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Urban greenspace composition and landscape context influence natural enemy community composition and function

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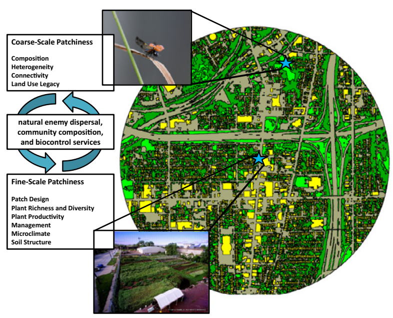
HIGHLIGHTS

- Urban greenspaces are a focus of conservation efforts targeted at beneficial arthropods.
- Greenspace composition can alter natural enemy community structure and food web dynamics.
- The spatial context of greenspace patches mediates community assembly and activity.

GRAPHICAL ABSTRACT



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ABSTRACT

Conservation research has historically been aimed at preserving high value natural habitats, but urbanization and its associated impacts have prompted broader mandates that include the preservation and promotion of biodiversity in cities. Current efforts within urban landscapes aim to support biodiversity and diverse ecosystem services such as storm water management, sustainable food production, and toxin remediation. Arthropod natural enemies provide biocontrol services important for the ecosystem management of urban greenspaces. Establishing habitat for these and other beneficial arthropods is a growing area of urban conservation. Habitat design, resource inputs, management, and abiotic conditions shape the value of greenspace habitats for arthropods. In general, larger patches with diverse plant communities support a greater abundance and diversity of natural enemies and biocontrol services, yet opposing patterns or no effects have also been documented. The surrounding landscape is likely a contributor to this variation in natural enemy response to patch-scale habitat design and management. Looking across rural–urban landscape gradients, natural enemy communities shift toward dominance by habitat generalists and disturbance tolerant species in urban areas compared to rural or natural communities. These changes have been linked to variation in habitat fragmentation, plant productivity and management intensity. In landscape-scale studies focusing solely within cities, variables such as impervious surface area and greenspace connectivity affect the community assembly of natural enemies within a patch. Given these findings, a greater mechanistic understanding of how both the composition and spatial context of urban greenspaces influence natural enemy biodiversity–biocontrol relationships is needed to advance conservation planning and implementation.

1. Introduction

Urbanization is a major contributor to native biodiversity loss (Hooper et al., 2005; McDonnell and Hahs, 2013). Urban landscapes are characterized by high levels of indigenous habitat

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fragmentation, high proportions of impervious surfaces, elevated pollution levels, and changes in local climates (such as heat island effects) relative to their surroundings (McIntyre et al., 2001). All of these factors influence the diversity, abundance, and activity of organisms found in urban areas. Traditionally conservation has focused primarily on preserving and restoring habitat within rural and natural landscapes, yet, with the Earth's surface so significantly shaped by human activity it is critical to understand how to preserve and promote species in human-dominated ecosystems such as cities (Miller and Hobbs, 2002; McDonald et al., 2008; McDonnell and Hahs, 2013; Vitousek et al., 1997). Within the last decade, the study of cities has grown from investigations of urban semi-natural areas to a focus on understanding entire cities as unique ecosystems (Humphries, 2012). Funding growth has also occurred. For example, in 2009, the US Forest Service and US National Science foundation invested $6 million USD to establish 21 Urban Long-Term Research Area Exploratory projects in cities across the US (Humphries, 2012).

A greater focus on the study and practice of urban conservation is important as many cities have been established within ecologically-important landscapes. Cities exist within riparian areas, ecological transition zones, and other species-rich locations that can represent important habitat for rare or declining species (Kuhn et al., 2004). Conservation in urban landscapes also provides the opportunity to study how environmental changes such as increased ambient temperatures will affect communities in nonurban areas. Further, as the majority of the world's people now live in cities, urban conservation also offers direct human benefits by connecting people with nature and enhancing provision of diverse ecosystem services (Dearborn and Kark, 2009).

To date, the field of landscape ecology has made fundamental advances into our understanding of pattern–process relationships. However, the field has had less impact on landscape planning and management (Nassauer and Opdam, 2008; Chisholm et al., 2014). Without understanding the mechanisms responsible for observed patterns in species abundance, richness, and activity, the results of conservation efforts are difficult to predict and hard to replicate even when desirable outcomes are achieved (Srivastava and Vellend, 2005). Urban greenspaces are highly diverse within and among cities, but generally consist of unbuilt areas that include some amount of vegetation cover such as parks, community gardens, cemeteries, playgrounds, and vacant lots. Therefore, understanding how the composition and landscape context of these varied greenspaces influence relationships between biodiversity, ecosystem functions, and ecosystem services is a critical task. An examination of arthropod natural enemies and their prey can provide significant insight into local and landscape factors that impact the structure and function of urban ecosystems. These arthropods are highly abundant, have relatively short generation times, and respond quickly to changes in the urban environment (McIntyre, 2000; McIntyre et al., 2001). In this review, we examine the theoretical basis and empirical relationships between natural enemy communities and their activity within urban greenspaces. We specifically address how plant community composition, quality and arrangement at local patch scales as well as the patch's context within the surrounding landscape influence patterns of natural enemy abundance, diversity, and biocontrol services.

2. Incorporating spatial structure to study natural enemy community composition and function

The design and dynamics of urban greenspaces are affected by both sociocultural and biophysical processes (Pickett et al., 1997, 2001, 2004, 2011). Both urbanization and deurbanization processes affect the value of urban habitats for conservation (Alberti, 2010; Gardiner et al., 2013). In growing cities, fragmentation and overall reductions in greenspace represent threats to biodiversity whereas cities that have witnessed economic and population decline are challenged with the management of a growing inventory of vacant greenspaces (Gardiner et al., 2013). Patch dynamics (Pickett and Rogers, 1997; Wu and Loucks, 1995) has become a unifying concept in landscape ecology which can be applied at multiple scales in order to study how these processes affect the spatial pattern of changing cities (Grimm et al., 2000; Pickett and Rogers, 1997; Pickett et al., 2001, 2011). Patch dynamics recognizes that a landscape is a mosaic of patches. Within this mosaic, the size, complexity and context of a patch will influence the species pool of organisms that colonize and impact ecosystem processes and services. Within an urban landscape, a patch hierarchy of fine and coarse-scale patchiness can be defined and quantified (Forman, 1995; Forman and Godron, 1986). Fine-scale patchiness encompasses microhabitat and local patch conditions such as plant species or functional trait diversity, vegetation and litter cover, soil structure or variation in temperature or relative humidity. Coarse-scale patchiness, including landscape-scale composition and habitat connectivity, is measured at larger landscapes scales and mediates the influence of fine-scale patchiness on biota by regulating the species pool of organisms supplied to a given greenspace. The change of individual patches at local scales and the pattern change in patch mosaics at broader scales give rise to system dynamics. Patch dynamics theory predicts that across scales spatial patchiness supports biodiversity and generates and controls fluxes of materials, energy, organisms and information through the environment (Pickett and Rogers, 1997; Wiens, 1992; Wiens et al., 1985).

Urban ecosystem management aims to apply our understanding of these relationships to support diverse ecosystem functions and services in cities. Many urban greenspace revitalization projects aim to enhance biodiversity across trophic levels. An assumption driving these projects is that establishing diverse plant communities to enhance fine-scale patchiness will support greater richness at higher trophic levels and enhanced ecosystem functions and services. This follows the Biodiversity–Ecosystem Function Hypothesis, which states that enhancing biological diversity (species, genotypes, etc.) supports increased ecosystem processes (Srivastava and Vellend, 2005). A significant body of research has tested this hypothesis (Hooper et al., 2005; Naeem et al., 1994; Loreau and Hector, 2001; Loreau et al., 2001). These studies began with plants (Hooper et al., 2005; Tilman, 1999; Tilman et al., 1997) and expanded to measure how entire food webs mediate ecosystem functions (Cardinale et al., 2006; Duffy et al., 2007). A correlation has emerged illustrating that species diverse communities produce more biomass and utilize a greater proportion of available resources than single species (Cardinale et al., 2006; Duffy et al., 2007). However, experiments examining predator and parasitoid biodiversity–ecosystem function relationships indicate high variation in the relationship between natural enemy diversity and prey capture (Bruno and Cardinale, 2008; Cardinale et al., 2003; Downing and Leibold, 2002; Duffy, 2002; Hawkins et al., 1992; Long et al., 2007;). In general, natural enemy richness is positively related to their total density; yet richness has been shown to both reduce (Finke and Denno, 2004) and strengthen (Finke and Snyder, 2008; Snyder et al., 2006) resource capture of prey. Why are these biodiversity–ecosystem function relationships less predictable? This may be due to different interactions mediating the impacts of natural enemy versus plant richness on ecosystem function (Bruno and Cardinale, 2008; Ives et al., 2005). Indirect and non-additive interactions such as facilitation and intraguild predation occur much more commonly among predators and parasitoids (Cardinale et al., 2003; Finke and Denno, 2002; Losey and