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Urban plants and climate drive unique arthropod interactions with unpredictable consequences

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Urban areas, a rapidly expanding land cover type, are composed of a mix of impervious surfaces, ornamental plants, and remnant habitat, which alters abiotic conditions and affects arthropod community assemblages and trophic interactions. Importantly, these effects often reduce arthropod diversity and may increase, reduce, or not change individual species or trophic interactions, which affects human and environmental health. Despite the pace of urbanization, drivers and consequences of change in urban arthropod communities remains poorly understood. Here, we review recent findings that shed light on the effects of urbanization on plants and abiotic conditions that drive arthropod community composition and trophic interactions, with discussion of how these effects conflict with human values and can be mitigated for future urbanization.

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Introduction

Urban landscapes are among the most rapidly expanding land cover type on the globe [1–3] and generally associated with reduced biodiversity [4,5] and fragmented vegetation [6]. Remnant patches of natural habitat stranded by urban development show a predictable decline in the plant and arthropod species associated with them [7,8]. However, much urban space is filled by maintained landscapes with plants from all over the world [9•], man-made structures [10], and unique atmospheric conditions [11,12]. These anthropogenic features create unique arthropod communities and ecological interactions that are hard to predict and may conflict with human values [7,13–15].

It has been documented for over a century that the abundance of some arthropods changes in urban habitats compared to surrounding natural areas [16–18]. In general, higher trophic levels and specialists are more sensitive than lower trophic levels and generalists to urbanization [19]. As a trophic level, herbivores [14] appear most resilient, with most urban plants supporting herbivores and herbivory to varying degrees. Even so, some herbivores become more abundant or feed more in urban conditions [20,21], while others decline or feed less [22,23••]. Within higher trophic levels, parasitoids in particular respond negatively to urbanization [24,25], whereas generalist predators like ants [23••,26] and spiders [27] often endure. Although each arthropod guild or trophic levels persists to some extent, it has become evident that arthropod communities and trophic interactions in cities are often distinct from those in natural ecosystems or other anthropogenic habitats like agricultural fields [19]. Urban plant communities can be quite diverse and, in many cases, more diverse than natural ecosystems [28,29]. However, most of the plants have not evolved with the indigenous arthropods. Thus, ecological interactions in urban landscapes occur among plants, herbivores, and natural enemies that may not otherwise interact.

In addition to unique plant communities, urban arthropods face unique abiotic conditions [11]. The urban heat island effect makes cities up to 12 °C hotter than their surrounding rural areas [12]. Some arthropod taxa, especially at high latitudes, benefit from this warming, whereas others are negatively affected [30•]. Other species migrate to cities from lower latitudes as the temperature is similar to their native conditions [31]. Thus, environmental conditions are strong filters to arthropod communities [32,33] and can intensify some interactions [34••] while reducing or redirecting others [35]. Therefore, even if an herbivore's preferred host or a predator's favorite prey is present, an interaction cannot occur if they cannot both exist in the same abiotic conditions.

Primary producers and climate have long been understood to drive arthropod communities and higher trophic level interactions [36,37]. The outcome of these interactions affects the beauty, carbon sequestration, and other services provided by urban plants, so understanding them will help us manage urban ecosystems to maximize beneficial services. Several studies have evaluated the landscape-scale and local drivers of arthropod communities [7,19,38], but few investigate trophic interactions at either scale. Thus, we focus our review on recent advances in how urban plant communities that are assembled by people, and the abiotic conditions that result from human infrastructure, affect interactions between plants, herbivores, and natural enemies, which affects people and the environment.

Urban habitats support unique arthropod communities and interactions

The effects of urbanization on arthropod communities and trophic interactions vary by scale (e.g. size, age) [39] and surrounding context (e.g. agricultural, rural), which can make their effects challenging to detect and predict [19,25,40]. For example, Kozlov *et al.* [23••] found that on average, insect herbivory was 16.5% lower on urban *Betula pubescens* than in nearby rural sites. This effect was present when comparing large cities (1–5 million people), but not medium or small cities (15–700 thousand), to their surrounding rural areas. In addition, across six regions in Switzerland, urban *Betula pendula* trees harbored arthropod communities distinct from those on rural *B. pendula*, but similar to geographically independent urban areas [41••]. Therefore, urban ecosystems create arthropod assemblages that are distinct from rural ecosystems but may be more like other cities.

Within a city, we often observe effects of vegetation patch size [19], complexity [42], cover [43••], and habitat connectivity [44] on arthropod abundance and diversity. Golf courses, among the largest habitat patches in urban landscapes, can support greater arthropod herbivore and predator richness than some urban parks and gardens [45]. Although larger patch size can sustain greater arthropod richness and biological control services, local features within a patch like floral resources, vegetation complexity, canopy cover, and composition may be more important drivers of higher trophic interactions in urban landscapes [42,46–48]. For example, Philpott and Bichier [40] found that local factors, like higher plant richness and abundance (within a 20×20 m plot), best predicted aphid predation rates in urban gardens. Given the effect of scale and local characteristics, it is critical to consider both when investigating effects of urbanization on ecological interactions.

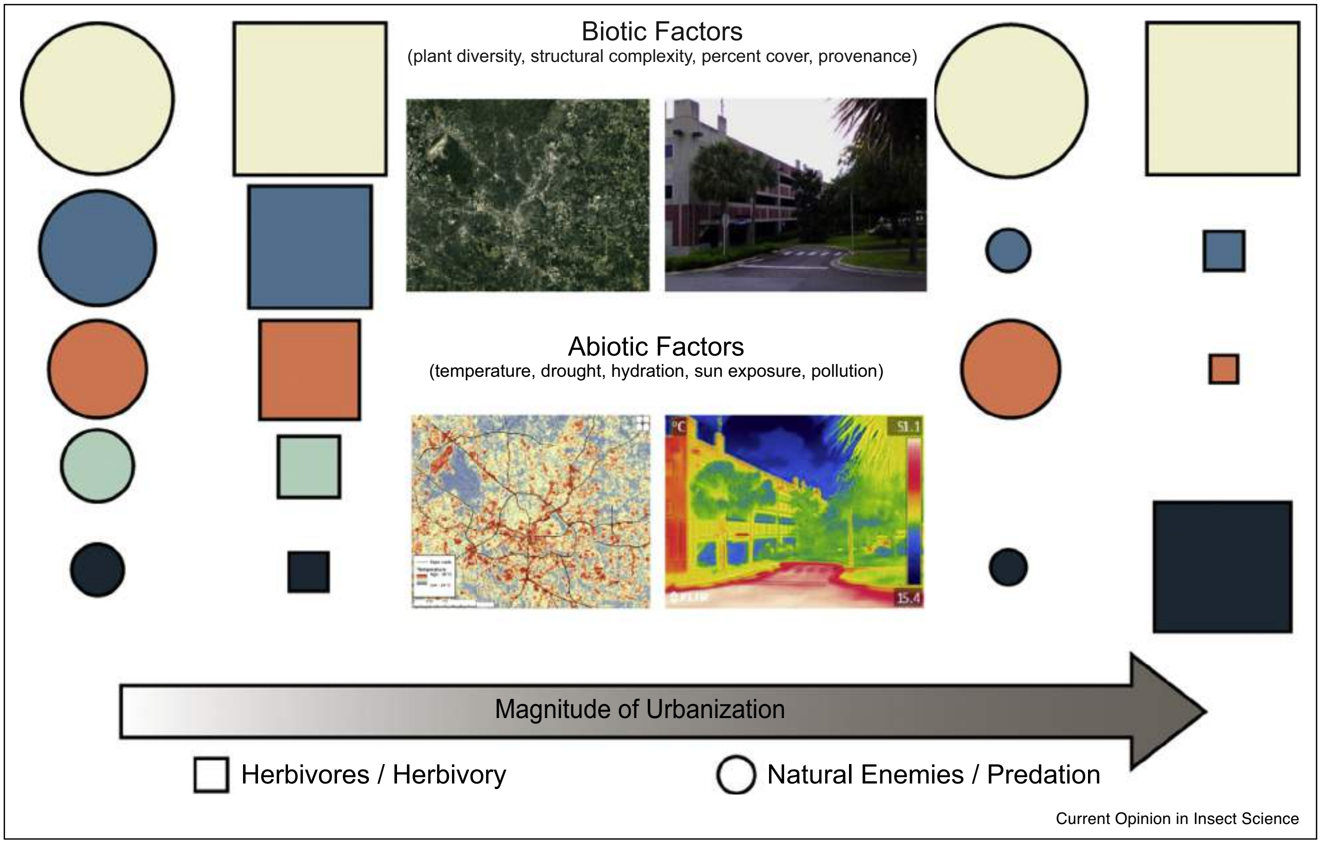
Since urban landscapes are characterized by a mosaic of fragmented vegetation, they are also comprised of a mosaic of abiotic conditions, which may differentially affect insect fitness and plant quality in those spaces [21,49,50]. Therefore, biotic and abiotic factors often interact to affect arthropod communities [51], which makes identifying a mechanism for the effects of urban features, like low tree canopy cover or plant density, difficult (Figure 1). For example, Shrewsbury and Raupp [52] found that the abundance of the herbivore, *Stephanitis pyrioides*, increased as urban tree canopy cover decreased, which was associated with fewer natural enemies but also more sun exposure. Dale and Frank [53] also found that herbivore abundance increased as tree canopy cover decreased, which also increased sun exposure and temperature. Despite changes in biotic factors like vegetation and natural enemies, temperature most strongly predicted herbivore fitness and abundance [53]. Therefore, abiotic factors like temperature may override the direct effects of biotic factors like plant density, diversity, or complexity, but are not as frequently measured [53,54]. Correlates of temperatures such as impervious surface cover are measured more often, but are also associated with canopy cover fragmentation, which complicates interpretation of results. Thus, measuring specific abiotic variables like temperature, CO_2, and soil moisture would help clarify observed effects.

Abiotic conditions filter arthropod communities

Warming and drought are often coincident in urban landscapes (except in desert cities, see [55]) where they can have complex effects on plants and insects. McClung and Ibanex [56] found that warming and drought synergistically reduced urban tree growth and altered urban forest composition over time. Changing the urban plant community can have cascading effects on herbivore communities and higher trophic levels that depend on them [57]. Similarly, many urban tree species are planted outside of their native range, which subjects them to abiotic conditions in which they did not evolve. Subsequent stress or atmospheric conditions can affect plant quality for herbivores by changing plant nutrient content or defense [58,59]. This can favor some herbivore species or guilds while excluding others [60]. For example, elevated nitrogen deposition associated with air pollution may increase the nutritional quality of plant foliage, increasing herbivore richness [61] or reducing herbivory by meeting nutrient requirements with less feeding [23••,62]. Warming and drought on urban *Acer rubrum* trees additively increases *Melanaspis tenebricosa* female body size and fecundity [63], which combine to reduce tree condition in warmer urban sites [49]. In addition, leaf stomata close in response to urban heat and drought, which reduces photosynthesis [50], but also changes leaf-level microclimates and affects trophic interactions that occur in that space [64]. Thus, arthropod communities are driven not only by the presence or absence of a host plant, but also plant physiological condition.

Warming also directly affects arthropod physiology, which can change arthropod abundance and behavior on urban plants [14]. For example, heat and drought reduce the hydration level of some arthropods, changing community composition and increasing herbivory as they seek moisture from plants [65]. Urban warming can also increase herbivore fecundity and population growth rates, contributing to 200 times greater abundance of an herbivore on hotter trees and negating natural enemy regulation [53]. Warm microclimates adjacent to buildings

Figure 1



As landscapes transition from natural areas to densely urbanized landscapes, or small towns to megacities, changes in biotic and abiotic factors occur. Although often investigated independently, these changes are frequently coupled and each affect arthropod communities. At large spatial scales, vegetated land cover and impervious surface cover translate to relatively cool and hot surface temperatures, respectively. At the local scale, more plant cover or complexity creates cooler microclimates than less plant cover or complexity. These changes may increase, reduce, or not affect arthropods and their trophic interactions. Above, the left side of the figure represents an arthropod community in a rural or natural area and the right side represents that community after extensive urbanization. Each color represents a trophic pair within an arthropod community. Circles are natural enemies or their predation services and squares are herbivores or herbivory. The size of each shape indicates the abundance of a species or magnitude of a trophic interaction.

increase overwinter survival of some insect herbivores, leading to greater herbivory on spring foliage [66]. Physiological changes in the fitness of some species can alter competition, which may exclude some species from urban areas altogether. For example, abiotic urban conditions can select for heat tolerant individuals, creating populations with higher critical thermal maximums as observed in ants [67•] and solitary bee communities [68]. Furthermore, arthropod species with origins in warmer climates may persist or establish in cities at higher latitudes or altitudes than the species would normally occur due to the urban heat island effect [69,70].

Although natural enemies tend to respond to prey density or vegetation characteristics, this may not hold true in urban ecosystems. For example, arboreal spider community composition on urban oak trees was more strongly associated with urban warming than prey density [54]. Some arthropod food webs are further complicated in urban areas where novel mutualisms facilitate herbivore outbreaks and inhibit top-down regulatory pressures. For example, an invasive ant, *Linepithema humile*, thrives in urban settings and facilitates outbreaks of a native herbivore, *Mesolecanium nigrofasciatum*, by protecting it from predation [71]. This herbivore reduces tree seed set and leaf growth, but not when *L. humile* are excluded from tree canopies [71]. Likewise, Rocha and Fellowes [72] found that aphid abundance increased with impervious surface cover (a common correlate of temperature) and was best explained by an increase in mutualistic ant abundance (*Myrmica rubra* and *Lasius niger*) and fewer predators. Using a manipulative experimental design, Turrini *et al.* [34••] found that syrphid fly predation reduced aphids in urban and rural sites, but was significantly less in urban sites, although a mechanism was not identified. Importantly, aphid feeding directly reduced root growth, so urban areas, defined as those with a 0.40 mean Normalized Difference Vegetation Index (NDVI) value within a 500 m buffer, reduced root biomass by disrupting the trophic cascade present in rural habitats (with a mean NDVI of 0.70). Illustrating the frequent interaction between biotic and abiotic factors, the authors also attributed reduced plant growth in the absence of herbivores or natural enemies to the direct effects of urban warming and pollution [34••].

Urban warming can indirectly affect insect abundance and distribution by altering plant and insect phenology [35,73,74]. Urban heat islands can shift plant flowering phenology, which disrupts pollinator resource utilization [74], and has implications for pollinator decline [75]. These effects may carry over to insects that serve dual functions as pollinators and predators. For example, the phenology of migratory syrphid flies is disrupted by urban warming, which reduces their abundance in urban compared to rural habitats and creates distinct communities of non-migratory species between land use types [73]. Urban warming also differentially affects predator-prey phenology, resulting in herbivore outbreaks on urban plants. *Parthenolecanium quercifex* phenology advances on trees in warmer urban landscapes while the phenology of its parasitoid does not, creating a temporal window of enemy-free space and facilitating higher herbivore fecundity and abundance [35].

Challenges in sustaining urban plants and their services

Urban plant composition is determined in part by consumer demands, aesthetic quality, design standards, and plant cost and availability [9•]. In some cases these decisions reduce urban tree diversity [9•,76] and predispose urban forests to devastation by exotic pests or climate change as observed with *Agrilus planipennis* and Dutch elm disease [77,78]. Increasing plant diversity is one approach to mitigating pest impacts, but it is not that simple. Exotic plants, a large portion of urban plantings [9•], generally support lower arthropod abundance and diversity than their native counterparts [79], which may disrupt ecological food webs [80] and contribute to the decline in urban biodiversity. For this reason, many argue against the use of exotic plants amidst already disturbed urban areas. However, exotic plants can still have use in urban settings where conditions are often vastly different from surrounding indigenous habitat [81••]. For example, Salisbury *et al.* [43••] found that sap-feeding herbivores were 30% more abundant on native than exotic ornamental plants. Although herbivores serve an important ecological function, sap-feeders are the most damaging and difficult to control arthropod pests of urban plants [14], and are repeatedly more abundant and damaging in urban than rural or natural areas [21,49,52,82]. Thus, strategic use of exotic plants in combination with natives may serve dual pest management and wildlife conservation functions in maintained urban landscapes.

Healthy plants in urban landscapes benefit people and the environment by reducing temperatures [12], sequestering carbon [83], capturing pollutants [84], and providing recreational or leisure space [85]. These benefits increase with plant growth, cover, and photosynthesis rates. Thus, biotic and abiotic factors within cities that often reduce these services [49,50,63] also increase maintenance costs and inputs [86]. Fortunately, local site characteristics, like impervious surfaces (a proxy of drought, heat, and pests) can be quantified and used to develop landscape design guidelines that reduce plant pests, increase urban plant condition, and reduce long-term maintenance costs [87•]. Since the way we design and maintain urban plantings often reduces beneficial insects [88] and increases plant pests [87•], it is critical that we bridge the common disconnect between landscape design, plant maintenance, and ecosystem services. To start, integrating new research evidence that informs plant selection based on diversity, provenance, and local site characteristics is critical for promoting ecosystem services that benefit people and the environment.

Knowledge gaps and research needs

The volume and pace of research focused on the ecology of arthropods in urban ecosystems has rapidly increased over recent decades. In result, we have a better understanding of the effects of urbanization on arthropod communities and trophic interactions. However, several knowledge gaps remain. Below, we have highlighted topics that we feel deserve attention for future investigations.

1 Abiotic factors other than temperature, like elevated carbon dioxide, ozone, nitrogen deposition, light, and anthropogenic noise, affect plant and animal behavior, physiology, and interactions [14,51,61,89]. However, relatively little research has investigated the direct and indirect effects of these abiotic factors on arthropods and trophic interactions.
2 Lawns, composed of various forbs and graminaceous plants, are arguably the most abundant habitat type in urban and residential landscapes and intimately linked to where humans live, work, and play. Plants in these spaces provide services like arthropod habitat, cooling, carbon sequestration, soil erosion control, and reduced noise and water runoff [90–92]. Despite this, and evidence that residential lawn plant communities are homogenized across large geographic scales [93•], relatively little research has focused on the identity, value, and ecological function of arthropods in residential lawns.
3 Research on the effects of urbanization on arthropod herbivores is often motivated by pest outbreaks or species of ecological concern, which has created a bias in the urban arthropod literature. Sedentary behavior, incomplete metamorphosis, high reproductive potential, and an abundant primary host plant seem to favor the success of herbivores in urban landscapes [14]. New

empirical data and meta-analyses of existing data are needed detailing which herbivores succeed or fail and the life history or behavioral traits that contribute to that result to direct future research and research applications.

4 Rapid urbanization will continue regardless of new strategies or technologies that make urban development more ecologically sustainable. Research on green infrastructure, like urban gardens, green roofs, and parks has made advancements, but represent only a small percentage of the urban environment [45,94]. Thus, identifying strategies that can facilitate the integration of ecological principles into existing and future urban infrastructure is increasingly important.

5 Although urban ecology research is being conducted globally, there is a bias in the primary literature towards work done in North America, South America, Europe, and Australia [95]. It is concerning that urban ecology focuses on the effects of urbanization, yet the largest and most rapidly urbanizing regions in the world (e.g. India, China, Indonesia) are not well represented in the primary literature. Therefore, research and literature reviews in these underrepresented regions will help direct future research efforts and inform urban ecology theory.

Conflict of interest statement

Nothing declared.

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References and recommended reading

Papers of particular interest, published within the period of review, have been highlighted as:

- • of special interest
- •• of outstanding interest

1. Nations U: **World urbanization prospects: the 2014 revision, highlights**. *Affairs DoEaS*. 2014.

2. Brown DG, Johnson KM, Loveland TR, Theobald DM: **Rural land-use trends in the conterminous United States, 1950–2000**. *Ecol Appl* 2005, **15**:1851-1863.

3. Alig RJ, Kline JD, Lichtenstein M: **Urbanization on the US landscape: looking ahead in the 21st century**. *Landsc Urban Plan* 2004, **69**:219-234.

4. McIntyre NE: **Ecology of urban arthropods: a review and a call to action**. *Ann Entomol Soc Am* 2000, **93**:825-835.

5. McKinney ML: **Urbanization, biodiversity, and conservation**. *BioScience* 2002, **52**:883-890.

6. McIntyre NE, Rango J, Fagan WF, Faeth SH: **Ground arthropod community structure in a heterogenous urban environment**. *Landsc Urban Plan* 2001, **52**:257-274.

7. McKinney ML: **Effects of urbanization on species richness: a review of plants and animals**. *Urban Ecosyst* 2008, **11**:161-176.

8. Rossetti MR, Tscharntke T, Aguilar R, Batary P: **Responses of insect herbivores and herbivory to habitat fragmentation: a hierarchical meta-analysis**. *Ecol Lett* 2017, **20**:264-272.

9. • Avolio ML, Pataki DE, Trammell TL, Endter-Wada J: **Biodiverse cities: the nursery industry, homeowners, and neighborhood differences drive urban tree composition**. *Ecol Monogr* 2018:1-18.

This paper illustrates the connection between nursery stock, human preference, and local urban landscape characteristics in determining urban forest composition. It identifies specific determinants of urban forest composition and important similarities and differences between municipal and residential trees.

10. Nowak DJ, Greenfield EJ: **Tree and impervious cover change in U.S. cities**. *Urban For Urban Green* 2012, **11**:21-30.

11. Arnfield AJ: **Two decades of urban climate research: a review of turbulence, exchanges of energy and water, and the urban heat island**. *Int J Climatol* 2003, **23**:1-26.

12. Oke TR, Crowther JM, McNaughton KG, Monteith JL, Gardiner B: **The micrometeorology of the urban forest [and discussion**. *Philos Trans R Soc B: Biol Sci* 1989, **324**:335-349.

13. Collier MJ, Devitt C: **Novel ecosystems: challenges and opportunities for the Anthropocene**. *Anthropocene Rev* 2016, **3**:231-242.

14. Raupp MJ, Shrewsbury PM, Herms DA: **Ecology of herbivorous arthropods in urban landscapes**. *Annu Rev Entomol* 2010, **55**:19-38.

15. Luck GW, Smallbone LT: **Species diversity and urbanisation: patterns, drivers and implications**. In *Urban Ecology*. Edited by Gaston KJ. New York, NY, USA: Cambridge University Press; 2010.

16. Putnam JD: **Biological and other notes on Coccidae**. *Proc Davenport Acad Sci* 1880, **2**:293.

17. Metcalf ZP: **The gloomy scale, an important enemy of shade trees in North Carolina**. *J Elisha Mitchell Sci Soc* 1912, **28**:88-91.

18. Kettlewell HBD: **Selection experiments on industrial melanism in the Lepidoptera**. *Heredity* 1955, **9**:323-342.

19. Burkman CE, Gardiner MM: **Urban greenspace composition and landscape context influence natural enemy community composition and function**. *Biol Control* 2014, **75**:58-67.

20. Cuevas-Reyes P, Gilberti L, González-Rodríguez A, Fernandes GW: **Patterns of herbivory and fluctuating asymmetry in *Solanum lycocarpum* St. Hill (Solanaceae) along an urban gradient in Brazil**. *Ecol Indic* 2013, **24**:557-561.

21. Meineke EK, Dunn RR, Sexton JO, Frank SD: **Urban warming drives insect pest abundance on street trees**. *PLoS ONE* 2013, **8**:e59687.

22. Bode RF, Gilbert AB: **Seed predators, not herbivores, exert natural selection on *Solidago* spp. in an urban archipelago**. *Environ Entomol* 2016, **45**:150-154.

23. •• Kozlov MV, Lanta V, Zverev V, Rainio K, Kunavin MA, Zvereva EL: **Decreased losses of woody plant foliage to insects in large urban areas are explained by bird predation**. *Global Change Biol* 2017, **23**:4354-4364.

Kozlov*et al.* use paired rural and urban sites across a large geographic range to evaluate the effects of plant quality, predation, and parasitism on the distribution and feeding activity of insect herbivores, particularly leaf mining and galling insects. Interestingly, herbivory was significantly less on urban than rural trees, but only when comparing large cities to their surrounding rural areas. Results present interesting implications regarding underlying plant quality effects on insect herbivory, demonstrate that trophic interactions may override abiotic drivers of herbivore success, and that these effects depend on the magnitude of urbanization.

24. Burks JM, Philpott SM: **Local and landscape drivers of parasitoid abundance, richness, and composition in urban gardens**. *Environ Entomol* 2017, **46**:201-209.

25. Nelson AE, Forbes AA: **Urban land use decouples plant-herbivore–parasitoid interactions at multiple spatial scales**. *PLoS ONE* 2014, **9**:e102127.

26. Thompson B, McLachlan S: **The effects of urbanization on ant communities and myrmecochory in Manitoba, Canada**. *Urban Ecosyst* 2007, **10**:43-52.

27. Lowe EC, Wilder SM, Hochuli DF: **Life history of an urban-tolerant spider shows resilience to anthropogenic habitat disturbance**. *J Urban Ecol* 2017:3.

28. Hope D, Gries C, Zhu W, Fagan WF, Redman CL, Grimm NB, Nelson AL, Martin C, Kinzig AP: **Socioeconomics drive urban plant diversity**. *Proc Natl Acad Sci USA* 2003, **100**:8788-8792.

29. Smith RM, Thompson K, Hodgson JG, Warren PH, Gaston KJ: **Urban domestic gardens (IX): composition and richness of the vascular plant flora, and implications for native biodiversity**. *Biol Conserv* 2006, **129**:312-322.

30. • Youngsteadt E, Ernst AF, Dunn RR, Frank SD: **Responses of arthropod populations to warming depend on latitude: evidence from urban heat islands**. *Global Change Biol* 2017, **23**:1436-1447.

This paper is uses a novel experimental approach to compare the effects of urban warming on urban arthropod communities across four cities and 6.6 degrees of latitude. Using this approach, the authors demonstrate that urban warming affects arthropod herbivores across geographically distinct cities; however, the magnitude and heterogeneity of that effect is dependent on latitude.

31. Menke SB, Guénard B, Sexton JO, Weiser MD, Dunn RR, Silverman J: **Urban areas may serve as habitat and corridors for dry-adapted, heat tolerant species; an example from ants**. *Urban Ecosyst* 2010, **14**:135-163.

32. Reese AT, Savage A, Youngsteadt E, McGuire KL, Koling A, Watkins O, Frank SD, Dunn RR: **Urban stress is associated with variation in microbial species composition-but not richness-in Manhattan**. *Int Soc Microb Ecol J* 2016, **10**:751-760.

33. Zvereva EL, Kozlov MV: **Consequences of simultaneous elevation of carbon dioxide and temperature for plant-herbivore interactions: a metaanalysis**. *Global Change Biol* 2006, **12**:27-41.

34. •• Turrini T, Sanders D, Knop E: **Effects of urbanization on direct and indirect interactions in a tri-trophic system**. *Ecol Appl* 2016, **26**:664-675.

Turriniet *al.* use a nice experimental design with paired urban and rural sites to evaluate the effects of urban ecosystems on multi-trophic interactions. This paper demonstrates the complexity of predator–herbivore–plant interactions in urban ecosystems while illustrating specific pathways by which urban factors can affect plant health.

35. Meineke EK, Dunn RR, Frank SD: **Early pest development and loss of biological control are associated with urban warming**. *Biol Lett* 2014, **10**:20140586.

36. Andrewartha HG, Birch LC: **Some recent contributions to the study of the distribution and abundance of insects**. *Annu Rev Entomol* 1960, **5**:219-242.

37. Hairston NG, Smith FE, Slobodkin LB: **Community structure, population control, and competition**. *Am Nat* 1960, **94**:421-425.

38. Faeth SH, Bang C, Saari S: **Urban biodiversity: patterns and mechanisms**. *Ann N Y Acad Sci* 2011, **1223**:69-81.

39. Bennett AB, Gratton C: **Local and landscape scale variables impact parasitoid assemblages across an urbanization gradient**. *Landscape Urban Plan* 2012, **104**:26-33.

40. Philpott SM, Bichier P: **Local and landscape drivers of predation services in urban gardens**. *Ecol Appl* 2017, **27**:966-976.

41. •• Knop E: **Biotic homogenization of three insect groups due to urbanization**. *Global Change Biol* 2016, **22**:228-236.

This paper compares arboreal arthropod communities across six cities and paired agricultural sites. The author demonstrates that urban factors can generate arthropod communities distinct from rural communities, but may homogenize geographically independent urban areas by differentially affecting generalists and specialists.

42. Fenoglio MS, Videla M, Salvo A, Valladares G: **Beneficial insects in urban environments: Parasitism rates increase in large and less isolated plant patches via enhanced parasitoid species richness**. *Biol Conserv* 2013, **164**:82-89.

43. •• Salisbury A, Al-Beidh S, Armitage J, Bird S, Bostock H, Platoni A, Tatchell M, Thompson K, Perry J: **Enhancing gardens as habitats for plant-associated invertebrates: should we plant native or exotic species?** *Biodivers Conserv* 2017, **26**:2657-2673.

Salisbury*et al.* use a common garden experiment to compare the effects of ornamental plant composition (native versus exotic) and canopy cover on arthropod communities. They find that exotic plantings require at least 28% more canopy cover to support an equivalent abundance of arthropods as native plants. However, the most abundant herbivores were sap-feeders, which recur as the most pestiferous insect group on urban plants.

44. Braaker S, Obrist MK, Ghazoul J, Moretti M: **Habitat connectivity and local conditions shape taxonomic and functional diversity of arthropods on green roofs**. *J Anim Ecol* 2017, **86**:521-531.

45. Mata L, Threlfall CG, Williams NS, Hahs AK, Malipatil M, Stork NE, Livesley SJ: **Conserving herbivorous and predatory insects in urban green spaces**. *Sci Rep* 2017, **7**:40970.

46. Delgado de la Flor YA, Burkman CE, Eldredge TK, Gardiner MM: **Patch and landscape-scale variables influence the taxonomic and functional composition of beetles in urban greenspaces**. *Ecosphere* 2017:8.

47. Egerer MH, Bichier P, Philpott SM: **Landscape and local habitat correlates of lady beetle abundance and species richness in urban agriculture**. *Ann Entomol Soc Am* 2017, **110**:97-103.

48. Egerer MH, Liere H, Lin BB, Jha S, Bichier P, Philpott SM: **Herbivore regulation in urban agroecosystems: Direct and indirect effects**. *Basic Appl Ecol* 2018.

49. Dale AG, Frank SD: **The effects of urban warming of herbivore abundance and street tree condition**. *PLOS ONE* 2014:9.

50. Meineke E, Youngsteadt E, Dunn RR, Frank SD: **Urban warming reduces aboveground carbon storage**. *Proc R Soc B* 2016:283.

51. Robinson EA, Ryan GD, Newman JA: **A meta-analytical review of the effects of elevated CO_2 on plant–arthropod interactions highlights the importance of interacting environmental and biological variables**. *New Phytol* 2012, **194**:321-336.

52. Shrewsbury PM, Raupp MJ: **Evaluation of components of vegetational texture for predicting azalea lace bug, *Stephanitis pyrioides* (Heteroptera: Tingidae), abundance in managed landscapes**. *Environ Entomol* 2000, **29**:919-926.

53. Dale AG, Frank SD: **Urban warming trumps natural enemy regulation of herbivorous pests**. *Ecol Appl* 2014, **24**:1596-1607.

54. Meineke EK, Holmquist AJ, Wimp GM, Frank SD: **Changes in spider community composition are associated with urban temperature, not herbivore abundance**. *J Urban Ecol* 2017, **3** juw010.

55. Bang C, Faeth SH: **Variation in arthropod communities in response to urbanization: seven years of arthropod monitoring in a desert city**. *Landsc Urban Plan* 2011, **103**:383-399.

56. McClung T, Ibáñez I: **Quantifying the synergistic effects of impervious surface and drought on radial tree growth**. *Urban Ecosyst* 2017, **21**:147-155.

57. Burghardt KT, Tallamy DW, Gregory Shriver W: **Impact of native plants on bird and butterfly biodiversity in suburban landscapes**. *Conserv Biol* 2009, **23**:219-224.

58. Herms DA, Mattson WJ: **The dilemma of plants: to grow or defend**. *Q Rev Biol* 1992, **67**:283-335.

59. Mattson WJ, Haack RA: **The role of drought in outbreaks of plant-eating insects**. *BioScience* 1987, **37**:110-118.

60. Koricheva J, Larsson S, Haukioja E: **Insect performance on experimentally stressed woody plants: a meta-analysis**. *Annu Rev Entomol* 1998, **43**:195-216.

61. Zvereva EL, Kozlov MV: **Responses of terrestrial arthropods to air pollution: a meta-analysis**. *Environ Sci Pollut Res* 2010, **18**:355-367.

62. Meunier CL, Gundale MJ, Sanchez IS, Liess A: **Impact of nitrogen deposition on forest and lake food webs in nitrogen-limited environments**. *Glob Chang Biol* 2016, **22**:164-179.

63. Dale AG, Frank SD: **Warming and drought combine to increase pest insect fitness on urban trees**. *PLOS ONE* 2017, **12**:e0173844.

64. Pincebourde S, Murdock CC, Vickers M, Sears MW: **Fine-scale microclimatic variation can shape the responses of organisms to global change in both natural and urban environments**. *Integr Compar Biol* 2016, **56**:45-61.

65. McCluney KE, Burdine JD, Frank SD: **Variation in arthropod hydration across US cities with distinct climate**. *J Urban Ecol* 2017:3.

66. Hart ER, Miller Jr FD, Bastian RA: **Tree location and winter temperature influence on mimosa webworm populations in a northern urban environment**. *J Arboricult* 1986, **12**:237-240.

67. • Diamond SE, Chick L, Perez A, Strickler SA, Martin RA: **Rapid evolution of ant thermal tolerance across an urban–rural temperature cline**. *Biol J Linnean Soc* 2017:121.

Diamondet *al.* demonstrate the evolutionary implications of urban abiotic conditions by investigating thermal responses of ant populations to urban warming and concluding that it may select for the rapid evolution of species or individuals with higher critical thermal maximums, which may shift urban arthropod community composition to those with higher thermal tolerance.

68. Hamblin AL, Youngsteadt E, Lopez-Uribe MM, Frank SD: **Physiological thermal limits predict differential responses of bees to urban heat-island effects**. *Biol Lett* 2017:13.

69. Kaiser A, Merckx T, Van Dyck H: **The Urban Heat Island and its spatial scale dependent impact on survival and development in butterflies of different thermal sensitivity**. *Ecol Evol* 2016, **6**:4129-4140.

70. Robinet C, Imbert C-E, Rousselet J, Sauvard D, Garcia J, Goussard F, Roques A: **Human-mediated long-distance jumps of the pine processionary moth in Europe**. *Biol Invas* 2012, **14**:1557-1569.

71. Brightwell RJ, Silverman J: **Invasive Argentine ants reduce fitness of red maple via a mutualism with an endemic coccid**. *Biol Invas* 2010, **12**:2051-2057.

72. Rocha EA, Fellowes MDE: **Does urbanization explain differences in interactions between an insect herbivore and its natural enemies and mutualists?** *Urban Ecosyst* 2018.

73. Luder K, Knop E, Menz MHM, Traveset A: **Contrasting responses in community structure and phenology of migratory and non-migratory pollinators to urbanization**. *Divers Distrib* 2018.

74. Neil K, Wu J: **Effects of urbanization on plant flowering phenology: a review**. *Urban Ecosyst* 2006, **9**:243-257.

75. Goulson D, Nicholls E, Botias C, Rotheray EL: **Bee declines driven by combined stress from parasites, pesticides, and lack of flowers**. *Science* 2015, **347**:1255957.

76. Kendal D, Dobbs C, Lohr VI: **Global patterns of diversity in the urban forest: is there evidence to support the 10/20/30 rule?** *Urban For Urban Green* 2014, **13**:411-417.

77. Raupp MJ, Cumming AB, Raupp EC: **Street tree diversity in eastern North America and its potential for tree loss to exotic borers**. *Arboricult Urban For* 2006, **32**:297-304.

78. Herms DA, McCullough DG: **Emerald ash borer invasion of North America: history, biology, ecology, impacts, and management**. *Annu Rev Entomol* 2014, **59**:13-30.

79. Tallamy DW: **Do alien plants reduce insect biomass?** *Conserv Biol* 2004, **18**:1689-1692.

80. Burghardt KT, Tallamy DW, van Kleunen M: **Plant origin asymmetrically impacts feeding guilds and life stages driving community structure of herbivorous arthropods**. *Divers Distrib* 2013, **19**:1553-1565.

81. •• Martinson HM, Bergmann EJ, Venugopal PD, Riley CB, Shrewsbury PM, Raupp MJ: **Invasive stink bug favors naive plants: testing the role of plant geographic origin in diverse, managed environments**. *Sci Rep* 2016, **6**:32646.

Martinsonet *al.* demonstrate the potential value of exotic plant species in urban forests by investigating the behavior and host preference of an exotic invasive insect herbivore. They find that the invasive herbivore preferentially attacks native plants with similar phylogenetic origins to their indigenous hosts, and that the relative abundance of native plants additively increases herbivore abundance.

82. Tooker JF, Hanks LM: **Influence of plant community structure on natural enemies of pine needle scale (Homoptera: Diaspididae) in urban landscapes**. *Environ Entomol* 2000, **29**:1305-1311.

83. Nowak DJ, Greenfield EJ, Hoehn RE, Lapoint E: **Carbon storage and sequestration by trees in urban and community areas of the United States**. *Environ Pollut* 2013, **178**:229-236.

84. Escobedo FJ, Nowak DJ: **Spatial heterogeneity and air pollution removal by an urban forest**. *Landsc Urban Plan* 2009, **90**:102-110.

85. Sarkar C, Webster C, Gallacher J: **Residential greenness and prevalence of major depressive disorders: a cross-sectional, observational, associational study of 94 879 adult UK Biobank participants**. *Lancet Planet Health* 2018, **2**:e162-e173.

86. Vogt J, Hauer RJ, Fischer BC: **The costs of maintaining and not maintaining the urban forest: a review of the urban forestry and arboriculture literature**. *Arboricult Urban For* 2015, **41**:293-323.

87. • Dale AG, Youngsteadt E, Frank SD: **Forecasting the effects of heat and pests on urban trees: impervious surface thresholds and the 'Pace-to-Plant' technique**. *Arboricult Urban For* 2016, **42**:181-191.

This paper is one of the first to use evidence of the effects of urban abiotic factors on herbivores and plant health to develop applications that can help urban planners and plant maintenance professionals increase urban tree condition and longevity. Specifically, authors develop a tool to easily quantify impervious surface cover and provide impervious surface thresholds that guide landscape design and plant selection decisions.

88. Unterweger PA, Wastian L, Betz O: **Influence of the reduction of urban lawn mowing on wild bee diversity (Hymenoptera, Apoidea)**. *J Hymenoptera Res* 2016, **49**:51-63.

89. Grenis K, Murphy SM: **Direct and indirect effects of light pollution on the performance of an herbivorous insect**. *Insect Sci* 2018.

90. Beard JB, Green RL: **The role of turfgrasses in environmental protection and their benefits to humans**. *J Environ Qual* 1994, **23**:1-16.

91. Dix ME, Baxendale FP: **Insect pests and arthropod predators associated with tree-turf landscapes**. *J Entomol Sci* 1997, **32**:257-271.

92. Rochefort S, Therrien F, Shetlar DJ, Brodeur J: **Species diversity and seasonal abundance of Collembola in turfgrass ecosystems of North America**. *Pedobiologia* 2006, **50**:61-68.

93. • Wheeler MM, Neill C, Groffman PM, Avolio M, Bettez N, Cavender-Bares J, Roy Chowdhury R, Darling L, Grove JM, Hall SJ *et al.*: **Continental-scale homogenization of residential lawn plant communities**. *Landsc and Urban Planning* 2017, **165**:54-63.

Wheeleret *al.* investigate residential lawn plant community composition across seven U.S. cities that span climatic variation in the continental U.S. Results suggest that increasing climatic differences (precipitation) are associated with increasingly dissimilar plant communities, although lawn plant communities across all sites were more similar to each other than to their reference natural habitats. Importantly, when planted turfgrass species were excluded, spontaneous, 'weedy' species were highly similar across all sites. These results have implications for the effects of climate, maintenance practices, and socioeconomic status on arthropod communities utilizing these ubiquitous habitats amidst urban ecosystems.

94. Quispe I, Fenoglio MS, Simon LR, Gavin B: **Host–parasitoid interactions on urban roofs: an experimental evaluation to determine plant patch colonisation and resource exploitation**. *Insect Conserv Divers* 2015, **8**:474-483.

95. Martin LJ, Blossey B, Ellis E: **Mapping where ecologists work: biases in the global distribution of terrestrial ecological observations**. *Front Ecol Environ* 2012, **10**:195-201.