or undertaken manipulative experiments.

Top-Down and Bottom-Up Effects of Pesticides

Pesticides can disrupt ecosystem processes at several spatial scales (116). Spider mites and scale insects are two taxa that commonly change dramatically following pesticide applications. Government agencies inadvertently created outbreaks of insects and mites in urban settings while conducting area-wide attempts to eradicate invasive exotic pests (24, 26, 29). Disruption of natural enemy communities and relaxation of top-down forces were implicated as the mechanisms associated with outbreaks of these pests (26, 29). Recently, populations of the spider mite *Tetranychus schoenei* were three orders of magnitude more abundant on elm trees treated with insecticides as part of an eradication program for *Anoplophora glabripennis*, in Central Park, New York (119). Both bottom-up and top-down forces were implicated in this outbreak, as spider mites were more fecund after consuming foliage of treated elms. Mites from treated trees were more toxic to predators (21, 142).

Municipalities attempting to manage biting and filth flies sometimes create secondary pest outbreaks. Prolonged applications of insecticides for mosquitoes and filth flies resulted in elevated and damaging levels of arthropods on street trees in California and Michigan, respectively (23, 100). Following cessation of pesticide applications, populations of herbivores declined dramatically as mortality caused by parasitoids and predators increased (90, 100). Chronic applications by commercial providers resulted in greater frequencies and elevated populations of coccid and diaspidid scales in managed landscapes, and residual organophosphate insecticides applied as blanket sprays reduced the abundance and activity of several taxa of natural enemies on treated trees (115). Incomplete applications of an insecticide to individual trees increased populations of a *F. externa* by altering both top-down and bottom-up

forces. Following an initial reduction in scale density on treated trees, scales then developed faster and were more fecund owing to an improvement in host quality. Moreover, a parasitoid and three predators were virtually eliminated from the lower crowns of partially treated trees (94).

Foliar applications of insecticides are not alone in their ability to increase populations of pests. Soil applications of the systemic insecticide imidacloprid have been linked to elevated populations of mites on trees including *P. multidigituli*, *Oligonychus ununguis*, *Nalepella tsugifolia*, and *T. schoenei*. Removal of top-down regulation by omnivorous predators and improved nutritional quality of hosts were implicated in greater abundance of spider mites following insecticide application (21, 119, 120, 133, 142). In controlled experiments that excluded predators, imidacloprid increased the fecundity of the twospotted spider mite, *Tetranychus urticae*, on burning bush, *Euonymus alatus*, and tomato (16, 142). In burning bush, the effect was restricted to plants growing in a low fertility treatment, as imidacloprid raised egg production to the same level observed on untreated plants growing in a high fertility regime (16). Imidacloprid also increased fecundity of the boxwood spider mite, *Eutetranychus buxi*, on *Buxus* and *T. schoenei* on *Ulmus* in the absence of predators (142). These studies provide evidence that imidacloprid can enhance host quality of woody plants for spider mites. Predatory insects that consumed prey exposed to imidacloprid through the host plant suffered reduced mobility, lower feeding rates, and greater mortality than those that ate prey from untreated plants (21), thereby providing evidence that both top-down and bottom-up effects may contribute to increased mite abundance following the application of insecticides.

SUMMARY POINTS

1. Empirical evidence does not a support a conclusion that herbivorous arthropods uniformly attain greatest richness or abundance along a gradient of increasing urbanization.

2. Small arthropods with sucking mouthparts, limited mobility, multiple generations on the same host plant, or other intimate associations with hosts such as scale insects, spider mites, lace bugs, aphids, gall midges, gall wasps, and dipterous leafminers, exclusively or generally increase along an urbanization gradient. These patterns are well supported empirically and in some cases mechanistically. Arthropods with these life-history characteristics appear to have the greatest likelihood of reaching outbreak population levels in response to urbanization.

3. Lepidoptera generally do not respond in simple linear fashion along an urbanization gradient. Many leaf-mining Lepidoptera respond just as strongly to habitat fragmentation and patch attributes as to urbanization, while several Macrolepidoptera exhibited a quadratic response with peak diversity linked to resources, for example, host availability, which was greatest at intermediate levels of urbanization. Habitat loss associated with fragmentation and degradation is especially disruptive to butterflies. Lepidopteran borers are an exception, and their response to urbanization is strong owing to relaxation of bottom-up effects, which is well supported theoretically. Conspicuous in their absence are studies on herbivorous Coleoptera, Symphyta, and many Heteroptera despite strong theoretical and experimental support that loss of bottom-up and top-down forces should alter patterns of their abundance along the urbanization gradient.

4. Fertilization almost always decreases tree resistance to herbivores and has the potential to increase their populations, especially in mites, scales, and adelgids that complete multiple generations on the same plant.

5. Applications of pesticides are well documented to increase populations of mites and scales. Few studies examined mechanisms but both top-down and bottom-up forces have been implicated.

6. It has been proposed that urban stress triggers insect outbreaks by enhancing host quality. However, this generalization is not well supported, except in the case of wood borers. We conclude that the effects of stress on host quality are variable and complex, possibly because of the nonlinear responses of plants to stress gradients.

7. Many features of urbanization constrain the availability of moisture and nutrients for plants and limit the impact of natural enemies in cities. This and the inherent low diversity of street tree communities greatly imperil the sustainability of urban forests confronted with an increasing stream of invasive species (85, 104, 113).

8. The contrived diversity of residential landscapes in suburbs and urban parks may be important for maintaining biodiversity and for restoring ecosystem function.

FUTURE ISSUES

1. Inferences derived from many studies conducted along urban gradients are limited owing to a failure to clearly define and assess relative contributions of environmental attributes that often covary or are otherwise confounded. Future research should attempt to clearly define and test specific features and characteristics of urbanization and independently examine mechanistic contributions of top-down and bottom-up factors.

2. Bottom-up and top-down dynamics relating to the increased presence of exotic plants and the introduction of exotic herbivores are poorly understood in urban systems. Future studies need to examine if exotic pests exploit naïve hosts that lack evolved defenses (Defense Free Space Hypothesis), if exotic plants support less diverse communities of herbivores, and whether this results in cascading effects that extend to higher and perhaps lower trophic levels.

3. Vegetational structure and diversity strengthens top-down impacts on herbivore populations. Future research should address what mix of plants should be used in urbanized areas to restore ecosystem function and how this mix should differ along various points of the urban gradient, for example, rural, suburban, and inner city, and at what spatial scale.

4. Impervious surfaces, a dominant feature of urbanization, have the potential to affect water availability, nutrient cycling, temperature and rates of development, and movement of herbivores and natural enemies. Further research needs to explore how these surfaces affect population dynamics, community structure, and ecosystem function. For example, do herbivores escape predators because cities are hot and herbivores race through vulnerable stages (Slow Growth–High Mortality Hypothesis)?

5. More studies need to examine the impact of urban stress and cultural management practices on host quality and arthropod outbreaks. These studies should characterize the intensity of stress, physiological responses of hosts, effects on host quality traits, and responses of various guilds or taxa of arthropods.

6. Considerable research is required before a robust predictive framework will emerge regarding the relative importance of bottom-up and top-down effects on population dynamics of phytophagous arthropods in urban environments.

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