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Herbivore regulation in urban agroecosystems: Direct and indirect effects

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Abstract

Urban agroecosystems can provide habitat for biodiversity and can benefit human communities through urban food provisioning. Moreover, urban agroecosystems could be managed so as to optimize ecosystem services like natural pest control provided by trophic interactions between natural enemies and herbivores. As in other ecosystems, predation and parasitism regulate herbivores in urban settings, but less is known about the relative importance of direct and indirect effects at local and landscape scales in highly managed urban agroecosystems. We collected data on herbivore (cabbage aphid) density and parasitism ratios (proportion of parasitized aphid "mummies") in 25 community gardens in three counties in the California central coast, USA. We used structural equation modeling to examine the effects of direct factors (host plant characteristics and parasitism) and indirect factors (soil, garden, and landscape characteristics) on herbivore density changes at two time points in the growing season (June and August). Aphid density, but not parasitism, varied across counties over the season, and there was a strong negative relationship between aphid density and parasitism. Direct effects were strong drivers of aphid density but not parasitism. In June, aphid density increased with host plant volume but decreased with greater floral density, while parasitism was only influenced by aphid density. In August, host plant volume similarly positively affected aphid density, and soil water holding capacity increased host plant volume. In addition, host plant density had a strong negative effect on parasitism. Urban gardeners may be able to reduce aphid pest densities by increasing floral resource density and strategically spatially distributing host plants throughout garden beds, though these processes depend on the season. The indirect effects of soil water holding capacity on aphid densities further suggest a critical role of human management on pest populations and pest control services through soil amendments and irrigation.

Keywords: Pest control; Urban agroecosystems; Path analysis

Introduction

Drivers of trophic interactions among predators and their prey may be fundamentally different in urban ecosystems from natural systems due to the anthropogenic alteration

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of local resource availability and urban landscape structure (Shochat et al., 2010). Plant nutrient and water availability, for example, are usually heavily supplemented in cities, thus reducing resource limitation for herbivores (Raupp, Shrewsbury, & Herms, 2010). Local vegetation simplification and habitat disturbance, fragmentation, and isolation that are characteristic of urban ecosystems (Faeth, Warren, Shochat, & Marussich, 2005; Niemelä, 2011) can strongly influence organisms in higher trophic levels (Marzluff, 2001; Burkman & Gardiner, 2014) to potentially alter interactions between herbivores and plants (Nelson & Forbes, 2014).

In particular, urban agroecosystems like community (i.e., allotment) gardens offer a model system in which to examine how changes in local management factors and surrounding landscape features affect insect communities and their interactions. In contrast to other urban ecosystems like turf-grass dominated parks managed by the city or private home gardens managed by individuals, urban community gardens are unique in that they have multiple plot holders and generally have high local vegetation complexity and high diversity of management practices (Guitart, Pickering, & Byrne, 2012). Furthermore, urban agroecosystems are usually small habitats isolated from one another and from other natural habitats (Faeth et al., 2005). Moreover, ecological knowledge gained from garden studies has practical application because bans on synthetic pest control inputs (e.g., organophosphates, pyrethroids) in many community gardens require efficient natural pest control of herbivores by natural enemies for urban agricultural sustainability (Oberholtzer, Dimitri, & Pressman, 2014).

Environmental factors such as local vegetation composition and complexity, as well as the amount of impervious cover (i.e., concrete and built surfaces) in the urban landscape can directly and indirectly affect higher trophic interactions like parasitism of herbivores across spatial scales (Pereira-Peixoto, Pufal, Staab, Martins, & Klein, 2016; Fenoglio, Werenkraut, Morales, & Salvo, 2017). For example, as predicted by the *resource concentration hypothesis* (Root, 1973), high host plant density in urban yards and parks increases the likelihood of pest outbreaks by directly increasing resource availability for herbivores (Dreistadt, Dahlsten, & Frankie, 1990; Shrewsbury & Raupp, 2006; Shrewsbury & Raupp, 2000). Similarly, as predicted by the *plant stress hypothesis* (White, 1969), soil nutrient and irrigation management can indirectly affect sap-sucking herbivore populations by altering host plant quality (Mattson, 1980; Hanks & Denno, 1993). These local-level factors can also have indirect effects on herbivore populations by altering the abundance, species composition, and the foraging behavior of their natural enemies (Hanks & Denno, 1993; Shrewsbury & Raupp, 2000, 2006). For example, *sensu* the *enemies hypothesis*, natural enemies should be more abundant and herbivore regulation more effective by delivering greater pest mortality in more structurally complex habitats with, for example, diverse vegetation (Root, 1973). Indeed, parasitism in urban contexts has been shown to increase with increasing habitat complexity through greater natural enemy richness in those habitats (Fenoglio, Videla, Salvo, & Valladeres, 2013).

Likewise, landscape-level factors, such as the amount of impervious cover, may directly affect herbivores through changes to micro-climate (e.g., heat island effects) and atmospheric conditions (Newman, 2003) and habitat isolation (Turrini, Sanders, & Knop, 2016). The amount of impervious cover can also indirectly affect herbivores by altering the populations and communities of their natural enemies (Bennett & Gratton, 2012a; Burkman & Gardiner, 2014) who may differ in sensitivity to urbanization (Fenoglio, Salvo, & Estallo, 2009; Fenoglio et al., 2013). For example, landscape-level environmental factors may subsequently change natural enemy-herbivore interactions (Shrewsbury & Raupp, 2000) and natural pest control provided by natural enemies through direct predation (Philpott & Bichier, 2017) and parasitism (Pereira-Peixoto et al., 2016). In sum, herbivore populations in urban community gardens can be affected by local factors through direct effects (e.g., by changing the availability and quality of their food) or through indirect ones (e.g., by changing the abundance of their natural enemy), as well as by landscape factors through direct effects (e.g., impervious cover can hinder their colonization to and from suitable habitats) or indirect ones (e.g., impervious cover can act as a colonization barrier to their natural enemies).

The strength of these direct and indirect effects may experience seasonal changes. The abundance and diversity of arthropod natural enemies can decrease over time in response to fluctuations in precipitation and temperatures (Bolger et al., 2000), and this can affect herbivore regulation through resource availability (Faeth et al., 2005). Moreover, the seasonal fluctuations that affect population-level resource availability and environmental stressors are combined with direct effects from human activities in cities that alter resources (Faeth et al., 2005). The altered patterns in resources and stressors due to temporal change and anthropogenic change can impact ecological predictions organized around direct versus indirect effects, resource concentration versus natural enemy regulation, at local versus landscape scales in urban systems (Dale & Frank, 2014). Thus even though we are beginning to understand the local and landscape factors that regulate herbivores through parasitism in urban systems (Fenoglio et al., 2013; Pereira-Peixoto et al., 2016), we still lack an understanding of local, landscape, and temporal factors in urban agroecosystems compared to rural agricultural landscapes.

In this study we aimed to investigate how local and landscape factors directly and indirectly affect insect herbivore regulation in urban agroecosystems (community gardens). We focus on the regulation of aphid herbivores – a prevalent sap-sucking pest in gardens – through parasitism by parasitic wasps as a trophic interaction that provides pest control services. Specifically, we asked: (1) How do local garden management factors (host plant characteristics, floral resources, and soil properties) and the landscape context of gardens (amount of surrounding impervious cover) affect

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