



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



Neal M. Williams^{a,*}, Rachael Winfree^b

^a Department of Entomology, University of California, 1 Shields Ave., Davis, CA 95616, United States

^b Department of Ecology, Evolution and Natural Resources, The State University, 119 Blake Hall, 93 Lipman Dr., Rutgers, New Brunswick, NJ 08901, United States

ARTICLE INFO

Article history:

Received 20 September 2012

Received in revised form 19 December 2012

Accepted 23 December 2012

Keywords:

Bees

Habitat loss

Land transformation

Pollen limitation

Urbanization

Woodland

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.

© 2013 Elsevier Ltd. All rights reserved.

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

* Corresponding author. Tel.: +1 530 752 9358; fax: +1 530 752 1537.

E-mail address: nmwilliams@ucdavis.edu (N.M. Williams).

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.

2.2. Pollinator visitation

We monitored insect flower visitors at the arrays of each focal plant species during peak bloom at each of the sites (*Claytonia* at 21 sites April 29–May 7; *Polemonium* at 19 of the 21 sites May 7–May 15). The number and identity of insects visiting female-phase flowers were recorded for each plant species on a single day at each site. Insects were considered to visit only if they made contact with sexual parts of the flower for >0.5 s. Observation was divided into twelve 5-min sample periods spread throughout the day. During each 5-min sample, observers also recorded the number of flowers watched ($n = 6–17$). From these data we calculated visitor rate, the number of visitors per flower per minute, and used this as our standard measure of abundance. Temperature, wind speed and light level were measured at each site at the start of observations and then after every fourth observation period. We measured light level at four points across the array at each recording event and then calculated average light intensity throughout the sampling day. Flower visitation data were collected only on days where temperatures exceeded 14.5 °C, wind speed was less than 2 m/s at 1 m above ground level, and skies were sunny or brightly overcast. We identified insects to a predetermined set of species and morpho-species during the observation periods and vouchered specimens to check species-level identification at the end of the day's observation periods (Table A1).

2.3. Pollination

We measured reproductive success for both target plant species in each site as the degree of pollen limitation $(S-O)/S$, where O is the mean number of seeds per fruit in un-manipulated open pollinated flowers, and S is the mean number of seeds per fruit in flowers that were open pollinated and then supplemented to saturation with pollen from three separate donor plants. To capture the pollination environment on the day we observed visitor communities, hand-supplemented pollination was completed at the end of the day's observation for each site, at which time we individually tagged un-manipulated and supplemented flowers. For *Claytonia*, we hand-pollinated the youngest female-phase flower on each of eight plants and paired each to a similar un-manipulated female flower on another plant within the same pot. For *Polemonium*, un-manipulated and supplemented flowers were on the same plant in each of eight pots. Although the ideal test of pollen limitation is to apply open and supplemented treatments to entire plants (Knight et al., 2006), thus controlling for potential resource re-allocation, our design targeted comparisons among sites and thus assessment of relative (not absolute) levels of pollination limitation. At the conclusion of the field study, we moved plants to a common garden until harvesting of mature fruits. Seed set was scored in the lab using a dissecting microscope to distinguish mature versus aborted seeds.

2.4. Landscape analysis

We used Arc GIS 9.2 (Environmental Systems Research Institute, Redlands, CA, USA) to analyze the landscape composition surrounding each study site. Land-use data were provided by the Delaware Valley Regional Planning Commission and had been digitized from aerial images taken in 2000. We simplified the 16 original land-use classes from that database to open water, woodland, agriculture, and developed (which contained suburban, urban, commercial classes; Table B1). Because our focus was on woodland plant species, we used proportion of woodland surrounding each site as our metric of landscape context. To determine the most appropriate scale for landscape analysis we first tested the effect on pollinator abundance of proportion woodland habitat in areas of increasing radius (500 m, 1000 m, 1500 m and

2000 m). R^2 values peaked at 1000 m; thus 1000 m was used as the spatial scale in subsequent landscape-scale analyses (see Steffan-Dewenter et al., 2002). We also calculated the proportion of woodland within 200 m and used this as a measure of local-scale woodland area. We used this approach rather than directly using contiguous patch area because in our study system, woodland patches are often oddly shaped such that measurements of continuous patch area resulted in inclusion of long fingers of woodland far beyond the flight radius of bees that would be visiting our arrays.

2.5. Statistical analysis

We used path analysis to quantify the different effects of habitat loss at landscape and local scales on pollination operating through changes to floral visitor abundance and diversity, as well as direct and indirect effects acting through differences in plant population size (Mitchell, 2001). Although it cannot be used to prove causation, path analysis identifies correlations among variables within a mechanistic path. Previous studies of biodiversity and landscape change have tested individual links in our overall path model, including the effects of landscape composition/isolation (Kremen et al., 2004; Ricketts et al., 2008), light level (Kilkenny and Gallo-way, 2008), and patch size on pollinator visitation (Slagle and Hendrix, 2009), as well as visitor abundance on reproductive success (Slagle and Hendrix, 2009; Steffan-Dewenter and Tschardt, 1999). Results of these previous studies support the a priori mechanistic hypotheses included in our path diagram.

Our replication at the landscape scale was necessarily limited; therefore we tested a single model (Fig. 1) that posits indirect effects of landscape (proportion of woodland at a 1 km radius) and local site characteristics (woodland area at 200 m, light level and

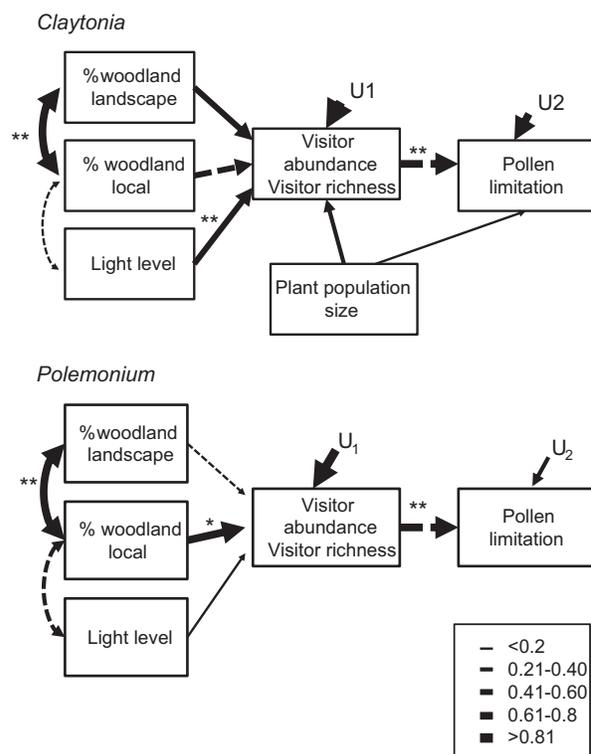


Fig. 1. Path models of landscape and local-scale effects of habitat loss on visitor abundance and pollination on (A) *Claytonia* and (B) *Polemonium*. Dashed arrows represent negative effects. Significance of effects, $P < 0.05 = *$, $P < 0.01 = **$.

plant population size) on pollen limitation acting through variation in visitor abundance and morpho-group richness, as well as direct effects of plant population size (number of *Claytonia* plants within 100 m) for *Claytonia*. Models for *Polemonium* did not include conspecific population size as a predictor variable because the only plants in the populations were those in our arrays and their number varied minimally among arrays. Path analysis was performed with SAS Proc CALIS (SAS STAT 9.3, 2009). Preliminary analysis showed that, as is commonly the case for pollinator communities (e.g. Kremen et al., 2002; Winfree et al., 2008), abundance and visitor species richness were strongly correlated (*Claytonia*, $r = 0.82$, $n = 21$, $P < 0.01$; *Polemonium*, $r = 0.81$, $n = 13$, $P < 0.01$). We ran separate analyses with each variable, but the two sets of results should not be interpreted as fully independent (Hoehn et al., 2008).

We screened for collinearity among predictors by examining variance inflation factors (VIF option of Proc REG, SAS STAT 9.3, 2009; Irwin, 2006). Local-scale woodland and proportion woodland at a landscape scale were correlated (*Claytonia*, $r = 0.77$; *Polemonium*, $r = 0.84$), but VIF values were moderate (*Claytonia*, 3.6 and 3.3; *Polemonium*, 2.2 and 2.4). Although this indicates that some imprecision may exist in path coefficients, it is not unreasonably large; for example, Quinn and Keough (2002) suggest values of 10 or more are a problem. VIFs for other predictor variables were less than 1.3.

To test for local and landscape effects on the composition of insect visitor communities at floral arrays we first ordinated floral visitors of each plant species and site using Non-metric Multi-Dimensional Scales (NMDSs) based on relative Sørensen distances to create a two-dimensional representation (Table D1; R 2.14.1 vegan package; Oksanen et al., 2011). We used a maximum of 20,000 random iterations with acceptable stress < 0.15 . We then tested for the relation of each landscape and local-scale predictor to the composition of flower-visitor communities among sites using a multivariate correlation analysis that partitions the linear component of each predictor on final NMDS axes (envfit R 2.14.1, Oksanen et al., 2011). Given low-stress solutions in the NMDS, this approach provides a metric of the effect of the predictors on community composition (Table D1). This analysis was based on morpho-species (Table A1).

3. Results

Visitor abundance and associated species richness strongly benefited pollination of both plant species. Pollen limitation in standardized arrays was significantly lower at those arrays that had more abundant and speciose flower visitors (Figs. 2 and 3, Table C1). However, although visitor abundance and richness varied dramatically among sites (*Claytonia*, < 0.001 –1.6 visitors per flower per hour, 1–5 species per hour; *Polemonium*, 0.05–1.8 visitors per flower per hour, 1–8 species per hour), neither variable was significantly affected by landscape context, measured as percent woodland within 1000 m, for either *Claytonia* or *Polemonium* (Figs. 4 and 5; Table C1). Only patch-level characteristics significantly affected pollinator visitation. Floral visitors of *Claytonia* were more abundant at arrays with higher light levels (Fig. 4; Table C1). *Polemonium* visitors were more abundant at arrays located at sites with more woodland at the local scale (percent woodland within 200 m; Fig. 5). Patterns for species richness mirrored those for visitor abundance, but were not significant for either effect. *Claytonia* population size did not significantly affect visitor abundance or diversity (Table C1).

The composition of pollinator communities visiting the arrays was significantly affected only by local-scale environmental factors and only for visitors of *Claytonia*. The proportion of woodland hab-

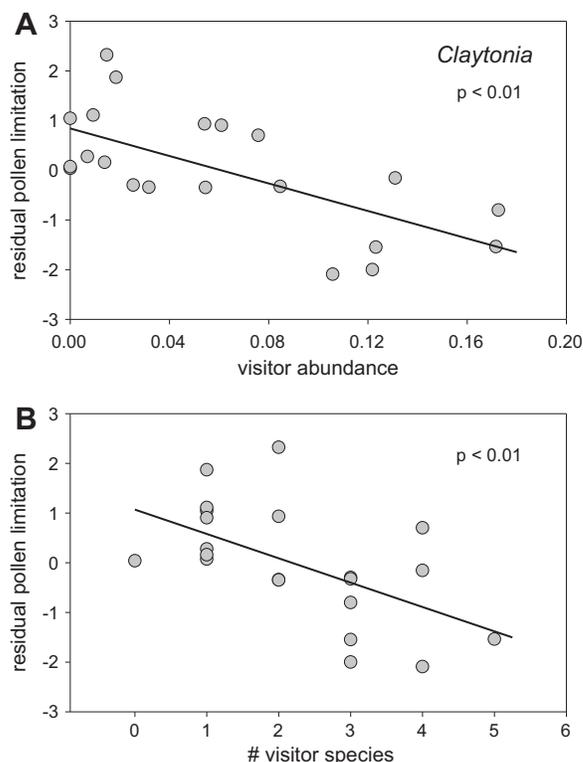


Fig. 2. Pollen limitation in *Claytonia* as a function of visitor (A) abundance and (B) richness. Y axis values are residuals from analysis of pollen limitation as a function of local and landscape variables allowing for visualization of the effects of floral visitors on pollination function.

itat in the landscape (1000 m radius) surrounding the study site did not significantly affect the composition of flower-visitor communities at either target plant species (*Claytonia* $r^2 = 0.22$, $p = 0.13$; *Polemonium* $r^2 = 0.04$, $p = 0.82$). Local-scale woodland area affected the composition of flower visitors at *Claytonia* arrays ($r^2 = 0.35$, $p = 0.04$), but not at *Polemonium* arrays ($r^2 = 0.01$, $p = 0.98$). Specifically, of the three taxa that dominated visitation to *Claytonia*, *Bombylius major* increased with local-scale woodland area, whereas *Lasioglossum (Dialictus)* spp. and *Andrena erigeniae* showed little change (Fig. 6). Other visitor species each occurred at only 1–3 sites and were thus too rare to confidently assess individual responses among sites. Although light level was important for determining abundance of flower visitors, it did not affect the composition of these visitor communities for either plant species (*Claytonia* $r^2 = 0.24$, $p = 0.11$; *Polemonium* $r^2 = 0.07$, $p = 0.71$). *Claytonia* abundance did not significantly affect composition of its flower visitor community ($r^2 = 0.30$, $p = 0.1$).

4. Discussion

Pollinator decline leading to increased pollen limitation is a primary mechanism through which habitat loss is posited to reduce native plant reproduction. Here, we simultaneously explored the effects of habitat loss caused by human activities on native pollinator communities, and on the pollination of two spring wildflowers, to quantify the effect of landscape change on plant reproduction acting through disruption of the pollination mutualism. We considered landscape and local factors to better understand the scale at which potential drivers most strongly affect pollinators and pollination.

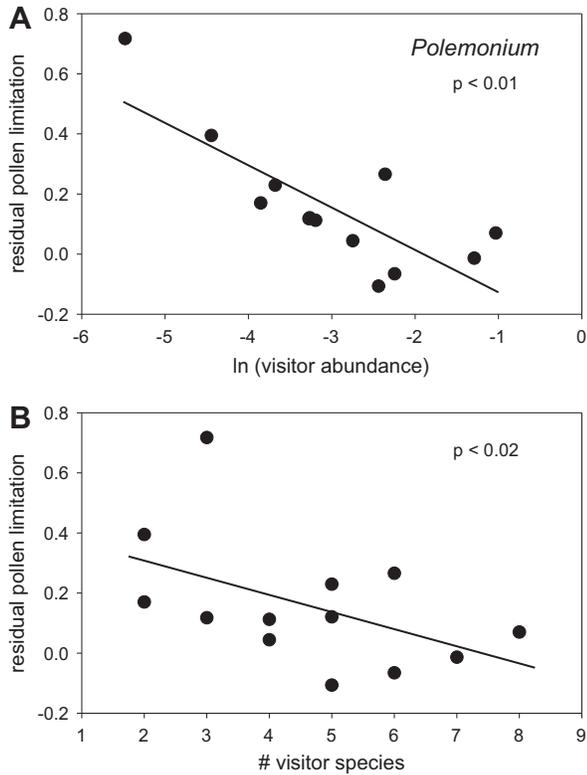


Fig. 3. Pollen limitation in *Polemonium* as a function of visitor (A) abundance and (B) richness. Y axis values are residuals from analysis of pollen limitation as a function of local and landscape variables allowing for visualization of the effects of floral visitor on pollination function.

4.1. Effects of pollinators on pollination

The abundance and correlated diversity of flower visitors were critical for successful plant reproduction. Seed set of *Claytonia* and *Polemonium* were significantly less pollen limited at sites with more abundant and speciose visitors at the study arrays. In addition, pollen limitation did not appear to be the result of plant population size for *Claytonia*, the one species for which we could test this effect. This result suggests seed set was not limited by a lack of genetic diversity or compatible mating partners (Aizen and Harder, 2007; Wagenius and Lyon, 2010; Wolf and Harrison, 2001) and reinforces the importance of abundant pollinators for successful reproduction. Investigation of endemic populations would be valuable nonetheless to explore the potential for genetic effects of woodland fragmentation on spring wildflower populations. Several other recent surveys have found similar patterns, where pollen limitation was greatest at sites with low visitor numbers and visitor diversity (Gomez et al., 2010; Gonzalez-Varo et al., 2009; Knight et al., 2005). As such our results support the role of biodiversity for ecosystem functioning and pollination in particular.

4.2. Landscape effects on pollinators

Despite substantial variation in pollinator abundance and diversity among sites and the critical role of these for pollination, landscape-scale habitat loss did not consistently affect pollinator community abundance, richness or composition. As a result, there was no one causal path linking landscape-scale change to pollinators and then to pollination. The lack of landscape-scale effect likely reflects a combination of factors. First, nearly all of the polli-

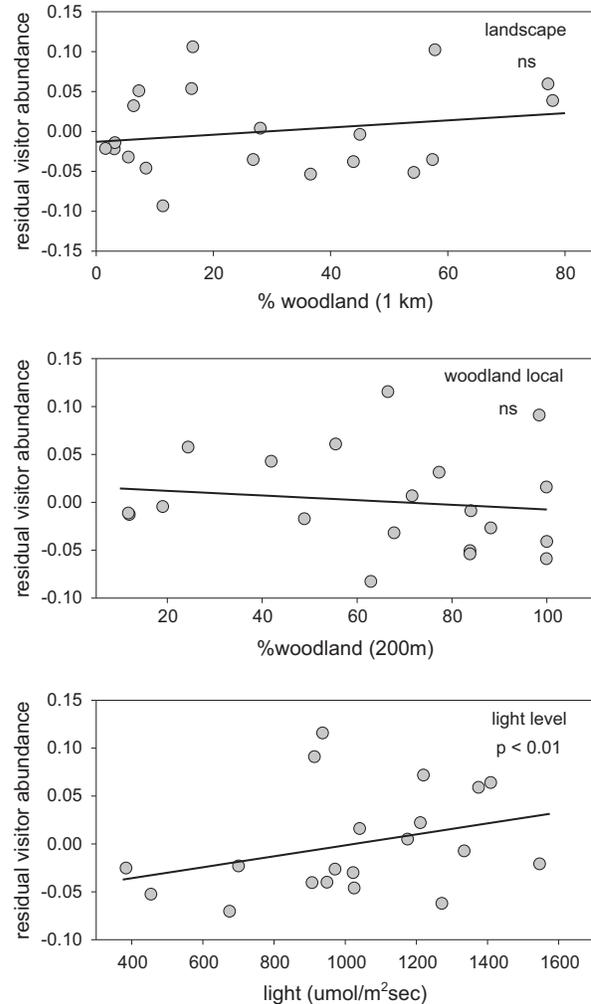


Fig. 4. Effects of landscape-level and local site factors on visitor abundance to *Claytonia* arrays.

nator species we observed were small vernal bees and flies with typical flight ranges of tens to a few hundred meters (based on body size, Greenleaf et al., 2007). Small body size combined with the relatively abundant floral resources from trees, shrubs, and forbs when *Claytonia* and *Polemonium* are blooming (Hightshoe, 1988), likely allow individuals to persist even in modest-sized woodland fragments during the spring (Müller et al., 2006). Such persistence would lead to weaker effects of habitat loss at the landscape scale and a stronger effect of local habitat area. Second, the quality of the matrix relative to the natural habitat it replaces moderates the effect of land-use change on pollinator populations (Holzschuh et al., 2010; Rundlof et al., 2008; Winfree, 2010). Other studies have found strong landscape-level effects where the quality of local habitat and matrix are relatively poor compared to natural habitats (Holzschuh et al., 2010; Kleijn and van Langevelde, 2006). In our study, the matrix was dominated by suburban and non-industrial urban areas, which in other regions have been shown to have abundant and diverse flower resources from gardens, parks and semi-natural habitats that support bee populations (Goulson et al., 2002; McFrederick and LeBuhn, 2006; Osborne et al., 2008; Tommasi et al., 2004). Resources from these surrounding habitats may have subsidized the forage used by insect pollinators within woodland fragments. Thus although woodland habitat was lost, it was in some cases replaced by relatively good habitat for bees

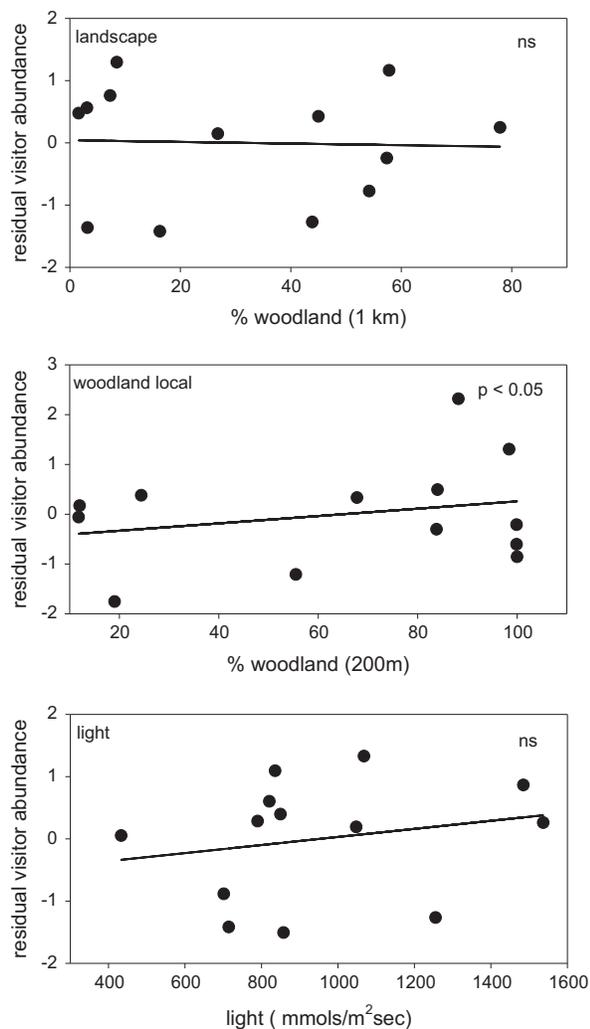


Fig. 5. Effects of landscape-level and local site factors on visitor abundance to *Polemonium* arrays.

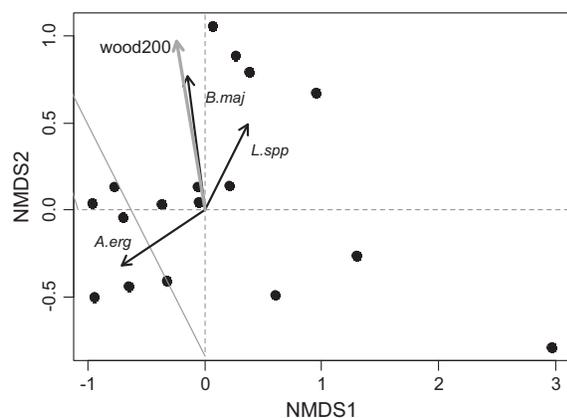


Fig. 6. Ordination of bee communities visiting *Claytonia* arrays (black circles), and the environmental vector for local-scale woodland area (Wood 200) plotted in the same two-dimensional space. Vectors for the three common morpho-species are plotted (*A. erg* = *Andrena erigeniae*, *L. spp* = *Lasioglossum Dialictus* sp., *B. maj* = *Bombylius major*). *Bombylius major* increases in the same direction as the environmental vector; however, both *A. erigeniae* and *Lasioglossum* sp. are nearly perpendicular to the direction of the environmental vector, indicating little change with local area of woodland.

and floral resources. Urbanization here may represent a habitat change rather than a clear loss. In addition, although one of our dominant pollinators was a fly (*Bombylius major*), its response to land use is tied to that of bees because it parasitizes them in its larval stage. Third, the pollinator communities we studied may have been filtered historically by the loss and conversion of woodland to agriculture. Forest in the Mid-Atlantic region was cleared for agriculture over a century ago and existing woodland fragments including those in urban landscapes are mostly secondary regrowth. This historic land transformation may have removed the pollinator species that cannot persist in fragmented landscapes. Such filtering is well documented for plant species within post-agricultural fragments (Vellend, 2004; Whitney and Foster, 1988). Although this question has rarely been investigated in bee communities, in other work in the Mid-Atlantic we have found that most bee species persist well with increasing forest loss, but a minority of species do not (Winfree, 2007).

4.3. Local-scale effects on pollinators

Local-scale habitat qualities better predicted pollinator abundance and diversity in our study than did landscape context. Pollinators were more abundant at *Claytonia* arrays in brighter locations. Light level at flowers is known to affect bee visitation (Kilkenny and Galloway, 2008), and is especially relevant for small species, which seek bright spots within forests (Herrera, 1995). The stronger effect of light environment on visitation to *Claytonia* than to *Polemonium* is consistent with its earlier flowering date. Air temperatures were much cooler during the weeks when *Claytonia* was blooming. At these times, radiant heat from sunlight may be particularly important to bees and other flower visiting insects for maintaining activity (Herrera, 1997; Schemske et al., 1978). For *Polemonium*, pollinators were more abundant at arrays in larger woodland fragments, although the local-area effect was highly variable. The effects of local-scale woodland area may have been weaker for *Claytonia* than for *Polemonium*, because *Claytonia* grows at woodland edges and clearings as well as inside woodlands. Its pollinators may move more readily into and out of woodland habitats, and their populations may be less tied to the area of local woodland.

For the pollinators of both plant species, the greater impact of woodland area at the local compared to the landscape scale likely reflects the smaller spatial scale over which the small-bodied pollinators in our system forage and disperse. The stronger effect of local-scale habitat factors that we found is particularly noteworthy because landscape-scale factors have been given greater attention in many studies of pollinator response to anthropogenic disturbance (reviewed in Winfree et al., 2011). However, a recent synthesis of how pollinators and crop pollination are affected by agricultural land transformation explicitly compared local- to landscape-scale effects, and found that local habitat factors were more important (Kennedy et al., in press), which is consistent with the results we report here.

Unlike some recent investigations of pollinator responses to landscape change (Aizen and Feinsinger, 1994; Cane et al., 2006; Carre et al., 2009; Verboven et al., 2012; Williams et al., 2010; Winfree et al., 2009), we did not find substantial differences in responses among pollinator species and as a result no strong shifts in community composition. Habitat loss might be expected to more strongly affect specialist bee species that rely on pollen from a single plant taxon, as has been documented for other trophic specialists in certain bee clades (Goulson et al., 2005; Kleijn and Raemakers, 2008). The sole specialist in our study, *A. erigeniae*, an oligolege of *Claytonia*, was only modestly affected by woodland area at a local scale and was, surprisingly, not affected by *Claytonia* population size. Instead it was most abundant where light levels

were highest, a pattern also seen in the generalist bees. Overall the composition of morphospecies visiting arrays matched our expectation based on our previous surveys of natural plant populations and previous research with *Claytonia* (Winfree et al., in preparation; Motten, 1986).

4.4. Conclusions—urbanization and the pollination of remnant plant populations

Urban development threatens many aspects of native biodiversity and associated ecosystem functions (Hahs et al., 2009; McKinney, 2006). However, against this general pattern, many native bee species do well in exurban and some suburban landscapes (Winfree et al., 2011), and the limited data on pollination vary from negative to positive effects of development. Those studies that report dramatic changes to pollinator communities and negative effects on plant reproduction tend to focus on tiny plant populations in fragments that would not support pollinators (e.g. Cheptou and Avendano, 2006), whereas those studies that report neutral or positive effects are in landscapes that have some habitats for pollinators (e.g., Cussans et al., 2010; Van Rossum, 2010; Verboven et al., 2012). Our own study falls in the latter category where pollination of spring wildflowers within fragments of native woodland appears to be relatively robust to changes in surrounding landscape.

Taken together, the significant relationship between diversity of pollinators and pollination function and the lack of a strong effect of woodland loss and associated fragmentation on pollinator communities have important implications for native plant populations and their floral visitors in fragmented landscapes. Seed set is an incomplete proxy for plant fitness (Gomez et al., 2010; Herrera, 2000) and is only one factor of many affecting plant population dynamics (Price et al., 2008). Nonetheless, it is likely that the loss of pollinators would dramatically reduce plant reproduction and impact long-term persistence of these plant populations. At the same time, it is encouraging for conservation that urban land-use at the landscape scale does not appear to negatively affect these spring wildflowers through pollination. The stronger effect of local-scale environment on pollinators also emphasizes the potential for site-level management as a tool to bolster pollinators and plants (Matteson and Langellotto, 2010). This is an encouraging outlook for conservation, because site-level management, such as improving habitat within private yards, parks, and municipal right of ways, is the scale of land use control within most cities and is thus a more tenable management option as compared with landscape-scale restoration.

Table A1

Species observed visiting *Claytonia* and *Polemonium* arrays with percentages of total visitors of each morpho-group. Data for each plant are summarized separately. “p” indicates the species was present and also part of the % calculated for the morpho-group. Identifications are based on vouchering at the end of observation periods.

Visitor morpho-group	Visitor species	<i>Claytonia virginica</i>	<i>Polemonium reptans</i>
Apoidea (bees)			
<i>Small Andrena</i>	<i>Andrena erigeniae</i>	42	
<i>Medium Andrena</i>	2 spp (no vouchers)	1.5	10.0
<i>Augochlora (green bee)</i>	<i>Augochlora pura</i>		19.5
<i>Ceratina</i>	<i>Ceratina calcarata</i>	1.5	17.5
	<i>Ceratina stearnsii</i>		p
<i>Lasioglossum (Dialictus)</i>	<i>Lasioglossum nr obscurum</i>	32.5	27.0
	<i>Lasioglossum sp.2</i>		p
<i>Halictus</i>	<i>Halictus sp. (no voucher)</i>		3.5
<i>Nomada</i>	<i>Nomada luteoloides</i>	4	2.5
	<i>N. form H</i>	p	
	<i>N. form K</i>	p	
<i>Osmia 2 sp.</i>	(no voucher)		5.5
Diptera (flies)			
<i>Bombylius</i>	<i>Bombylius major</i>	13	8.5
<i>Tachinidae</i>	(no voucher)	3.5	0.5
<i>Syrphidae</i>	(no voucher)	2	0.5

Table B1

Translation of original land classes from Delaware Valley Regional Planning Commission 2000 to those used to assess landscape context along woodland-urban gradient.

	DVPC land class	Simplified land class
1	Agriculture	Agriculture
2	Woodland	Woodland
3	Water	Water
4	Commercial	
5	Community services	
6	Manufacturing: light industrial	
7	Mining	
8	Parking	
9	Recreation	
10	Residential: mobile home	Developed
11	Residential: multi-family	
12	Residential: row home	
13	Residential: single-family detached	
14	Transportation	
15	Utility	
16	Vacant	

Acknowledgements

Lisa Mandel, Alison Parker, and Caroline Polger provided excellent assistance in field and lab. Jessica Forrest and Sandra Gillespie and three anonymous reviewers provided very helpful comments on the manuscript. Research was supported by NSF DEB0516205 and Bryn Mawr College.

Appendix A

Flower visitor species .

Appendix B

GIS Land Classification Summary and Supplemental Analysis of Urban (Developed) land class based on quality for native bees and other insect flower visitors .

Appendix C

Path coefficients .

Table C1

Table of path coefficients from best-fit path models.

Path	Spatial scale of effect	Coeff.	SE	P value
<i>Claytonia</i>				
<i>Visitor abundance</i>				
Visitor rate ^a –pollen limitation	Local	–0.68	0.12	<0.01
Plant population size–pollen limitation	Local	–0.09	0.17	ns
% Woodland (1000 m)–visitor rate	Landscape	0.55	0.32	ns
% woodland (200 m)–visitor rate	Local	–0.41	0.40	ns
Light level–visitor rate	Local	0.34	0.03	<0.01
Plant population size–visitor rate	Local	0.32	0.27	ns
<i>Visitor richness</i>				
Visitor richness–pollen limitation	Local	–0.58	0.15	<0.01
Plant population size–pollen limitation	Local	–0.18	0.18	ns
% Woodland (1000 m)–visitor richness	Landscape	0.39	0.35	ns
% Woodland (200 m)–visitor richness	Local	–0.22	0.43	ns
Light level–visitor richness	Local	0.24	0.22	ns
Plant population size–visitor richness	Local	0.08	0.30	ns
<i>Correlation among predictors^b</i>				
% woodland (1000 m)–% woodland (200 m)	Landscape–local	0.77	0.09	<0.01
% woodland (200 m)–light level	Local–local	–0.14	0.20	ns
% woodland (200 m)–plant population size	Local–local	0.60	0.14	<0.01
<i>Polemonium</i>				
<i>Visitor abundance</i>				
Visitor rate–pollen limitation	Local	–0.792	0.107	<0.01
% Woodland (1000 m)–visitor rate	Landscape	–0.094	0.404	ns
% Woodland (200 m)–visitor rate	Local	0.740	0.376	<0.05
Light level–visitor rate	Local	0.169	0.257	ns
<i>Visitor richness</i>				
Visitor richness–pollen limitation	Local	–0.502	0.216	<0.02
% Woodland (1000 m)–visitor richness	Landscape	–0.001	0.376	ns
% Woodland (200 m)–visitor richness	Local	0.680	0.354	ns
Light level–visitor richness	Local	–0.059	0.214	ns
<i>Correlation among predictors^b</i>				
% Woodland (1000 m)–% woodland (200 m)	Landscape–local	0.835	0.87	<0.01
% Woodland (200 m)–light level	Local–local	–0.274	0.262	ns

Note: Values correspond to model structures shown in Fig. 1. Significance values for standardized path analysis are interpreted based on *t* statistics with rule infinite degrees of freedom following suggestion of SAS/STAT Proc Calis (SAS_Institute 2011).

^a In our analysis, visitor abundance was measured as a rate, visitors per flower per min.

^b Correlations among predictors are identical in models using visitor abundance or richness, but differ between plant species because of differences in the numbers of sites used.

Table D1

Ordination of bee communities among sites.

	Final dimensionality	Final stress ^a	Random iterations
Claytonia	2	0.059	20,000
Polemonium	2	0.124	20,000

^a Follows formula of (Clarke, 1993) ranging from 0 to 1.

Appendix D

See Table D1.

References

- Aguilar, R., Ashworth, L., Galetto, L., Aizen, M.A., 2006. Plant reproductive susceptibility to habitat fragmentation: review and synthesis through a meta-analysis. *Ecology Letters* 9, 968–980.
- Ahrne, K., Bengtsson, J., Elmqvist, T., 2009. Bumble bees (*Bombus* spp. along a gradient of increasing urbanization. *Plos One* 4.
- Aizen, M.A., Feinsinger, P., 1994. Forest fragmentation, pollination, and plant reproduction in a Chaco dry forest, Argentina. *Ecology* 75, 330–351.
- Aizen, M.A., Harder, L.D., 2007. Expanding the limits of the pollen-limitation concept: effects of pollen quantity and quality. *Ecology* 88, 271–281.
- Cane, J.H., Minckley, R.L., Kervin, L.J., Roulston, T.H., Williams, N.M., 2006. Complex responses within a desert bee guild (Hymenoptera: Apiformes) to urban habitat fragmentation. *Ecological Applications* 16, 632–644.
- Carre, G., Roche, P., Chifflet, R., Morison, N., Bommarco, R., Harrison-Cripps, J., Krewenka, K., Potts, S.G., Roberts, S.P.M., Rodet, G., Settele, J., Steffan-Dewenter, I., Szentgyorgyi, H., Tscheulin, T., Westphal, C., Woyciechowski, M., Vaissiere, B.E., 2009. Landscape context and habitat type as drivers of bee diversity in European annual crops. *Agriculture Ecosystems and Environment* 133, 40–47.
- Cheptou, P.O., Avedano, L.G., 2006. Pollination processes and the Allee effect in highly fragmented populations: consequences for the mating system in urban environments. *New Phytologist* 172, 774–783.
- Clarke, K.R., 1993. Non-parametric multivariate analyses of change in community structure. *Australian Journal of Ecology* 18, 117–143.
- Concepcion, E.D., Diaz, M., Kleijn, D., Baldi, A., Batary, P., Clough, Y., Gabriel, D., Herzog, F., Holzschuh, A., Knop, E., Marshall, E.J.P., Tschamntke, T., Verhulst, J., 2012. Interactive effects of landscape context constrain the effectiveness of local agri-environmental management. *Journal of Applied Ecology* 49, 695–705.
- Cussans, J., Goulson, D., Sanderson, R., Goffe, L., Darvill, B., Osborne, J.L., 2010. Two bee-pollinated plant species show higher seed production when grown in gardens compared to arable farmland. *PLoS One* 5, e11753. <http://dx.doi.org/10.1371/journal.pone.0011753>.
- Ghazoul, J., 2005. Pollen and seed dispersal among dispersed plants. *Biological Reviews* 80, 413–443.
- Gomez, J.M., Abdelaziz, M., Lorite, J., Munoz-Pajares, A.J., Perfectti, F., 2010. Changes in pollinator fauna cause spatial variation in pollen limitation. *Journal of Ecology* 98, 1243–1252.
- Gonzalez-Varo, J.P., Arroyo, J., Aparicio, A., 2009. Effects of fragmentation on pollinator assemblage, pollen limitation and seed production of Mediterranean myrtle (*Myrtus communis*). *Biological Conservation* 142, 1058–1065.
- Goulson, D., Hanley, M.E., Darvill, B., Ellis, J.S., Knight, M.E., 2005. Causes of rarity in bumblebees. *Biological Conservation* 122, 1–8.
- Goulson, D., Hughes, W.O.H., Derwent, L.C., Stout, J.C., 2002. Colony growth of the bumblebee, *Bombus terrestris*, in improved and conventional agricultural and suburban habitats. *Oecologia* 130, 267–273.
- Greenleaf, S.S., Williams, N.M., Winfree, R., Kremen, C., 2007. Bee foraging ranges and their relationship to body size. *Oecologia* 153, 589–596.
- Hadley, A.S., Betts, M.G., 2012. The effects of landscape fragmentation on pollination dynamics: absence of evidence not evidence of absence. *Biological Reviews* 87, 526–544.

- Hahs, A.K., McDonnell, M.J., McCarthy, M.A., Vesk, P.A., Corlett, R.T., Norton, B.A., Clemants, S.E., Duncan, R.P., Thompson, K., Schwartz, M.W., Williams, N.S.G., 2009. A global synthesis of plant extinction rates in urban areas. *Ecology Letters* 12, 1165–1173.
- Herrera, C.M., 1995. Floral biology, microclimate, and pollination by ectothermic bees in an early-blooming herb. *Ecology* 76, 218–228.
- Herrera, C.M., 1997. Thermal biology and foraging responses of insect pollinators to the forest floor irradiance mosaic. *Oikos* 78, 601–611.
- Herrera, C.M., 2000. Flower-to-seedling consequence of different pollination regimes in an insect-pollinated shrub. *Ecology* 81, 15–29.
- Hightshoe, G.L., 1988. Native Trees Shrubs, and Vines for Urban and Rural America. John Wiley and Sons, New York, NY.
- Hoehn, P., Tschamtkke, T., Tylianakis, J.M., Steffan-Dewenter, I., 2008. Functional group diversity of bee pollinators increases crop yield. *Proceedings of the Royal Society Biological Sciences Series B* 275, 2283–2291.
- Holzschuh, A., Steffan-Dewenter, I., Tschamtkke, T., 2010. How do landscape composition and configuration, organic farming and fallow strips affect the diversity of bees, wasps and their parasitoids? *Journal of Animal Ecology* 79, 491–500.
- Irwin, R.E., 2006. The consequences of direct versus indirect species interactions to selection on traits: pollination and nectar robbing in *Ipomopsis aggregata*. *American Naturalist* 167, 315–328.
- Jennersten, O., 1988. Pollination in *Dianthus deltooides* (Caryophyllaceae): effects of habitat fragmentation on visitation and seed set. *Conservation Biology* 2, 359–366.
- Kennedy, C., Lonsdorf, E., Neel, M., Williams, N., Ricketts, T., Winfree, R., Bommarco, R., Brittain, C., Cariveau, L., Carvalheiro, N., Chacoff, S., Cunningham, B., Danforth, D., Dudenhöffer, J., Elle, E., Gaines, H., Garibaldi, L.A., Gratton, C., Holzschuh, A., Isaacs, R., Javorek, S., Jha, S., Klein, A., Krewenka, K., Mandelik, Y., Mayfield, M., Morandin, L., Neame, L., Otieno, M., Park, M., Potts, S., Rundlöf, M., Steffan-Dewenter, I., Taki, H., Tuell, J., Viana, B., Westphal, C., Greenleaf, S., Kremen, C., A global quantitative synthesis of local and landscape effects on wild bee pollinators in agroecosystems. *Ecology Letters* (in press).
- Kilkenny, F.F., Galloway, L.F., 2008. Reproductive success in varying light environments: direct and indirect effects of light on plants and pollinators. *Oecologia* 155, 247–255.
- Kleijn, D., Raemakers, I., 2008. A retrospective analysis of pollen host plant use by stable and declining bumble bee species. *Ecology* 89, 1811–1823.
- Kleijn, D., van Langevelde, F., 2006. Interacting effects of landscape context and habitat quality on flower visiting insects in agricultural landscapes. *Basic and Applied Ecology* 7, 201–214.
- Klein, A.M., Vaissiere, B.E., Cane, J.H., Steffan-Dewenter, I., Cunningham, S.A., Kremen, C., Tschamtkke, T., 2007. Importance of pollinators in changing landscapes for world crops. *Proceedings of the Royal Society B – Biological Sciences* 274, 303–313.
- Knight, T.M., Steets, J.A., Ashman, T.-L., 2006. A quantitative synthesis of pollen supplementation experiments highlights the contribution of resource reallocation to estimates of pollen limitation. *American Journal of Botany* 93, 271–277.
- Knight, T.M., Steets, J.A., Vamasi, J.C., Mazer, S.J., Burd, M., Campbell, D.R., Dudash, M.R., Johnston, M.O., Mitchell, R.J., Ashman, T.-L., 2005. Pollen limitation of plant reproduction: pattern and process. *Annual Review of Ecology Evolution and Systematics* 36, 467–497.
- Kremen, C., Williams, N.M., Aizen, M.A., Gemmill-Herren, B., LeBuhn, G., Minckley, R., Packer, L., Potts, S.G., Roulston, T., Steffan-Dewenter, I., Vazquez, D.P., Winfree, R., Adams, L., Crone, E.E., Greenleaf, S.S., Keitt, T.H., Klein, A.M., Regetz, J., Ricketts, T.H., 2007. Pollination and other ecosystem services produced by mobile organisms: a conceptual framework for the effects of land-use change. *Ecology Letters* 10, 299–314.
- Kremen, C., Williams, N.M., Bugg, R.L., Fay, J.P., Thorp, R.W., 2004. The area requirements of an ecosystem service: crop pollination by native bee communities in California. *Ecology Letters* 7, 1109–1119.
- Kremen, C., Williams, N.M., Thorp, R.W., 2002. Crop pollination from native bees at risk from agricultural intensification. *Proceedings of the National Academy of Sciences of the United States of America* 99, 16812–16816.
- Krewenka, K.M., Holzschuh, A., Tschamtkke, T., Dormann, C.F., 2011. Landscape elements as potential barriers and corridors for bees, wasps and parasitoids. *Biological Conservation* 144, 1816–1825.
- Loveland, T.R., Acevedo, W., 2011. Land Cover Change in the Eastern United States. US Department of Interior & US Geological Survey. <<http://landcover.trends.usgs.gov/east/regionalSummary.html>>.
- Matlack, G.R., 1994. Plant species migration in a mixed-history forest landscape in eastern North America. *Ecology* 75, 1491–1502.
- Matteson, K.C., Langellotto, G.A., 2010. Determinates of inner city butterfly and bee species richness. *Urban Ecosystems* 13, 333–347.
- McFrederick, Q.S., LeBuhn, G., 2006. Are urban parks refuges for bumble bees *Bombus* spp. (Hymenoptera: Apidae)? *Biological Conservation* 129, 372–382.
- McKinney, M.L., 2006. Urbanization as a major cause of biotic homogenization. *Biological Conservation* 127, 247–260.
- Mitchell, R.J., 2001. Path analysis. In: Scheiner, S.M., Gurevitch, J. (Eds.), *Design and Analysis of Ecological Experiments*. Oxford university Press, New York, NY, pp. 217–234.
- Motten, A.F., 1986. Pollination ecology of the spring wildflower community of a temperate deciduous forest. *Ecological Monographs* 56, 21–42.
- Müller, A., Diener, S., Schnyder, S., Stutz, K., Sedivy, C., Dorn, S., 2006. Quantitative pollen requirements of solitary bees: implications for bee conservation and the evolution of bee-flower relationships. *Biological Conservation* 130, 604–615.
- Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H., Wagner, H., 2011. *vegan: Community Ecology Package*. In R Package Version 2.0-2.
- Ollerton, J., Winfree, R., Tarrant, S., 2011. How many flowering plants are pollinated by animals? *Oikos* 120, 321–326.
- Osborne, J.L., Martin, A.P., Shortall, C.R., Todd, A.D., Goulson, D., Knight, M.E., Hale, R.J., Sanderson, R.A., 2008. Quantifying and comparing bumblebee nest densities in gardens and countryside habitats. *Journal of Applied Ecology* 45, 784–792.
- Price, M.V., Campbell, D.R., Waser, N.M., Brody, A.K., 2008. Bridging the generation gap in plants: pollination, parental fecundity, and offspring demography. *Ecology* 89, 1596–1604.
- Quinn, G.P., Keough, M.J., 2002. *Experimental Design and Data Analysis for Biologists*. Cambridge University Press.
- Ricketts, T.H., Dinerstein, E., Olson, D.M., Loucks, C.J., Eichbaum, W., DellaSalla, D., Kavanagh, K., Hedao, P., Hurlley, P., Carney, K., Abell, R., Walters, S., 1999. *Terrestrial Ecoregions of North America: A Conservation Assessment*. Island Press, Washington, DC.
- Ricketts, T.H., Imhoff, M., 2003. Biodiversity, urban areas, and agriculture: locating priority ecoregions for conservation. In *Conservation Ecology. The Resilience Alliance*.
- Ricketts, T.H., Regetz, J., Steffan-Dewenter, I., Cunningham, S.A., Kremen, C., Bogdanski, A., Gemmill-Herren, B., Greenleaf, S.S., Klein, A.M., Mayfield, M.M., Morandin, L.A., Ochieng, A., Viana, B.F., 2008. Landscape effects on crop pollination services: are there general patterns? *Ecology Letters* 11, 499–515.
- Ries, L., Debinski, D.M., 2001. Butterfly responses to habitat edges in the highly fragmented prairies of Central Iowa. *Journal of Animal Ecology* 70, 840–852.
- Rodrigues, J.J.S., Brown Jr., K.S., Ruzsyczk, A., 1993. Resources and conservation of Neotropical butterflies in urban forest fragments. *Biological Conservation* 64, 3–9.
- Rundlöf, M., Nilsson, H., Smith, H.G., 2008. Interacting effects of farming practice and landscape context on bumblebees. *Biological Conservation* 141, 417–426.
- SAS_Institute, 2011. *SAS/STAT 9.3 User's Guide*. SAS Institute, Cary, NC.
- Schemske, D.W., Willson, M.F., Melampy, M.N., Miller, L.J., Verner, L., Schemske, K.M., Best, L.B., 1978. Flowering ecology of some spring woodland herbs. *Ecology* 59, 351–366.
- Slagle, M.W., Hendrix, S.D., 2009. Reproduction of *Amorpha canescens* (Fabaceae) and diversity of its bee community in a fragmented landscape. *Oecologia* 161, 813–823.
- Steffan-Dewenter, I., Munzenberg, U., Burger, C., Thies, C., Tschamtkke, T., 2002. Scale-dependent effects of landscape context on three pollinator guilds. *Ecology* 83, 1421–1432.
- Steffan-Dewenter, I., Tschamtkke, T., 1999. Effects of habitat isolation on pollinator communities and seed set. *Oecologia* 121, 432–440.
- Theobald, D.M., 2005. Landscape patterns of exurban growth in the USA from 1980 to 2020. *Ecology and Society* 10, 32.
- Tommasi, D., Miro, A., Higo, H.A., Winston, M.L., 2004. Bee diversity and abundance in an urban setting. *The Canadian Entomologist* 136, 851–869.
- Van Rossum, F., 2010. Reproductive success and pollen dispersal in urban populations of an insect-pollinated hay-meadow herb. *Perspectives in Plant Ecology Evolution and Systematics* 12, 21–29.
- Vellend, M., 2004. Parallel effects of land-use history on species diversity and genetic diversity of forest herbs. *Ecology* 85, 3043–3055.
- Verboven, H.A.F., Brys, R., Hermy, M., 2012. Sex in the city: reproductive success of *Digitalis purpurea* in a gradient from urban to rural sites. *Landscape and Urban Planning* 106, 158–164.
- Wagenius, S., Lyon, S.P., 2010. Reproduction of *Echinacea angustifolia* in fragmented prairie is pollen-limited but not pollinator-limited. *Ecology* 91, 733–742.
- Ward, M., Johnson, S.D., 2005. Pollen limitation and demographic structure in small fragmented populations of *Brunsvigia radulosa* (Amaryllidaceae). *Oikos* 108, 253–262.
- Washitani, I., Osawa, R., Namai, H., Niwa, M., 1994. Patterns of female fertility in heterostylous *Primula sieboldii* under severe pollinator limitation. *Journal of Ecology* 82, 571–579.
- Whitney, G.G., Foster, D.R., 1988. Overstorey composition and age as determinants of the understorey flora of woods in central New England USA. *Journal of Ecology* 76, 867–876.
- Williams, N.M., Crone, E.E., Roulston, T.H., Minckley, R.L., Packer, L., Potts, S.G., 2010. Ecological and life-history traits predict bee species responses to environmental disturbances. *Biological Conservation* 143, 2280–2291.
- Winfree, R., 2010. The conservation and restoration of wild bees. In: Ostfeld, R.S., Schlesinger, W.H. (Eds.), *The Year in Ecology and Conservation Biology*. Annals of the New York Academy of Sciences, New York, pp. 169–197.
- Winfree, R., Aguilar, R., Vázquez, D.P., LeBuhn, G., Aizen, M.A., 2009. A meta-analysis of bees' responses to anthropogenic disturbance. *Ecology* 90, 2068–2076.
- Winfree, R., Bartomeus, I., Cariveau, D.P., 2011. Native pollinators in anthropogenic habitats. *Annual Review of Ecology, Evolution, and Systematics* 42, 1–22.
- Winfree, R., Williams, N.M., Gaines, H., Ascher, J.S., Kremen, C., 2008. Wild bee pollinators provide the majority of crop visitation across land-use gradients in New Jersey and Pennsylvania, USA. *Journal of Applied Ecology* 45, 793–802.
- Winfree, R., Griswold, T., Kremen, C., 2007. Effect of human disturbance on bee communities in a forested ecosystem. *Conservation Biology* 21, 213–223.
- Wolf, A.T., Harrison, S.P., 2001. Effects of habitat size and patch isolation on reproductive success of the serpentine morning glory. *Conservation Biology* 15, 111–121.