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Review

Planting gardens to support insect pollinators

Ania A. Majewska [1,2]* and Sonia Altizer [1,2]

[1]Odum School of Ecology, University of Georgia, 140 E. Green Street, Athens, GA 30602, U.S.A.
[2]Center for the Ecology of Infectious Disease, University of Georgia, Athens, GA 30602, U.S.A

Abstract: *Global insect pollinator declines have prompted habitat restoration efforts, including pollinator-friendly gardening. Gardens can provide nectar and pollen for adult insects and offer reproductive resources, such as nesting sites and caterpillar host plants. We conducted a review and meta-analysis to examine how decisions made by gardeners on plant selection and garden maintenance influence pollinator survival, abundance, and diversity. We also considered characteristics of surrounding landscapes and the impacts of pollinator natural enemies. Our results indicated that pollinators responded positively to high plant species diversity, woody vegetation, garden size, and sun exposure and negatively to the separation of garden habitats from natural sites. Within-garden features more strongly influenced pollinators than surrounding landscape factors. Growing interest in gardening for pollinators highlights the need to better understand how gardens contribute to pollinator conservation and how some garden characteristics can enhance the attractiveness and usefulness of gardens to pollinators. Further studies examining pollinator reproduction, resource acquisition, and natural enemies in gardens and comparing gardens with other restoration efforts and to natural habitats are needed to increase the value of human-made habitats for pollinators.*

Keywords: bee, butterfly, conservation, disease, habitat restoration, predators

Siembra jardines para dar soporte a los insectos polinizadores

Resumen: *La declinación mundial de insectos polinizadores ha dado pie a esfuerzos de restauración, incluyendo la jardinería amigable con los polinizadores. Los jardines pueden proporcionar néctar y polen para los insectos adultos y también pueden ofrecer recursos reproductivos, como sitios de anidación y plantas hospederas para las orugas. Realizamos una revisión y un meta-análisis para examinar cómo las decisiones que toman los jardineros relacionadas a la selección de plantas y el mantenimiento del jardín influyen se la supervivencia, abundancia y diversidad de los polinizadores. También consideramos las características de los paisajes vecinos y los impactos de los enemigos naturales de los polinizadores. Nuestros resultados indicaron que los polinizadores respondieron positivamente a la alta diversidad de especies de plantas, la vegetación leñosa, el tamaño del jardín y la exposición al sol, mientras que respondieron negativamente a la separación entre los jardines y los sitios naturales. Las características intrínsecas de los jardines tuvieron una mayor influencia sobre los polinizadores que los factores del paisaje vecino. El creciente interés por la jardinería para polinizadores resalta la necesidad de entender como los jardines contribuyen a la conservación y como algunas características de los jardines pueden incrementar lo útil y atractivo de los jardines para los polinizadores. Se requieren estudios más profundos que examinen la reproducción de los polinizadores, la adquisición de recursos y los enemigos naturales en los jardines, y también que comparen a los jardines con otros esfuerzos de restauración y con los hábitats naturales para incrementar el valor de los hábitats para polinizadores creados por humanos.*

Palabras Clave: abeja, conservación, depredadores, enfermedades, mariposa, restauración del hábitat

摘要: 为应对全球昆虫传粉者的减少, 人们发起了生境恢复工作, 如培植传粉者友好的花园。花园不仅为成体昆虫提供了花 **蜜和花粉**, 还能提供繁殖资源, 如筑巢地和毛虫的寄主植物 。 **我**们通过文献综述和荟萃分析, 研究了花园管理者在植物选择和花园维护方面的决策如何影响传粉者的生存、丰度及多样性, 并将周围景观特征及传粉者天敌的影响纳入考虑。结果表明, 较高的植物物种多样性、木本植被覆盖、较大的花园面积和阳光照射

*email majewska@uga.edu
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对传粉者有积极作用，而花园生境与自然环境的分隔则对传粉者有负面影响。花园内部特征比周围景观因素对传粉者的影响更大。人们对为传粉者建造花园的日益浓厚的兴趣，突显了我们需要更好地理解花园如何促进对传粉者的保护以及花园的一些特征如何提高其对传粉者的吸引力和有用性。未来仍需进一步研究传粉者在花园中的繁殖情况、资源需求及其天敌的影响，并将花园与自然生境和其它恢复项目比较，以提升传粉者的人工生境的价值。【翻译：胡怡思；审校：聂永刚】

关键词: 保护，生境恢复，捕食者，疾病，蝴蝶，蜜蜂

Introduction

Widespread pollinator declines are caused by multiple factors, including pesticides, disease, and habitat loss that reduces the availability of flowers, nesting sites, and egg-laying opportunities for pollinators (Goulson et al. 2015). As humans continue to modify natural landscapes, habitat restoration has become increasingly important for recovering pollinator populations (Menz et al. 2011) and has been implemented in a variety of landscapes, including agricultural zones, roadsides, and urban gardens. Indeed, planting floral resources, such as hedgerows, crop margins, and right-of-ways, can increase the abundance and diversity of bees, butterflies, and pollinating flies (Hannon & Sisk 2009; Pywell et al. 2011; Wojcik & Buchmann 2012). A habitat restoration strategy that has received less scientific attention involves planting gardens for insect pollinators. Gardens are patches of human-managed habitats, where a variety of plant species are intentionally planted, typically on private property and in public green spaces, such as parks in urban and suburban landscapes. Although gardens tend to be created for aesthetic display, these areas can support substantial biodiversity (Owen 2010; Speak et al. 2015; Threlfall et al. 2017). Interest in the benefits gardens may offer wildlife has prompted a recent surge of studies into how these habitats influence pollinator abundance, diversity, and survival. Synthesizing this research is crucial to predicting the importance of gardens for insect pollinator conservation.

The number of guides for pollinator gardening has increased since the 1980s (Supporting Information), and wildlife conservation organizations (e.g., National Wildlife Federation) with specific gardening-for-wildlife initiatives provide plant lists and gardening recommendations online to the public. The number of books on how to garden for pollinators (e.g., Mader et al. 2011) and websites continues to increase alongside public concern for pollinators. Existing guides encourage gardeners to provide abundant and diverse plant species that offer nectar and pollen (Black et al. 2016; Frey & LeBuhn 2016). Reproductive resources, such as caterpillar host plants and 'bee hotels', are encouraged to provide egg-laying sites for butterflies, moths, bees, and wasps (Mader et al. 2011). Gardeners also face maintenance decisions regarding weed removal, pests, pruning, fertilizing, and watering to sustain ecologically useful and aesthetically pleasing gardens (Black et al. 2016).

Because gardens can offer many resources (Fig. 1), they are often assumed to benefit insect pollinators. Although garden habitats can support a high diversity of pollinators (Matteson et al. 2008; Owen 2010), gardens may not generate the same outcomes as observed in larger-scale restoration efforts, in part owing to differences in plant composition, habitat complexity, management, spatial scale, and impacts of surrounding landscapes (e.g., Winfree et al. 2011; Kennedy et al. 2013; Threlfall et al. 2017). Moreover, pollinator interactions with natural enemies, such as predators and pathogens, could be affected by gardens in ways that limit future pollinator recruitment (Goulson et al. 2015; Satterfield et al. 2015). Understanding the circumstances under which gardens are beneficial or detrimental to pollinators is crucial for maximizing the conservation potential of these habitats.

We reviewed how garden features influence pollinator diversity, abundance, and survival and identify underlying ecological mechanisms that may contribute to different outcomes. We began by synthesizing information on how local garden traits and landscape-scale factors may benefit or harm insect pollinators utilizing gardens. We then conducted a meta-analysis of empirical studies characterizing pollinator abundance, diversity, presence, or visitation associated with local garden features (including plant selection and garden management practices) and landscape-scale factors (including urbanization and distance to natural habitats). We also identified needs for future research, including studies on pollinator mortality in gardens and estimates of garden effects on pollinator reproduction to determine the conditions under which gardens simply attract pollinators versus contribute positively to their fitness.

Mechanisms by which Garden Characteristics Influence Pollinator Populations

Plant Selection

Gardeners are faced with an array of choices when creating a garden. Decisions on how many and which plant species to choose can be guided by books and websites on gardening for pollinators (e.g., www.pollinator.org/guides.htm). However, these resources typically provide genus-level recommendations based on personal observations rather than on comprehensive data (Garbuzov & Ratnieks 2014). Although forbs, such as asters (Asteraceae), represent the bulk of plants on pollinator garden lists, woody vegetation, including tree and shrub species, are also recommended to provide nectar, pollen, shelter, and shade (Black et al. 2016).

In addition to plants that provide nectar and pollen, other plants provide food for the caterpillar stages of Lepidoptera (i.e., host plants), and some plants serve both functions. Caterpillar host plants in gardens can boost local population size (*Passiflora* spp.) (Fleming et al. 2005), although their presence does not necessarily increase fecundity. For example, Levy and Connor (2004) found that pipevine swallowtails (*Battus philenor*) using host plants in gardens have higher egg mortality compared with those at natural sites, although they did not examine factors responsible for mortality differences.

Citing adaptations to local conditions, native plants (i.e., species that evolved with soils, climate, fauna, and other flora in a given region) are often considered a better choice for gardens than exotic species (i.e., not native to the continent on which they are now found) and are thought to be preferred by pollinators (e.g., Mader et al. 2011), in part because exotic plants may not produce the olfactory or visual cues needed by native insects or because they may not be as palatable as native plants (Corbet et al. 2001; Keane & Crawley 2002; Novotny & Basset 2005). Yet, in a garden setting, if exotic plants provide the same key resources as native plants, both types could be used by pollinators. Many exotic plants in gardens can maintain flowers and foliage significantly longer than native counterparts. These shifts in resource availability can alter pollinator community composition, plant–pollinator networks, foraging behavior (Gotlieb et al. 2011), and the timing of pollinator reproduction (Satterfield et al. 2015). Studies comparing pollinator abundance and diversity in gardens with native versus exotic plants show mixed results, and the debate concerning the relative benefits of native and exotic plants in gardens continues, motivating the need for future studies examining the impacts of plant choice on insect pollinators.

Garden Management Practices to Maintain Aesthetic Appeal

Gardeners undertake numerous maintenance practices, including weeding, mulching, and cleaning their gardens (Clayton 2007; Goddard et al. 2013), and at times apply chemicals, mainly fertilizers and pesticides (Robbins et al. 2001), all of which can influence insect pollinators. Weeding creates aesthetic appeal but tends to lower habitat utility for pollinators. Weeds, or any undesired plants not intentionally planted, such as dandelions (*Taraxacum* spp.), can serve as foraging resources for pollinators (Larson et al. 2014; MacIvor et al. 2014) or as host plants (e.g., milkweed [*Asclepias* spp.] for monarchs). Removal of unwanted vegetation and application of weed suppressing barriers, such as mulch, increase aesthetics, but decrease the complexity and structural diversity of the area, potentially reducing the attractiveness and use by pollinators. Mulching serves to retain soil moisture, yet might block ground-nesting species, such as plasterer, mining, and andrenid bees from accessing bare ground for nest excavation and building (Cane 2015; Fortel et al. 2016). More complex gardens can offer a greater diversity of substrates for nesting or for hiding from predators (see "Natural Enemies" below). Simultaneously, weeding and mulching likely reduce competition for resources and allow remaining plants to invest more resources in growth and reproduction (Johnson 1971), potentially increasing nectar and pollen of cultivated plants. Studies in agroecosystems suggest that a diversity of beneficial weeds enhances pollinator populations (Nicholls & Altieri 2013; Landis 2017), but how weeding affects the abundance and diversity of pollinators in gardens has seldom been studied.

Clearing practices, such as pruning and removal of dead vegetation, may also affect pollinators by unintentionally removing certain life stages. Nonmobile stages, including eggs and pupae or adults overwintering on dead vegetation, are most vulnerable during clearing events. Such practices may decrease pollinator abundance, as has been documented in other area types (e.g., lower butterfly abundance on mowed fields [Dover et al. 2011]). The timing of weeding, clearing, and mulching is important, as evidenced by recommendations to delay the clearing of dead vegetation until later in the growing season, allowing for the emergence of cavity-nesting pollinators and emergence of overwintering butterflies (Black et al. 2016).

Many pollinator habitat guides also recommend leaving brush piles, snags, or stumps in gardens to serve as natural nesting resources for cavity-nesting pollinators, and these features can also be used by other wildlife, such as birds, rodents, and reptiles as foraging and reproductive sites (Mader et al. 2011). Features such as brush piles often run counter to the aesthetic inclinations of gardeners who prefer well-groomed sites cleared of dead vegetation with mulch or other substrates covering the ground. Some gardeners provide artificial nests (e.g., bee hotels; Fig. 1) that can be used by cavity-nesting pollinators, including carpenter, leaf-cutting, and mason bees (Fortel et al. 2016; MacIvor 2017). One study indicated that artificial nests increased local population sizes of some species (Gruber et al. 2011). Other research suggests that artificial nests are rarely used by the targeted species (Fussell & Corbet 1992; MacIvor & Packer 2015), and their use depends on nest design and sun exposure (Gaston et al. 2005).

Insect pollinators can be exposed to pesticides in gardens (Botías et al. 2017). Ornamental plants sold at garden centers can be treated with systemic insecticides, such as neonicotinoids, which are then expressed by plant tissues (Lentola et al. 2017). Gardeners might also intentionally apply insecticides to eliminate plant pests

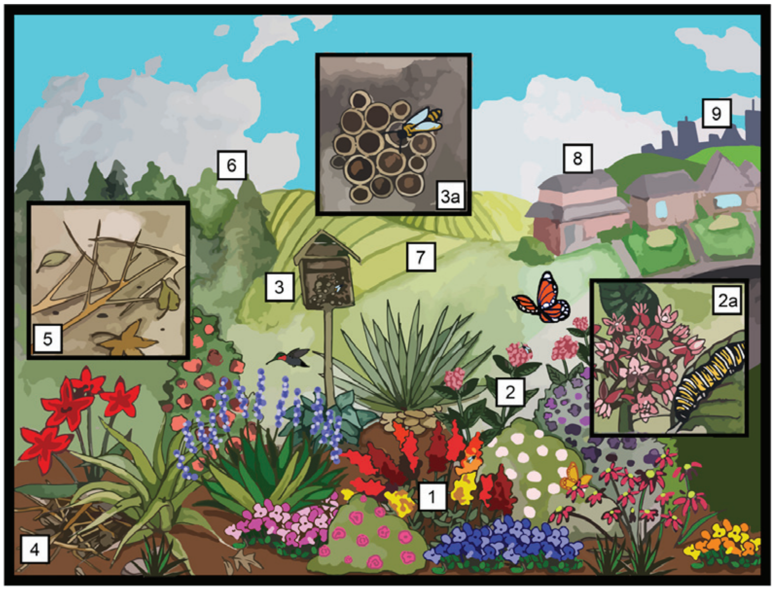

Figure 1. Gardening for pollinators books and guides encourage the planting of (1) a variety of colorful flowering species that provide nectar and pollen for adults throughout the growing season and (2) host plants for caterpillars, such as (2a) milkweed for monarchs. Pollinator gardeners also include structural elements, such as (3) artificial nest boxes for (3a) cavity-nesting bees and wasps and (4) a brush pile for overwintering, shelter from harsh weather, or nesting. (5) Bare soil patches allow ground-nesting pollinators to form belowground habitats. The surrounding landscape, which may include (6) natural forest, (7) crops, and (8) residential and urban areas, can also influence the diversity and abundance of pollinator visitors to a garden. Artwork by R. L. Atkins.

(e.g., aphids) or house pests (e.g., cockroaches) near the boundary of structures. Drift from chemicals applied for tick control, mosquito spraying, and other applications can occur from nearby areas (Ginsberg et al. 2017). The negative effects of pesticides on pollinators in agriculture are well documented (Desneux et al. 2007), and the amounts of chemicals used in residential areas can be similar to those found in proximity to agriculture (Kolpin et al. 1998), suggesting the impact on garden pollinators may be significant, depending on the timing and frequency of the pollinators' garden use.

Importance of Surrounding Habitats

Gardens are a part of a larger mosaic, and surrounding areas can influence the diversity and abundance of visiting pollinators. Clusters of gardens may support higher biodiversity (Vergnes et al. 2012; Braaker et al. 2014), and connected gardens (i.e., within dispersal distance of pollinators) can increase the diversity of pollinators in a community (Hanski et al. 1995; Goddard et al. 2010). Gardens can also be located near vacant lots, reserves, or remnants of forest (Rudd et al. 2002), and some butterflies can use even corridors of low-quality habitat for interpatch movement (Haddad & Tewksbury 2005). Habitat connectivity allows additional species of pollinators to utilize gardens, particularly dietary specialists and those that require multiple habitat types to complete life cycles (Westrich 1996; Wray & Elle 2015). For example, while gardens can offer host plants, such as dill (Apiaceae) for black swallowtails (*Papilio polyxenes*), adults also require other locations for displaying to attract mates (Lederhouse 1982).

Urban landscapes can harbor diverse communities of wild insect pollinators (Hall et al. 2017), although urbanization generally decreases pollinator diversity and abundance (Bates et al. 2011; Tonietto et al. 2011). Compared with rural areas, urban pollinators tend to represent generalist, highly mobile, stress-tolerant species (Fetridge et al. 2008; Bergerot et al. 2010). The presence of environmental contaminants and the mortality associated with roads (e.g., car strikes; Harrison & Winfree 2015) can harm some pollinators in urban gardens. Urbanized areas also tend to be dominated by exotic plants (Lowenstein & Minor 2016), which can decrease some pollinator species. Although little is known about insect movement in urban environments (LaPoint et al. 2015), features, such as buildings, have been shown to disrupt the movements of bumble bees (Jha et al. 2013).

Agricultural fields surrounding gardens have mixed effects on pollinators. Proximity to crop fields pollinated by managed honeybees can promote disease in wild pollinators, and exposure to agrochemicals can negatively affect pollinator survival and health (Desneux et al. 2007). Seasonal mass flowering events of crops might provide additional forage and boost pollinator populations. Indeed, the number of bee brood cells was higher in artificial nests in gardens next to rapeseed fields compared to gardens located in other landscapes (Pereira-Peixoto et al. 2014), suggesting that the reproduction was augmented by increased foraging resources.

Impacts of Natural Enemies

Gardens can attract pollinator natural enemies, including predators, parasitoids, and parasites. Otoshi et al. (2015) found that the density and richness of spiders, all of which are predators, increased with the abundance and diversity of ornamental plants in gardens. Maintenance activities, such as weeding, may decrease habitat complexity and structural diversity, which could expose pollinators to greater predation risk if more complex habitats offer more hiding sites from predators (Karban et al. 2013; Grof-Tisza et al. 2015). Yet, ecological theory suggests that complex habitats can also increase predation risk (Langellotto & Denno 2004). Indeed, predatory heteropteran bugs (i.e., true bugs) are more common in gardens, parks, and gulf courses with greater vegetation volume (Mata et al. 2017). Further work is needed to examine the role of habitat complexity in predator–prey relationships in a garden setting.

Pathogens, parasitoids, brood parasites, and kleptoparasites can affect pollinator fitness in gardens. Gardens frequented by managed honeybees (*Apis mellifera*) or bumblebees (*Bombus* spp.) can pose pathogen spillover risks to wild pollinators because managed pollinators tend to harbor high levels of infectious diseases (Murray et al. 2013; Fürst et al. 2014). Some generalist pathogens of bees (e.g., *Nosema* spp.) can spread between multiple pollinator species indirectly via flowers (McArt et al. 2014), such that shared foraging sites can become disease hotspots. Moreover, when densities of insect pollinators are high in gardens, mortality risk from parasitoids might be elevated. For instance, buff-tailed bumblebees (*Bombus terrestris*) had higher parasitoid nest infestation in gardens where bee densities were higher (Goulson et al. 2002). Garden isolation from other pollinator habitats can lead to crowding and elevated parasitism. The number of parasitized brood cells in artificial nest boxes increases as the abundance of cavity-nesting pollinators increases, and the strongest parasitism occurs in gardens isolated from similar sites (Pereira-Peixoto et al. 2016). This may occur if both pollinators and their natural enemies are aggregated into few available habitat patches, although artificial nest boxes in general might present an easy target for parasitoids. Finally, studies of monarch butterflies and a protozoan parasite (*Ophryocystis elektroscirrha*) suggest that gardens can increase the exposure to infection when exotic host plants extend the phenology of breeding activity and parasite transmission (Satterfield et al. 2015).

Meta-analysis of Garden Characteristics Effects on Pollinators

Past work indicates that garden design, maintenance, and surrounding habitats can influence pollinator visitation, diversity, abundance, and demography. We conducted a meta-analysis of prior studies to address the following questions: Does the selection of native plants, higher plant diversity, and greater floral abundance increase pollinator abundance and diversity? Are certain garden management practices, such as mulching and chemical use, particularly detrimental to pollinators in gardens? What landscape factors are associated with positive and negative effects on pollinators in gardens? Is natural enemy pressure similar in gardens versus natural habitats? We compiled sufficient data to test 4 factors related to plant selection: native versus non-native plantings (e.g., proportion of garden covered by native plants), flower abundance (e.g., proportion of flowering plants), plant species diversity (e.g., plant species richness), and woody vegetation (e.g., shrub and tree presence). We tested 3 garden management factors: use of chemical biocides (e.g., fungicides and pesticides), habitat diversity (e.g., index of the variety of features, such as a pond present in garden), and the proportion of mulch cover. We examined 2 other garden traits commonly measured in studies of pollinator gardens: garden size (e.g., area) and sun exposure (e.g., light availability measured using a photometer). We examined 6 landscape-level factors: urbanization metrics (e.g., proportion impervious surface within 1000 m radius), green space (e.g., proportion green space within 500 m of a garden), distances to agricultural fields, and distances to water bodies, coast, and forest. Because relatively few studies quantified natural enemies in gardens, we were unable to test factors associated with enemy risk.

Data Collection and Statistical Approach

We searched for published studies in ISI Web of Science and Google Scholar. We focused our search on articles published between January 1920 and November 2017. We used the following search string: (*pollinator** OR *pollinat** OR *butterfly* OR *bee*) OR ("*pollinator conservation*") AND (*garden** OR *gardening*) NOT: ("*honeybee*" OR "*honey bee*" OR "*common garden*") to narrow the search to pertinent studies. The final data set included studies from 2004 to 2017. We also searched bibliographies of recent papers, which added 5 studies to our data set.

We included studies examining relationships between garden attributes and measures of pollinator abundance, diversity, presence, or visitation. Studies were included if at least 3 replicate sampling sites were examined (to allow for estimation of sampling variance [Moher et al. 2009]). From each study, we recorded the type of test statistic (e.g., F, z, χ^2), test statistic value, sample size, and directionality (positive or negative) of the relationship between garden attributes and pollinators. Next, we followed Rosenthal and DiMatteo (2001) to convert the test statistics into correlation-based r between garden attributes and pollinator measures. When the value of test statistic was not reported, we followed Bentz et al. (2016) and used the reported p value and sample size to calculate r. We assigned negative values to effect sizes for which the garden attributes significantly decreased pollinators (Viechtbauer 2010). The directional r effect sizes were converted into Fisher's Z with R package metafor (Bonett 2007) to stabilize the variance (Borenstein et al. 2009).

We recorded pollinator species, family, and order examined in each study. We recorded the pollinator measure tested (e.g., abundance) and the garden attribute tested against each measure. Attributes for which we gathered fewer than 3 lines of data across all studies were later excluded. Additional details on criteria for study inclusion and descriptive analyses are given in Supporting Information. The resulting data set included 178 records from 24 studies testing relationships between garden attributes and pollinator measures.

Correlates of Pollinator Measures in Gardens

We examined the direction and strength of pollinator responses to within-garden characteristics and external landscape factors. The within-garden features included 4 factors related to plant selection: flower abundance, plant species diversity, native versus non-native planting, and woody vegetation; 3 garden management-related factors: chemical use, habitat diversity, and mulch cover; and 2 other traits: garden size and sun exposure. We examined 6 landscape-level factors based on the habitats surrounding gardens: urbanization metrics, green space, and distances to agricultural fields, water bodies, coast, and forest. A full description of the attributes and their assignments, along with example studies, is provided in Supporting Information.

We fit random-effects models (REMs) with observation, study, and pollinator family as random effects (Konstantopoulos 2011). Attribute type (within vs. external factor) was a fixed factor. The random effect of observation was nested within a published study to account for unit-level heterogeneity and study pseudoreplication because most studies (21 of 24) contained >1 effect size. We fit REMs with restricted maximum likelihood to obtain unbiased estimates of variance components (Higgins & Thompson 2002; Nakagawa & Santos 2012).

We examined the degree to which particular features predicted variation in effect sizes. We built separate univariate mixed-effects models (MEMs) for plant selection, garden management, other traits, and the landscape factors, with the same random effects as REMs. We performed post hoc comparisons to test whether coefficients differed significantly from zero, while adjusting for the potentially inflated false-discovery rate (Benjamini & Hochberg 1995; Hothorn et al. 2017). We repeated the above analyses on data without the 5 studies added from bibliographies of recent papers and found similar results (Supporting Information).

Meta-analysis Results

Of the 178 pollinator–garden interactions identified, data were primarily from Lepidoptera and Hymenoptera (Fig. 2). Most studies measured effects on pollinators based on overall abundance or diversity; fewer studies

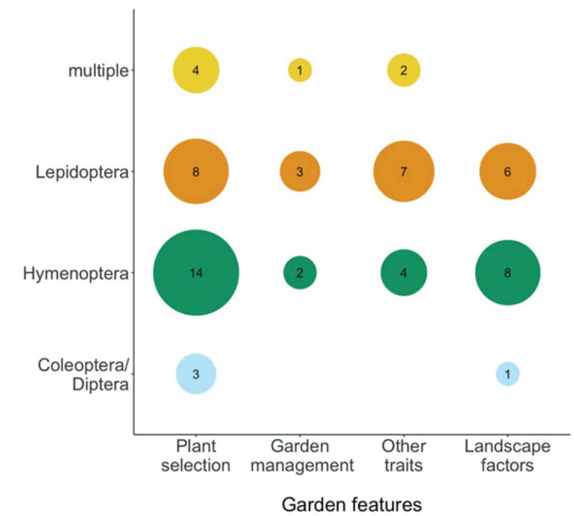

Figure 2. Distribution of data across pollinator taxonomic groups and garden features used in a meta-analysis of studies on the effects of garden characteristics on insect pollinators (size of circles and numbers indicate the number of unique pollinator–garden attribute interactions examined). Multiple is any combination of 1 or more insect pollinator orders. Garden feature categories include plant selection, which relates to the choice of plants in a garden (e.g., native versus non-native plants); garden management, which are features and practices to maintain the garden and its aesthetic appeal (e.g., chemical use); other traits include features commonly examined in pollinator garden studies (e.g., garden size); landscape factors refer to attributes of garden's surrounding landscape (e.g., degree of urbanization).

measured presence or other responses (Supporting Information). Most of the studies included in the meta-analysis were recent (published in the last 5 years), and the diversity of pollinator types examined increased over time (Fig. 3). The best studied garden attributes were size, native versus non-native plants, and flower abundance (Fig. 4).

The REM for the entire data set showed significant heterogeneity in pollinator effects across all studies and attributes ($I^2 = 0.99$; $Q_M = 4139.65$, df $= 177$, $p < 0.001$) (Fig. 4). Within-garden features had overall stronger effect sizes than landscape-level attributes ($z = 6.39$, $p < 0.001$). Univariate MEM analyses of plant-selection features tested separately indicated that pollinators responded positively to flower abundance, plant diversity, and woody vegetation metrics (Fig. 4a). The MEM analyses of garden management showed that pollinators were not influenced significantly by chemical use, habitat diversity, or mulch cover (Fig. 4b). Garden size and sun exposure positively influenced pollinators (Fig. 4c). Post hoc comparisons showed that only plant

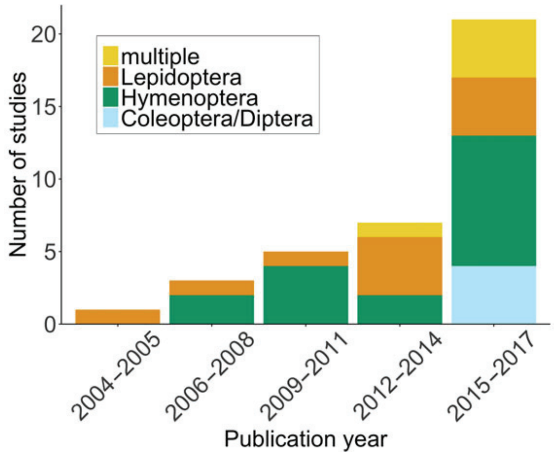

Figure 3. Number of studies in a meta-analysis of the effects of garden characteristics on insect pollinators by year of publication and pollinator guild (multiple, >1 pollinator guild).

diversity ($z = 6.66$, $p < 0.001$), woody vegetation metrics ($z = 3.24$, $p = 0.004$), garden size ($z = 5.37$, $p < 0.001$), and sun exposure ($z = 2.63$, $p = 0.02$) had effect sizes that were significantly different from zero, although flower abundance was nearly significant ($z = 2.30$, $p = 0.06$). Univariate MEMs of landscape factors showed that greater distances to agricultural fields and coastal zones negatively influenced pollinators (Fig. 4d). Post hoc comparisons showed that effect sizes for distance to field and coast showed marginal difference from zero ($p \leq 0.1$).

Discussion

Pollinator gardens are growing in popularity and can be important conservation tools for a diversity of pollinators that have declined in recent decades (Goulson et al. 2015; Thomas 2016). Simultaneously, a need remains for scientifically informed recommendations for elements of garden design and best practices to ensure that gardens contribute positively to pollinator abundance, reproduction, and survival. Our review and meta-analysis showed that relationships between garden attributes and pollinators vary widely. A handful of garden features, especially plant diversity, woody vegetation, and garden size, were consistently associated with positive effects on pollinators. Greater plant diversity species and floral traits could better attract and support diverse assemblages of pollinators (Ghazoul 2006). Higher plant diversity is also expected to extend the resource phenology needed to support numerous pollinators in gardens. Woody plants in gardens, such as shrubs and trees, may result in a higher quality habitat for insect pollinators by providing additional food, shade, and shelter from strong winds. This finding reinforces recommendations for gardens and other pollinator restoration efforts to plant species-rich floral mixtures and to include shrubs and trees (Winfree 2010; Havens & Vitt 2016).

Our results pointed to multiple maintenance strategies that may affect the utility of gardens for pollinators, yet information was only available for a subset of these strategies for the meta-analysis, and none showed consistent significant effects on pollinators. Indeed, many within-garden characteristics identified in the review showed weak or no relationships based on the meta-analysis. Much like our review, which pointed to both positive and negative consequences of exotic plants for pollinators, the meta-analysis showed no consistent directional association between native versus non-native plants and pollinators, perhaps because in some cases exotic plants can adequately substitute for resources provided by native plants (Severns & Warren 2008; Majewska et al. 2018). For example, Salisbury et al. (2015) compared flying insect visitors to experimental plots and concluded that gardens containing mostly native plant species, but also some exotic plants, could provide optimal resources for pollinating insects by extending the flowering season. Majewska et al. (2018) found that the diversity and abundance of butterflies visiting experimental gardens was similar for assemblages of native versus exotic plant species. Similarly, in terms of chemical use, it seems likely that both positive and negative relationships exist and may produce stronger net relationships if parsed out at finer scales. For example, slug treatments and fungicides may improve the quality and health of treated plants, allowing for greater investment in flowers (Muratet & Fontaine 2015), and thereby attract more pollinators, which could nonetheless experience sublethal effects of the chemicals. Exposure to some pesticides can negatively impact pollinators (e.g., Desneux et al. 2007), and we caution against conclusions of no effects of garden chemical use on pollinator survival or health.

Multiple studies showed that landscapes surrounding pollinator habitats can predict species diversity and composition. In support of this idea, our meta-analysis suggested that proximity to areas representing a source of specialist pollinators or with additional foraging and reproductive resources, such as pastures, may enhance pollinator communities found in gardens. Specifically, our results showed that pollinators respond negatively to increasing distances of gardens from agricultural fields and coastline; however, this was examined only for moths (Lepidoptera) and the effect was not statistically significant. Similarly, our results indicate that proximity to habitats unsuitable for pollinators, such as highly urbanized landscapes, may decrease pollinator use of gardens, presumably owing to limited habitats and resources (Tonietto et al. 2011; Wray & Elle 2015). Landscape-level factors showed weaker associations with pollinators than within-garden attributes, suggesting that patch-scale

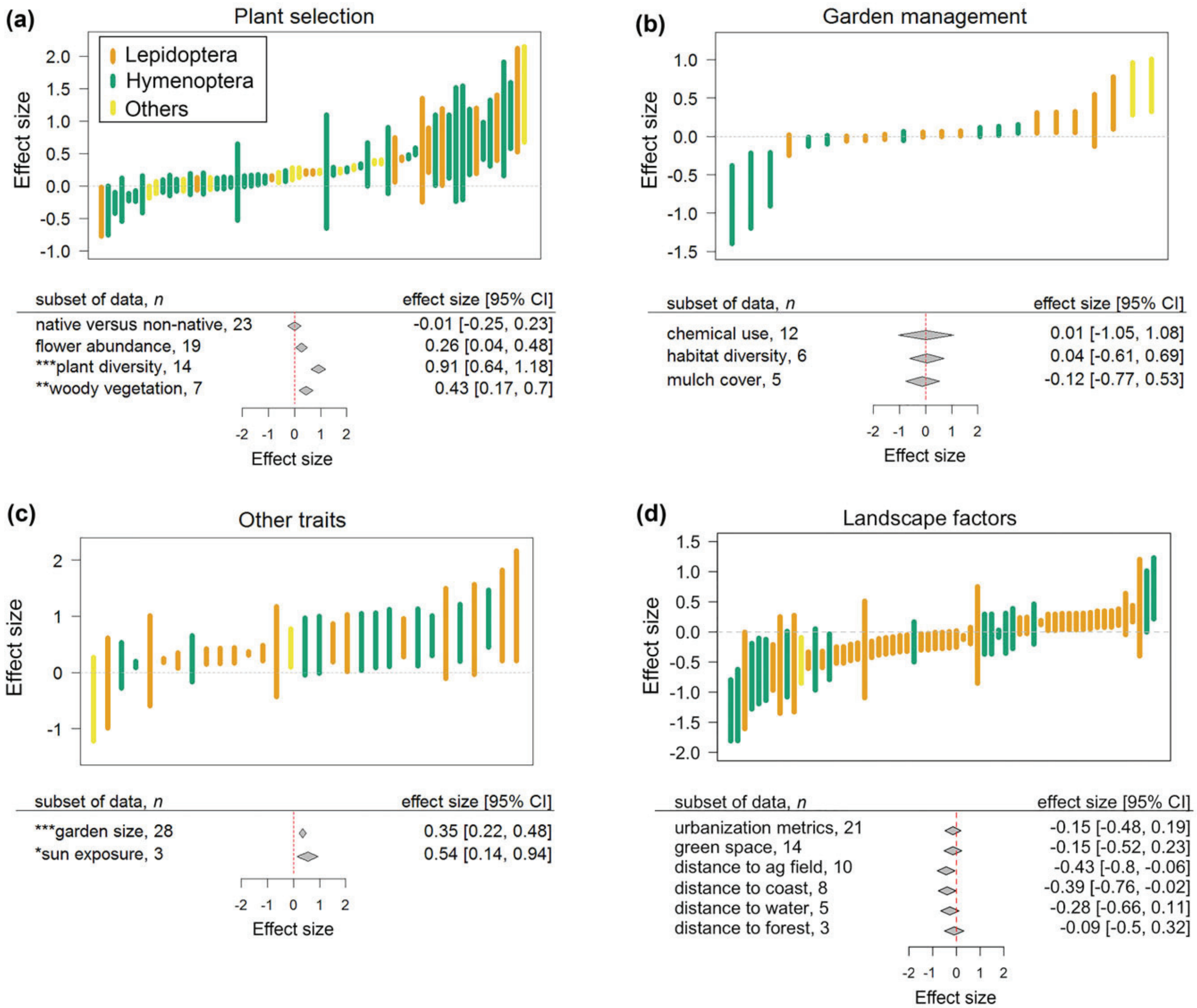

*Figure 4. Distribution of Fisher's Z effect sizes for observed relationships between 4 garden attributes and effects on pollinators (top) and summary of effect sizes based on features tested (beneath each forest plot): (a) plant selection, (b) garden management, (c) other commonly examined traits, and (d) landscape factors (for description of each category see Methods and Supporting Information) (vertical lines, 95% CI for effect sizes of pollinator–garden attribute interactions; CIs above horizontal dashed line, garden attributes positively influenced pollinators; CIs below horizontal dashed line, negative effects on pollinators; subset of data, n, number of pollinator–garden attribute interactions corresponding to each level; significance: *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$).*

garden features play a key role in determining the abundance and diversity of pollinators visiting gardens.

Several factors, including natural enemies and artificial nest boxes, could not be included in our meta-analysis due to the small number of studies that examined these topics. This represents a crucial gap where future work is needed (Table 1). Multiple types of resources can be used for pollinators for nesting and reproduction. Some of these, such as caterpillar host plants, may be easy to monitor, whereas others, such as natural ground nests, may be difficult to monitor, possibly accounting for lack of information on the topic. Importantly, as artificial nests for cavity-nesting pollinators become more popular, this could present an opportunity to ask how augmentation of nest sites by gardeners might benefit reproductive success of cavity-nesting pollinators. Similarly, studies of predation on pollinators in gardens are needed. Direct visual observations of predation are challenging because most pollinators (and their predators) are relatively small in size and highly mobile. Focusing on predation and parasitism of nonmobile immature stages in artificial structures or hosts plants represents a more practical approach that would yield insights into the effect of gardens on pollinator population biology (Table 1). This information is critical for evaluating gardens' relative contribution to pollinator population

Table 1. Outstanding research questions on how gardens and specific garden attributes might influence insect pollinator diversity, abundance, and health.

Question	Research need
Are measures of pollinator diversity and population biology similar in gardens relative to natural habitats?	intensive monitoring of multiple life stages in replicate gardens and natural sites comparison of pollinator fecundity, survival, predation, and parasitism in gardens versus natural sites longitudinal assessments in gardens and natural sites to quantify seasonal and longer term effects
What garden design elements or management practices result in garden habitats acting as sources, sinks, or ecological traps for pollinators?	experimental manipulations of garden features (e.g., native versus exotic plants, nesting resources) and practices (e.g., weeding, fertilizer, and pesticide use) to quantify pollinator responses across multiple life stages in terms of survival, reproduction, predation, and parasitism assessment of pollinator survival and natural enemy pressure in gardens with and without specific features or practices and examination of the relative importance of predation versus parasitism as causes of pollinator mortality in gardens
What are the effects of the habitats surrounding gardens on pollinators?	examination of pollinator fecundity, survival, predation, and parasitism in gardens surrounded by agricultural, urban and natural habitats

biology, their role in pollinator restoration, and to inform best gardening practices that maximize the benefit of gardens for pollinators.

As human-dominated landscapes continue to expand, gardens may aid in mitigating the negative effects of habitat loss for wild insect pollinators, their associated organisms, and other fauna (e.g., birds, bats, and small mammals). However, gardens are much more complex than generally assumed and subject to widely variable aesthetic preferences and management practices. Our review and meta-analysis underscore the need to understand which garden traits attract insect pollinators and under what circumstances gardens support pollinator conservation and act as population sources, versus conditions under which gardens may act as sinks. Despite the popularity of pollinator-friendly gardening, work examining pollinator population dynamics in response to gardens (and garden traits) lags behind the proliferation of books and online resources currently available. Further work is needed to develop an evidenced-based approach to evaluate the consequences of garden characteristics and educate gardeners about their importance. Ultimately, more studies comparing pollinator population health and ecology in gardens versus natural pollinator habitats will improve current understanding of the role gardens play in supporting diverse and healthy pollinator populations.

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Supporting Information

Pollinator gardening books published by year (Appendix S1), meta-analysis details, including data collection procedures (Appendix S2), and detailed meta-analysis results along with the list of studies included (Appendix S3) are available online. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

Literature Cited

Bates AJ, Sadler JP, Fairbrass AJ, Falk SJ, Hale JD, Matthews TJ. 2011. Changing bee and hoverfly pollinator assemblages along an urban-rural gradient. PLOS ONE **6** (e23459) https://doi.org/10.1371/journal.pone.0023459.

Benjamini Y, Hochberg Y. 1995. Controlling the false discovery rate: a practical and powerful approach to multiple testing. Journal of the Royal Statistical Society. Series B (Methodological) **57:**289–300.

Bentz AB, Becker DJ, Navara KJ. 2016. Evolutionary implications of interspecific variation in a maternal effect: a meta-analysis of yolk testosterone response to competition. Royal Society Open Science **3:**160499.

Bergerot B, Fontaine B, Renard M, Cadi A, Julliard R. 2010. Preferences for exotic flowers do not promote urban life in butterflies. Landscape and Urban Planning **96:**98–107.

Black SH, Borders B, Fallon C, Lee-Mader E, Sherpherd M. 2016. Gardening for butterflies: how you can attract and protect beautiful, beneficial insects. Timber Press, Portland, Oregon.

Bonett DG. 2007. Transforming odds ratios into correlations for meta-analytic research. The American Psychologist **62:**254–255.

Borenstein M, Hedges LV, Higgins J, Rothstein HR. 2009. Converting among effect sizes. Pages 45–49 in Borenstein M, editor. Introduction to meta-analysis. John Wiley & Sons, West Sussex, United Kingdom.

Botías C, David A, Hill EM, Goulson D. 2017. Quantifying exposure of wild bumblebees to mixtures of agrochemicals in agricultural and urban landscapes. Environmental Pollution **222:** 73–82.

Braaker S, Ghazoul J, Obrist M, Moretti M. 2014. Habitat connectivity shapes urban arthropod communities: the key role of green roofs. Ecology **95:**1010–1021.

Cane JH. 2015. Landscaping pebbles attract nesting by the native ground-nesting bee *Halictus rubicundus* (Hymenoptera: Halictidae). Apidologie **46:**728–734.

Clayton S. 2007. Domesticated nature: motivations for gardening and perceptions of environmental impact. Journal of Environmental Psychology **27:**215–224.

Corbet SA, Bee J, Kanchon D, Gale S, Gorringe E, Ferla Bl, Moorhouse T, Trevail A, Van Bergen Y, Vorontsova M. 2001. Native or exotic? Double or single? Evaluating plants for pollinator-friendly gardens. Annals of Botany **87:**219–232.

Desneux N, Decourtye A, Delpuech J-M. 2007. The sublethal effects of pesticides on beneficial arthropods. Annual Review of Entomology **52:**81–106.

Dover J, Rescia A, Fungariño S, Fairburn J, Carey P, Lunt P, Arnot C, Dennis R, Dover C. 2011. Land-use, environment, and their impact on butterfly populations in a mountainous pastoral landscape: individual species distribution and abundance. Journal of Insect Conservation **15:**207–220.

Fetridge ED, Ascher JS, Langellotto GA. 2008. The bee fauna of residential gardens in a suburb of New York City (Hymenoptera: Apoidea). Annals of the Entomological Society of America **101:**1067–1077.

Fleming TH, Serrano D, Nassar J. 2005. Dynamics of a subtropical population of the zebra longwing butterfly *Heliconius charithonia* (Nymphalidae). Florida Entomologist **88:**169–179.

Fortel L, Henry M, Guilbaud L, Mouret H, Vaissière BE. 2016. Use of human-made nesting structures by wild bees in an urban environment. Journal of Insect Conservation **20:**239–253.

Frey K, LeBuhn G. 2016. The bee-friendly garden: design an abundant, flower-filled yard that nurtures bees and supports biodiversity. Ten Speed Press, New York.

Fürst M, McMahon DP, Osborne J, Paxton R, Brown M. 2014. Disease associations between honeybees and bumblebees as a threat to wild pollinators. Nature **506:**364–366.

Fussell M, Corbet SA. 1992. Flower usage by bumble-bees: a basis for forage plant management. Journal of Applied Ecology **29:**451–465.

Garbuzov M, Ratnieks FL. 2014. Listmania: the strengths and weaknesses of lists of garden plants to help pollinators. BioScience **64:**1019–1026.

Gaston KJ, Smith RM, Thompson K, Warren PH. 2005. Urban domestic gardens (II): experimental tests of methods for increasing biodiversity. Biodiversity and Conservation **14:**395–413.

Ghazoul J. 2006. Floral diversity and the facilitation of pollination. Journal of Ecology **94:**295–304.

Ginsberg HS, Bargar TA, Hladik ML, Lubelczyk C. 2017. Management of arthropod pathogen vectors in North America: minimizing adverse effects on pollinators. Journal of Medical Entomology **54:**1463–1475.

Goddard MA, Dougill AJ, Benton TG. 2010. Scaling up from gardens: biodiversity conservation in urban environments. Trends in Ecology & Evolution **25:**90–98.

Goddard MA, Dougill AJ, Benton TG. 2013. Why garden for wildlife? Social and ecological drivers, motivations and barriers for biodiversity management in residential landscapes. Ecological Economics **86:**258–273.

Gotlieb A, Hollender Y, Mandelik Y. 2011. Gardening in the desert changes bee communities and pollination network characteristics. Basic and Applied Ecology **12:**310–320.

Goulson D, Hughes W, Derwent L, Stout J. 2002. Colony growth of the bumblebee, *Bombus terrestris*, in improved and conventional agricultural and suburban habitats. Oecologia **130:**267–273.

Goulson D, Nicholls E, Botías C, Rotheray EL. 2015. Bee declines driven by combined stress from parasites, pesticides, and lack of flowers. Science **347:**1255957.

Grof-Tisza P, Holyoak M, Antell E, Karban R. 2015. Predation and associational refuge drive ontogenetic niche shifts in an arctiid caterpillar. Ecology **96:**80–89.

Gruber B, Eckel K, Everaars J, Dormann CF. 2011. On managing the red mason bee (*Osmia bicornis*) in apple orchards. Apidologie **42:**564.

Haddad NM, Tewksbury JJ. 2005. Low-quality habitat corridors as movement conduits for two butterfly species. Ecological Applications **15:**250–257.

Hall DM, Camilo GR, Tonietto RK, Ollerton J, Ahrné K, Arduser M, Ascher JS, Baldock KC, Fowler R, Frankie G. 2017. The city as a refuge for insect pollinators. Conservation Biology **31:**24–29.

Hannon LE, Sisk TD. 2009. Hedgerows in an agri-natural landscape: potential habitat value for native bees. Biological Conservation **142:**2140–2154.

Hanski I, Pakkala T, Kuussaari M, Lei G. 1995. Metapopulation persistence of an endangered butterfly in a fragmented landscape. Oikos **72:**21–28.

Harrison T, Winfree R. 2015. Urban drivers of plant–pollinator interactions. Functional Ecology **29:**879–888.

Havens K, Vitt P. 2016. The importance of phenological diversity in seed mixes for pollinator restoration. Natural Areas Journal **36:**531–537.

Higgins J, Thompson SG. 2002. Quantifying heterogeneity in a meta-analysis. Statistics in Medicine **21:**1539–1558.

Hothorn T, Bretz F, Westfall P, Heiberger RM, Schuetzenmeister A, Scheibe S. 2017. R package multcomp: simultaneous inference in general parametric models. Version 1.4-8.

Jha S, Stefanovich L, Kremen C. 2013. Bumble bee pollen use and preference across spatial scales in human-altered landscapes. Ecological Entomology **38:**570–579.

Johnson BJ. 1971. Effect of weed competition on sunflowers. Weed Science **19:**378–380.

Karban R, Mata TM, Grof-Tisza P, Crutsinger G, Holyoak MA. 2013. Non-trophic effects of litter reduce ant predation and determine caterpillar survival and distribution. Oikos **122:**1362–1370.

Keane RM, Crawley MJ. 2002. Exotic plant invasions and the enemy release hypothesis. Trends in Ecology & Evolution **17:**164–170.

Kennedy CM, Lonsdorf E, Neel MC, Williams NM, Ricketts TH, Winfree R, Bommarco R, Brittain C, Burley AL, Cariveau D. 2013. A global quantitative synthesis of local and landscape effects on wild bee pollinators in agroecosystems. Ecology Letters **16:**584–599.

Kolpin DW, Barbash JE, Gilliom RJ. 1998. Occurrence of pesticides in shallow groundwater of the United States: initial results from the National Water-Quality Assessment Program. Environmental Science & Technology **32:**558–566.

Konstantopoulos S. 2011. Fixed effects and variance components estimation in three-level meta-analysis. Research Synthesis Methods **2:**61–76.

Landis DA. 2017. Designing agricultural landscapes for biodiversity-based ecosystem services. Basic and Applied Ecology **18:**1–12.

Langellotto GA, Denno RF. 2004. Responses of invertebrate natural enemies to complex-structured habitats: a meta-analytical synthesis. Oecologia **139:**1–10.

LaPoint S, Balkenhol N, Hale J, Sadler J, Ree R. 2015. Ecological connectivity research in urban areas. Functional Ecology **29:**868–878.

Larson JL, Kesheimer AJ, Potter DA. 2014. Pollinator assemblages on dandelions and white clover in urban and suburban lawns. Journal of Insect Conservation **18:**863–873.

Lederhouse RC. 1982. Territorial defense and lek behavior of the black swallowtail butterfly, *Papilio polyxenes*. Behavioral Ecology and Sociobiology **10:**109–118.

Lentola A, David A, Abdul-Sada A, Tapparo A, Goulson D, Hill E. 2017. Ornamental plants on sale to the public are a significant source of pesticide residues with implications for the health of pollinating insects. Environmental Pollution **228:**297–304.

Levy JM, Connor EF. 2004. Are gardens effective in butterfly conservation? A case study with the pipevine swallowtail, *Battus philenor*. Journal of Insect Conservation **8:**323–330.

Lowenstein DM, Minor ES. 2016. Diversity in flowering plants and their characteristics: integrating humans as a driver of urban floral resources. Urban Ecosystems **19:**1735–1748.

MacIvor JS. 2017. Cavity-nest boxes for solitary bees: a century of design and research. Apidologie **48:**311–327.

MacIvor JS, Cabral J, Packer L. 2014. Pollen specialization by solitary bees in an urban landscape. Urban Ecosystems **17:**139–147.

MacIvor JS, Packer L. 2015. ‘Bee Hotels’ as tools for native pollinator conservation: a premature verdict? PLOS ONE **10** (e0122126) https://doi.org/10.1371/journal.pone.0122126.

Mader E, Shepherd M, Vaughan M, Black SH, LeBuhn G. 2011. Attracting native pollinators: protecting North America’s bees and butterflies. Storey Publishing, North Adams, Massachusetts.

Majewska AA, Sims S, Wenger SJ, Davis AK, Altizer S. 2018. Do characteristics of pollinator-friendly gardens predict the diversity, abundance, and reproduction of butterflies? Insect Conservation and Diversity **11:**370–382.

Mata L, Threlfall CG, Williams NS, Hahs AK, Malipatil M, Stork NE, Livesley SJ. 2017. Conserving herbivorous and predatory insects in urban green spaces. Scientific Reports **7:**40970.

Matteson KC, Ascher JS, Langellotto GA. 2008. Bee richness and abundance in New York City urban gardens. Annals of the Entomological Society of America **101:**140–150.

McArt SH, Koch H, Irwin RE, Adler LS. 2014. Arranging the bouquet of disease: floral traits and the transmission of plant and animal pathogens. Ecology Letters **17:**624–636.

Menz MH, Phillips RD, Winfree R, Kremen C, Aizen MA, Johnson SD, Dixon KW. 2011. Reconnecting plants and pollinators: challenges in the restoration of pollination mutualisms. Trends in Plant Science **16:**4–12.

Moher D, Liberati A, Tetzlaff J, Altman DG, Group P. 2009. Preferred reporting items for systematic reviews and meta-analyses: the PRISMA statement. PLoS Medicine **6** (e1000097) https://doi.org/10.1371/journal.pmed.1000097.

Muratet A, Fontaine B. 2015. Contrasting impacts of pesticides on butterflies and bumblebees in private gardens in France. Biological Conservation **182:**148–154.

Murray TE, Coffey MF, Kehoe E, Horgan FG. 2013. Pathogen prevalence in commercially reared bumble bees and evidence of spillover in conspecific populations. Biological Conservation **159:**269–276.

Nakagawa S, Santos ES. 2012. Methodological issues and advances in biological meta-analysis. Evolutionary Ecology **26:**1253–1274.

Nicholls CI, Altieri MA. 2013. Plant biodiversity enhances bees and other insect pollinators in agroecosystems. A review. Agronomy for Sustainable Development **33:**257–274.

Novotny V, Basset Y. 2005. Host specificity of insect herbivores in tropical forests. Proceedings of the Royal Society of London, Series B: Biological Sciences **272:**1083–1090.

Otoshi MD, Bichier P, Philpott SM. 2015. Local and landscape correlates of spider activity density and species richness in urban gardens. Environmental Entomology **44:**1043–1051.

Owen J. 2010. Wildlife of a garden: a thirty-year study. Royal Horticultural Society, Peterborough, United Kingdom.

Pereira-Peixoto MH, Pufal G, Martins CF, Klein A-M. 2014. Spillover of trap-nesting bees and wasps in an urban–rural interface. Journal of Insect Conservation **18:**815–826.

Pereira-Peixoto MH, Pufal G, Staab M, Feitosa Martins C, Klein A. 2016. Diversity and specificity of host–natural enemy interactions in an urban–rural interface. Ecological Entomology **41:**241–252.

Pywell R, Meek W, Hulmes L, Hulmes S, James K, Nowakowski M, Carvell C. 2011. Management to enhance pollen and nectar resources for bumblebees and butterflies within intensively farmed landscapes. Journal of Insect Conservation **15:**853–864.

Robbins P, Polderman A, Birkenholtz T. 2001. Lawns and toxins: an ecology of the city. Cities **18:**369–380.

Rosenthal R, DiMatteo MR. 2001. Meta-analysis: recent developments in quantitative methods for literature reviews. Annual Review of Psychology **52:**59–82.

Rudd H, Vala J, Schaefer V. 2002. Importance of backyard habitat in a comprehensive biodiversity conservation strategy: a connectivity analysis of urban green spaces. Restoration Ecology **10:**368–375.

Salisbury A, Armitage J, Bostock H, Perry J, Tatchell M, Thompson K. 2015. Enhancing gardens as habitats for flower-visiting aerial insects (pollinators): Should we plant native or exotic species? Journal of Applied Ecology **52:**1156–1164.

Satterfield DA, Maerz JC, Altizer S. 2015. Loss of migratory behaviour increases infection risk for a butterfly host. Proceedings of the Royal Society of London, Series B: Biological Sciences **282:**20141734.

Severns P, Warren A. 2008. Selectively eliminating and conserving exotic plants to save an endangered butterfly from local extinction. Animal Conservation **11:**476–483.

Speak A, Mizgajski A, Borysiak J. 2015. Allotment gardens and parks: provision of ecosystem services with an emphasis on biodiversity. Urban Forestry & Urban Greening **14:**772–781.

Thomas JA. 2016. Butterfly communities under threat. Science **353:**216–218.

Threlfall CG, Mata L, Mackie JA, Hahs AK, Stork NE, Williams NS, Livesley SJ. 2017. Increasing biodiversity in urban green spaces through simple vegetation interventions. Journal of Applied Ecology **54:**1874–1883.

Tonietto R, Fant J, Ascher J, Ellis K, Larkin D. 2011. A comparison of bee communities of Chicago green roofs, parks and prairies. Landscape and Urban Planning **103:**102–108.

Vergnes A, Le Viol I, Clergeau P. 2012. Green corridors in urban landscapes affect the arthropod communities of domestic gardens. Biological Conservation **145:**171–178.

Viechtbauer W. 2010. Conducting meta-analyses in R with the metafor package. Journal of Statistical Software **36:**1–48.

Westrich P. 1996. Habitat requirements of central European bees and the problems of partial habitats. Pages 1–16 in Matheson A, Buchman S, O’Toole C, Westrich P, Williams I, editors. The conservation of bees. Academic Press, London.

Winfree R. 2010. The conservation and restoration of wild bees. Annals of the New York Academy of Sciences **1195:**169–197.

Winfree R, Bartomeus I, Cariveau DP. 2011. Native pollinators in anthropogenic habitats. Annual Review of Ecology, Evolution, and Systematics **42:**1–22.

Wojcik VA, Buchmann S. 2012. Pollinator conservation and management on electrical transmission and roadside rights-of-way: a review. Journal of Pollination Ecology **7:**16–26.

Wray JC, Elle E. 2015. Flowering phenology and nesting resources influence pollinator community composition in a fragmented ecosystem. Landscape Ecology **30:**261–272.