



Local habitat characteristics but not landscape urbanization drive pollinator visitation and native plant pollination in forest remnants



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ABSTRACT

Habitat loss from urban development threatens native plant populations in many regions of the world. In addition to direct plant mortality, urban intensification potentially impacts pollinator communities and in turn disrupts the pollination mutualisms that are critical to the viability of native plant populations. We placed standardized flowering plant arrays into woodlands along a gradient of increasing urban land use to simultaneously quantify landscape-scale and local-scale effects on pollinators and on reproduction of two spring ephemeral wildflowers (*Claytonia virginica* and *Polemonium reptans*) in woodland fragments in the Mid-Atlantic Region of North America. Greater pollinator abundance and associated diversity significantly reduced the degree of pollen limitation, demonstrating that pollinator populations are critical to successful pollination of these plant populations. However, landscape-scale habitat loss did not reduce pollinator abundance or diversity. Habitat loss at the landscape scale therefore does not appear to drive changes in pollination in this woodland system. Rather, local-scale habitat characteristics were more important, with pollinators being more abundant in brighter woodland patches for one plant species, and in larger patches for the other species. Because we found abundant pollinators and adequate pollination even in isolated, urban woodland fragments, our results are encouraging for the conservation of both plants and pollinators in urban landscapes.

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1. Introduction

Pollination is a critical ecological function in natural and managed systems worldwide (Klein et al., 2007). An estimated 85% of angiosperm species depend on animal pollination (Ollerton et al., 2011) making it fundamental to the persistence of natural plant populations as well as to crop production. However, habitat loss and fragmentation from agricultural intensification and urban expansion threaten pollinators and diminish pollination on which plant populations and functioning ecosystems depend (Kremen et al., 2007; Williams et al., 2010; Winfree et al., 2009).

Landscape-scale effects such as isolation from natural habitat reduce pollinator abundance, diversity and pollination (Ricketts et al., 2008; Winfree et al., 2009), and have been the focus of most recent research. However, local habitat quality can mitigate the effect of landscape change (e.g., Concepcion et al., 2012; Kleijn and van Langevelde 2006; Rundlof et al., 2008), and local scale qualities such as plant density, patch size, perimeter length may have different effects on pollinator's populations and their behavior than those operating at the landscape scale (Hadley and Betts, 2012). In addition, much of what we know about the effects of landscape

change on pollination is based on studies of crop plants, set within agricultural landscapes (Ricketts et al., 2008). However, this knowledge may not be easily transferable to wild plants within habitat fragments because the spatial configuration and characteristics of habitats are often qualitatively different for crops versus for native vegetation. As a result, both pollinator community responses and foraging behavior may differ between the two contexts leading to differential effects of habitat loss on pollination (Cane et al., 2006; Krewenka et al., 2011; Ries and Debinski, 2001; Slagle and Hendrix, 2009). Studies of remnant plant populations and their pollinator communities are needed to understand the impacts of habitat loss on these interactions and the implication for conservation.

Numerous studies have quantified the effects of habitat loss and fragmentation on plant reproduction (reviewed in Aguilar et al., 2006), and a growing number of studies document the impact of land-use changes on pollinator communities (Winfree et al., 2011). Few studies, however, have simultaneously quantified the effects of habitat loss on pollinator communities and the resultant effects on reproduction of native plants (but see Aizen and Feinsinger, 1994; Gonzalez-Varo et al., 2009; Jennersten, 1988; Slagle and Hendrix, 2009; Verboven et al., 2012). Such simultaneous investigation provides a way to partition direct effects of habitat loss on plant reproduction from indirect effects operating through

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changes to pollinator communities and the pollination process (Aguilar et al., 2006; Kremen et al., 2007). Habitat loss can directly impact plant reproduction via limitation of seed set post-pollination (e.g., reduced nutrients or moisture in fragments). Indirect effects acting through changes to pollinator communities and their visitation patterns in response to habitat loss can decrease pollination success by reducing the quantity or quality of pollen transferred or altering plant mating patterns (Aizen and Harder, 2007; Knight et al., 2005; Ward and Johnson, 2005; Washitani et al., 1994; Cheptou and Avendano, 2006). Some effects, such as reduction in plant population size may have direct and indirect effects on pollination, either by limiting the number of pollen donors and compatible mating (Aizen and Harder, 2007; Wolf and Harrison, 2001), or altering pollinator visitation (reviewed in Ghazoul, 2005). All of these changes have implications for the long-term fate of native plant populations in fragmented landscapes.

Urban, suburban and exurban expansion are primary drivers of habitat loss and fragmentation and continue at a rapid pace throughout North America (Loveland and Acevedo, 2011; Theobald, 2005); however, relatively little is known about the persistence of pollinators or pollination function in such built landscapes as compared to in agricultural landscapes (Cussans et al., 2010; Verboven et al., 2012). Some studies have found that the diversity and abundance of pollinating insects decreases along rural to urban gradients (Ahrne et al., 2009; Rodrigues et al., 1993). However, sensitivity to urbanization varies among species (Osborne et al., 2008; Rodrigues et al., 1993), and some bee species are equally or more abundant in natural vegetation fragments within urban landscapes compared to extensive natural areas (Cane et al., 2006; McFrederick and LeBuhn, 2006; Osborne et al., 2008). Furthermore, although negative effects of urbanization on pollinators have been found in tiny isolated plant populations within an urban matrix (e.g., Cheptou and Avendano, 2006), the impact can be minimal or even positive where the urban matrix is less hostile to pollinators (Cussans et al., 2010; Verboven et al., 2012). In such cases urbanization might represent habitat change rather than habitat loss. As a result, effects of urbanization on pollinators and concomitantly on native plant pollination are difficult to predict, and may not be entirely negative (Matteson and Langellotto, 2010).

To simultaneously measure pollinator activity and the extent to which insufficient pollination reduces plant reproduction along an urbanization gradient, we used a phytometer experiment in which we placed standardized arrays of spring wildflowers within woodland habitats that differed in the extent of forest cover versus urban land cover in the surrounding landscape, and also in local habitat variables such as woodland fragment size. This experimental approach allowed us to control the direct effects of landscape change on native plant reproduction, in order to better isolate the indirect effects as mediated by pollinators. We used a path analysis framework to test the following hypotheses: (1) landscape-level loss of habitat negatively affects pollinator communities; (2) changes to local habitat quality associated with fragmentation negatively affect pollinators; (3) reduction of pollinator abundance and species richness decrease pollination and plant reproduction; (4) reduced plant population size in fragments decreases plant reproduction directly, or indirectly through changes in pollinator communities.

2. Methods

2.1. Study system and sites

The study was carried out in the Northeastern Coastal Forest ecoregion (further described in Ricketts et al., 1999) in the

vicinity of Philadelphia, Pennsylvania, USA. Native habitats consist primarily of deciduous hardwood woodlands. This region has among the highest human population density in the USA, and continued development around major cities has converted agricultural and woodland habitat to exurban, suburban, and commercial land use that threatens endemic biodiversity (Ricketts and Imhoff, 2003). Although agriculture, not suburban development, was the original driver of forest fragmentation (Matlack, 1994), woodland fragments now exist within a landscape dominated by urban, suburban and agricultural land.

We measured pollinators and plant reproduction of two native spring wildflower species, *Claytonia virginica* and *Polemonium reptans* (hereafter *Claytonia* and *Polemonium*). Both species have generalized/actinomorphic flowers and are dependent on insect pollinators for successful reproduction (Motten, 1986, NMW unpublished). Our experimental design controlled for variation in plant genetic background and condition, edaphic factors and moisture for both species. Plants were grown in pots containing a standard soil mixture and placed in a common garden within a natural woodland until the experiment. *Claytonia* tubers were obtained in the winter from three local populations, and *Polemonium* plants were purchased from four different wildflower preserves the previous season. Plants from the different source populations were assigned randomly to sites to ensure a diverse but consistent genetic background among arrays. During the experiment, plants were uniformly watered across all arrays. At the end of the field study for each plant species, all plants were returned to the common garden to complete seed development.

We selected 21 study sites such that all were within mature, relatively undegraded woodland habitat, but the land cover surrounding each site at a 1 km radius varied from 2% to 78% woodland with the remainder being predominantly suburban and urban development. To avoid confounding effects of agricultural habitat we selected sites that fell primarily along a gradient of wooded to developed land (agricultural land cover surrounding most of the study sites varied from 0% to 6%, with the exception being three sites with 20%, 21%, and 35% agricultural cover within 1 km). Tree communities were dominated by *Liriodendron tulipifera*, *Quercus* spp. and lesser numbers of *Acer platanoides*, *Acer rubrum* and *Fagus grandifolia*. All study sites were at least 1.1 km apart, with all but one pair separated by >2.1 km, and a median inter-site distance of 16.4 km.

To standardize microsite environment among sites, plants of both species were placed in standardized potted arrays within a light gap, such that the experimental plants would receive direct sun for at least part of the day even after trees had leafed out. Nonetheless, mean light level at the plant array ranged from 450 to 1500 mmols m⁻² s⁻¹ PAR. The spatial extent, 4 m², and density of flowers within the potted arrays were standardized among all sites. Most arrays contained ten 8 L pots of each species, although at some sites an extra pot was added to equalize flower density. The two species flowered sequentially. *Claytonia* pots contained 5–7 flowering stems for a total of 40–70 total flowers per array, followed by *Polemonium* for which pots contained single large plants with 20–30 open flowers for a total of 160–200 flowers per array. Nearly all sites had natural populations of *Claytonia* growing within 50 m of the array. The estimated number of *Claytonia* inflorescences within 100 m of the array ranged from 0 to ~10,000 among sites, and this number was uncorrelated with area of woodland at local or landscape scales ($r = 0.06, -0.07$). In contrast, although *Polemonium* existed at several of our sites based on historical records, it is now largely extirpated in our study area. Only two individual plants were found at a single study site and these were located over 100 m from the study array.

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