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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

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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, CO₂, 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

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