

ECOLOGY OF ORGANISMS IN URBAN ENVIRONMENTS

Urban drivers of plant–pollinator interactions

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1. Plant–pollinator interactions are affected by global change, with largely negative impacts on pollination and plant reproduction. Urban areas provide a unique and productive study system for understanding the impacts of many global change drivers on plant–pollinator interactions.
2. We review the mechanistic pathways through which urban drivers alter plant–pollinator interactions. The literature on urban drivers of plant–pollinator interactions is small but growing and has already produced exciting insights about how population processes or pollinator behaviour interacts with landscape urban drivers to affect pollination outcomes.
3. Habitat loss and fragmentation can change flower visitation rates and pollination success through changes in pollinator foraging behaviour or through population-level effects on pollinators. Urban environments, where impermeable surface provides an inhospitable matrix, may allow researchers to identify habitat fragments more clearly than in many other environments.
4. Recent studies have found that non-native plants are not differently preferred by pollinators relative to native plants, therefore removing the basis for expecting pollinator-mediated competition between native and non-native plants in urban habitats. However, non-native species together with managed vegetation may have powerful effects in urban habitats via changes in community-level plant phenology and consequent changes in pollinator phenology.
5. The current level of climate warming has not caused plants and pollinators to become detectably temporally separated, although at the same time, diversity among species' phenological responses could buffer plant–pollinator interactions from climate variation. Due to the urban warming effect, cities provide a promising system for better understanding the warming effects on plant–pollinator interactions.
6. Environmental contaminants such as soil nitrogen and heavy metal pollution have been examined with respect to plant–pollinator interactions in small-scale, mechanistic studies. The extent to which environmental contaminants drive plant–pollinator interactions in actual urban landscapes is, however, currently unknown.
7. Important knowledge gaps that require research attention include understanding the consequences of plant and pollinator trait filtering on plant–pollinator interactions, and expanding the literature to include underrepresented biomes and pollinator taxa.

Key-words: Climate warming, environmental contaminants, habitat fragmentation, mutualism, non-native species, plant–animal interaction, pollination, urbanization

Introduction

Pollination is emerging as a model system for studying global change impacts on species interactions. The potential exists for integrating questions about global change with the physiological, behavioural and reproductive processes that characterize the plant–pollinator mutualism, because

there is a large and long-standing literature on the mechanistic aspects of pollination. Research on urban drivers of plant–pollinator interactions is particularly promising because it could accomplish at least three important scientific goals. First, as a study system, urban environments provide spatial concentrations of major global change drivers, such as habitat loss and global warming, expressed at high local intensity and replicated across the world's biogeographic regions. As such, urban ecosystems may be

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productively treated as natural experiments in which to understand global change processes. Secondly, urban land use is a driver of global change in its own right, and therefore, studies on specific urban drivers or combinations of drivers are needed to predict the effects of future urban expansion, which is expected to increase globally by 285% between 2000 and 2030 (Seto, Güneralp & Hutrya 2012). Finally, urban plant–pollinator interactions provide pollination services to urban crops (Werrell *et al.* 2009) and wild plants (Andrieu *et al.* 2009). Understanding how urban drivers affect pollination services will be increasingly important for food production and biodiversity conservation goals as urban land use expands.

We identify four major categories of urban drivers shown to affect urban plant–pollinator interactions (Fig. 1): habitat loss and fragmentation, the introduction of non-native species, urban warming and environmental contaminants including nitrogen deposition and pollution. The first two have been relatively well studied in agricultural and natural systems, as demonstrated in recent reviews or meta-analyses of the effects of land use change and fragmentation on pollinators (Winfree, Bartomeus & Cariveau 2011), on plant–pollinator interactions (Ferreira, Boscolo & Viana 2013) and on pollination (Aguilar *et al.* 2006), and the effects of invasions on plant–pollinator interactions (Morales & Traveset 2009). In order to avoid overlap with these previous reviews, we focus on studies that have at least some sites in urban habitat and emphasize the role of these drivers in a specifically urban context. While the effects of climate warming on plant–pollinator interactions have received much recent attention (Burkle & Alarcón 2011), no studies have yet taken advantage of the opportunities created by urban warming for space-for-time substitution climate studies. Finally, environmental drivers such as pollution have received little attention as drivers of plant–pollinator interactions in any landscape context, although they have been the subject of small-scale laboratory and field experiment studies. For this fourth section, we therefore synthesize smaller-scale studies to understand how these environmental drivers may operate at the landscape scales at which urbanization occurs. In order to focus on the four specific drivers, we avoid extensively citing a larger number of studies using urbanization gradient designs that fail to isolate any particular urban drivers.

The objective of this review is to trace potential pathways through which each specific urban driver may alter plant–pollinator interactions. Therefore, we focus on the relatively small number of studies that measure interactions in a way that provides some mechanistic link between urban drivers and the mutualistic partner benefits (Fig. 1). Urban drivers acting on various life-history traits shape urban plant and animal communities and thereby constrain potential interaction identities. For example, the introduction of non-native plants directly impacts composition of the urban plant community, which then affects plant–pollinator interactions via pollinator preferences or

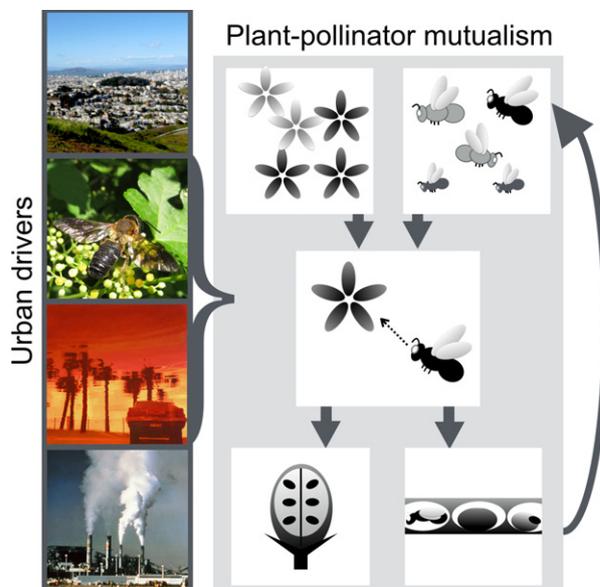


Fig. 1. Fragmentation, non-native and managed species, urban warming and environmental contaminants (left column) are specific urban drivers that directly affect plant–pollinator interactions at different stages of the plant–pollinator mutualism process (right column). Arrows indicate processes endogenous to the plant–pollinator mutualism, which includes a positive feedback loop between the rewards from individual interactions and plant and pollinator community structure (right). (i) Urban drivers filter plant and pollinator species by acting on life-history traits unrelated to the pollination mutualism, such as soil preferences and nesting habitats; (ii) Urban drivers simultaneously affect conditions for interaction between persisting plants and animals, which include spatial and temporal overlap and attraction between potential partners; (iii) Once an interaction has occurred, urban drivers can affect the rewards received by plants or pollinators.

plant bloom time (Section 2: ‘Non-native and managed species’). Urban drivers can also directly affect the interaction rates of plants and animals that persist in the urban environment. For example, urban warming may alter their temporal overlap (Section 3: ‘Urban warming and climate change’), and environmental contaminants can interrupt attraction (Section 4: ‘Environmental contaminants’). Finally, once an interaction occurs, urban drivers can alter the mutualistic costs and rewards to one or both partners, which may have population-level effects that lead to changes in the urban species community (Fig. 1). For example, habitat fragmentation can promote transfer of pollen between closely related plants and result in low seed set or offspring vigour (Section 1: ‘Habitat loss and fragmentation’).

Habitat loss and fragmentation

The process of urbanization is characterized by spatially disjointed development of built-up areas, such that urban landscapes contain fragments of open space such as vacant lots, reserves, parks and gardens. Pollinator population and pollinator foraging dynamics are two mechanisms through which urban habitat loss and fragmentation might

affect pollinators and subsequent pollination service to plants. Future studies of fragmentation as an explicit urban driver may explain heterogeneous responses of pollinator life-history traits, such as body size, to urbanization.

Habitat loss and fragmentation may alter pollinator visitation to plants by causing declines in pollinator populations and changes in pollinator community composition, as predicted by species–area relationships or pollinator resource requirements. These processes can affect pollination function, especially for plant species dependent upon a particular pollinator. For example, loss of a rare pollinator from small natural habitat fragments in an urban matrix led to pollen limitation in six dependent orchid species (Pauw 2007). For plant species not dependent on a particular pollinator, the loss of habitat-specific pollinators from small fragments may be offset by neutral or positive responses in other pollinator species. This was found in two studies in which smaller fragments lost some pollinator species while simultaneously receiving an influx of pollinator species associated with the surrounding matrix (Cane *et al.* 2006; Winfree *et al.* 2014), potentially buffering plant–pollinator interactions. A pollen limitation experiment done along a rural-to-urban gradient provided mixed support for this hypothesis, finding that declining forest fragment size reduced pollinator flower visitation, pollinator species richness and pollination in one but not another woodland herb (Williams & Winfree 2013).

Studies from urban areas have supported the prediction, based on optimal foraging theory, that pollinators will avoid travelling to smaller, more isolated resource patches or will otherwise alter their visitation behaviour in order to offset costs in time and energy (Pyke 1980). These studies use one of the two major methods: measuring pollinator visitation rates and behaviours at focal patches, or tracking pollinator movement between patches. Flower visitation rates and seed set both decreased in smaller plant populations for an unmanaged weed (*Crepis sancta*) growing in small-scale urban fragments (the small dirt patches surrounding street trees). Furthermore, selfing rates were higher in small fragmented urban populations than in large continuous rural populations (Cheptou & Avendaño 2006). On the pollinator side, although visitation to urban fragment populations was lower, the time spent at each flower was longer, suggesting that pollinators were more fully exploiting each flower's resources to recoup energy spent flying longer distances (Andrieu *et al.* 2009). Together, these papers demonstrate that urban fragmentation can alter plant–pollinator interactions via pollinator behavioural responses to small-scale habitat fragmentation.

Pollen analogue methods such as fluorescent dye provide a way to determine whether habitat connectivity facilitates pollinator movement and thus functional connectivity between urban plant populations (see LaPoint *et al.* 2015 for definition of functional connectivity). A study of fluorescent dye movement among urban populations of a forest understorey herb (*Primula elatior*) showed that habitat

corridors increased pollinator movement between connected habitat fragments, thus mitigating the effects of fragmentation (Van Rossum & Triest 2012). In contrast, almost no dye was detected in unconnected fragments. This result might suggest that the urban matrix is hostile to pollinator foraging movements and therefore pollen transfer; however, a parallel study in a meadow herb (*Centaurea jacea*) found that pollinators successfully transferred dye over 2 km through urban matrix habitat between parks (Van Rossum 2010). A potential explanation for this difference is that urban habitats tend to be open or savannah-like rather than forested (Matteson, Grace & Minor 2013), so the perceived contrast between plant habitat fragment and urban matrix may be stronger for pollinators of *P. elatior*, a forest understorey plant, than for pollinators of *C. jacea*, a meadow plant.

We identify three areas where future studies can improve our understanding of urban fragmentation as a driver of plant–pollinator interactions. First, while fragmentation of natural habitat is a necessary consequence of urbanization, the assumption that floral resources are more fragmented in urban habitats is rarely tested and may not hold true in some types of urban land use or at some times of the year. One study found no difference in flower abundance or distribution between survey transects in urban parks versus residential neighbourhoods (Matteson, Grace & Minor 2013). Secondly, because habitat associations are generally unknown for pollinators (Winfree, Bartomeus & Cariveau 2011), pollinators can exhibit idiosyncratic responses to fragmentation when matrix habitat includes alternative foraging resources (e.g. Winfree *et al.* 2014). Because extensive areas of impermeable surface cover prevent most plant growth, urban areas have potential strength as fragmentation study systems, in that fragmentation may be defined commensurately across many plant and pollinator species.

Finally, the role of pollinator mobility in mediating the response of plant–pollinator interactions to urban fragmentation is unknown. Bee body size, which is directly related to foraging range (Greenleaf *et al.* 2007), does not consistently respond to urban fragmentation, with some studies concluding that small-bodied bees are more sensitive (e.g. Cane *et al.* 2006) and other studies concluding that small-bodied bees respond positively to urbanization (e.g. Wray, Neame & Elle 2014). We expect that this variability reflects a trade-off between the ability to access widely distributed resources and the ability to thrive on locally scarce resources (Fig. 2). In the diagrammed example, a study comparing areas *a* and *b* would conclude that fragmentation is associated with high mobility, large body size and connectivity among plant populations. On the other hand, a study comparing areas *a* and *c* would conclude that fragmentation is associated with low mobility, smaller body size and isolation of plant populations. Understanding the importance of pollinator movement in acquiring necessary resources in different landscapes is an important step in reconciling conflicting findings.

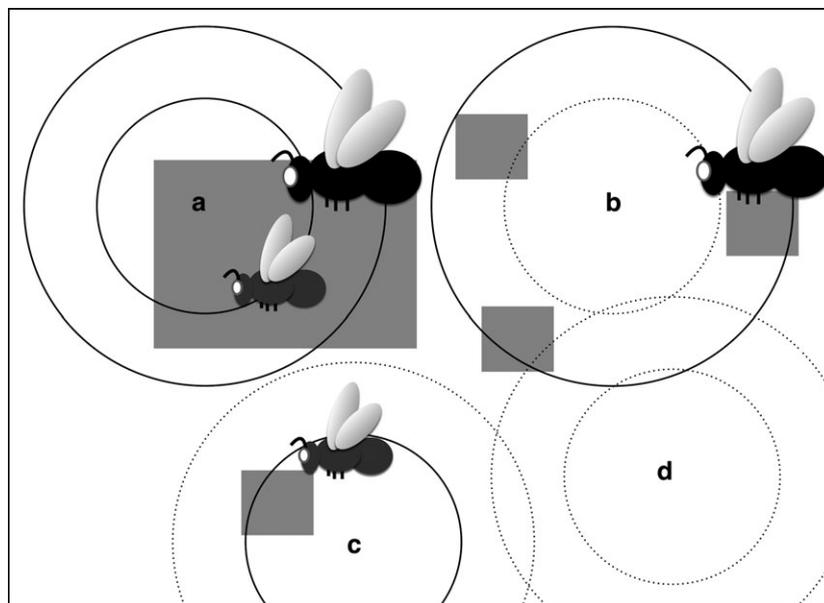


Fig. 2. This diagram explores potential outcomes in the interaction between fragmentation of flowering plant habitat, pollinator nesting habitat and the flight ranges of central-place foraging pollinators. Grey patches represent plant habitat fragments; letters show locations of pollinator nest sites in fragments or matrix, and circles show flight diameters of nesting female bees varying by body size. Dotted lines indicate flight ranges containing too few floral resources for successful pollinator nesting. At nest site a, both large and small pollinators persist; at nest site b, only the larger pollinator can access enough flowering plant habitat fragments; at nest site c, only the small pollinator can persist on the limited available resources; nest site d has too few resources for either pollinator.

Non-native and managed species

Urban plant communities are characterized by high proportions of invasive and non-native species, many of which are also actively managed (e.g. in gardens; Pickett *et al.* 2011). Half of invasive urban plants with known introduction pathways have been deliberately introduced as ornamentals (La Sorte *et al.* 2014). Managed or ornamental species may in some cases be native but are similarly subject to anthropogenic selection filters and intensively managed to produce novel communities, especially in affluent neighbourhoods (Hope *et al.* 2003). We first consider the effects of non-native and managed plant species on urban plant–pollinator interactions and then discuss the effects of non-native and managed pollinators.

NON-NATIVE AND MANAGED PLANTS

Pollinator preference is an important mechanism for competitive effects of non-native plants on native neighbouring plants. A meta-analysis found that non-native neighbours typically have negative effects on both visitation and reproductive success in focal native plants, particularly when the two plant species have phenotypically similar flowers (Morales & Traveset 2009). However, there is likely a persistent study design issue in the selection of dominant, showy non-native plants that can be expected *a priori* to have strong effects. Recent studies conducted in urban settings have improved research design by comparing pollinator visitation between multiple native and non-native plant

species, while controlling for differences in plant species' abundances. In New Jersey suburban habitat, pollinator interaction with non-native plants was dramatically higher than that in natural forest, but in proportion to the higher abundance of non-native plants (Williams *et al.* 2011). A European study used experimental arrays of congeneric or con-familial native and non-native plants set in replicated rural, semi-urban and urban landscape contexts. They found that while visitation to all plants decreased across the urban gradient, pollinators did not prefer native or non-native plants at any level of the treatment (Chrobok *et al.* 2013). Similarly, native and wild-type plants sold as garden ornamentals did not consistently differ from cultivars and hybrids in attracting pollinators in a common garden experiment (Garbuzov & Ratnieks 2014). These studies suggest that, in aggregate, pollinators do not perceive the non-native status of plants. This conclusion does not preclude the possibility that urban floras are more likely to include highly attractive or rewarding plants for other reasons, such as human preference for mass-flowering ornamentals or for garden plants that attract charismatic animal pollinators such as butterflies and hummingbirds. Comparing the distributions of plant attractiveness to pollinators between urban and natural habitats would be an informative first step in asking whether pollinator preference is an important driver of urban plant–pollinator interactions.

The ability of pollinators to avail themselves of non-native and ornamental plants is likely an important condition for thriving in urban habitats. Specialist (oligolectic)

pollinators are sometimes found to be absent or depleted in urban areas (Cane *et al.* 2006; Matteson 2008). However, there is no clear evidence that non-native plant invasion is a primary driver, as compared to other urban drivers of host plant decline, or other pollinator life-history traits correlated with specialization and responses to urbanization. We suspect that the presence of preferred plant genera, families or trait groups is more important to the persistence of specialist pollinators than are geographic origins of the plants.

High concentrations of non-native and managed plants in urban areas might have strong impacts on plant-pollinator interactions by altering seasonal availability of pollinator foraging resources. For several reasons, non-native plants might extend or shift community bloom phenology in urban relative to surrounding environments. First, the timing of bloom appears to be conserved by geographic origin, as demonstrated by a study of three Mediterranean-climate regions that found non-native plants may bloom later, earlier or in sync with native plants, but in all cases retained the basic phenology of their source region (Godoy *et al.* 2009). Furthermore, a greenhouse study found that non-native cultivated species consistently germinate earlier than native plants, suggesting that human selection for convenient phenological qualities places a strong trait selection filter on many non-native plants before they are transported (Chrobok *et al.* 2011). Similarly, ornamental plantings may be consciously designed to provide long-season bloom, either through selection of assemblages with complementary bloom periods or through selection or breeding of long-blooming plants (Garbuzov & Ratnieks 2014). People also extend the growing season for flowering forbs in parks, gardens and lawns through management practices, in particular irrigation in arid environments and tree removal in temperate forested environments. Deforestation or tree thinning extends the duration of floral resource availability by removing light limitation following early summer canopy closure (Winfree *et al.* 2014). Finally, urban warming may shift or lengthen plant species' flowering phenology, discussed further in detail in the following section.

Several lines of evidence suggest that urban pollinator phenologies have changed to match those of non-native and managed urban vegetation. One way this could occur is through habitat filtering and, ultimately, selection against pollinator species adapted to the phenology of native plants. For example, bee species in natural desert habitats had short periods of activity matched with the timing of natural bloom, while irrigated gardens supported pollinator species with longer periods of activity that can take advantage of longer growing season unlimited by water (Gotlieb, Hollender & Mandelik 2011). Similarly, in a study of bees in oak-savannah fragments in different landscape contexts, bee species captured in forest-surrounded fragments had early flight seasons corresponding with the spring and early summer bloom period of native

plants, while bee species captured in urban-surrounded fragments had late flight seasons, presumably sustained by late-blooming plants in urban habitat (Wray, Neame & Elle 2014). Future research is needed to confirm the mechanistic links between temporal shifts in flower resources and shifts in community composition towards pollinators with longer or later flight seasons. Higher generalism of urban pollinators might be an important confounding factor, since specialization may constrain flight seasons to a temporally narrow subset of plant bloom periods. Pollinator specialization did not differ between urban and natural habitats in the two studies cited here (Gotlieb, Hollender & Mandelik 2011; Wray, Neame & Elle 2014).

A second way pollinators, particularly social colony nesters, may adapt to different bloom phenology is by lengthening their flight season to match longer period of bloom. For example, during a mild winter in southern England, three colonies of *Bombus terrestris* collected large amounts of nectar and pollen from non-native ornamentals in an urban park (Stelzer *et al.* 2010). Finally, across landscapes with urban and non-urban habitat types, pollinator species with longer flight seasons could respond to shifts in bloom phenology by foraging in different habitats depending on which offers the most resources at a given time. For example, seasonal changes in foraging activity between urban and rural habitats have been observed by decoding honeybee dances to determine worker flight directions and distances (Beekman & Ratnieks 2000).

NON-NATIVE AND MANAGED POLLINATORS

As for non-native plants, strong effects of non-native pollinators have been found in many research projects focusing on a few unusually dominant, invasive species, especially *Apis mellifera* and *Bombus terrestris*, both of which have been widely introduced for agricultural purposes. Managed *Apis* is emerging as an urban driver of plant-pollinator interactions because bee-keeping in cities is rising, even while the total number of managed and feral *Apis mellifera* colonies is falling in both the USA and Europe (Potts *et al.* 2010). *Apis* has been shown to affect plant-pollinator interactions negatively as disease reservoirs for wild pollinators (Fürst *et al.* 2014), but could potentially have positive effects through its role as a long-season supergeneralist that can rescue plants from other pollinator declines. Furthermore, managed pollinators are at least partly uncoupled from the positive feedbacks inherent to mutualisms; for example, bee-keepers supplement their bees' diets with sugar-water to tide them over periods of low bloom and replace failed hives. Therefore, managed *Apis* may buffer plant-pollinator networks from cascading extirpations, as has been hypothesized for managed plants (Keitt 2009). Given the recent increases in urban bee-keeping, and the variation among towns that do or do not allow it, there are opportunities for researchers to use urban areas as a system for studying the role of managed *Apis* in the environment.

Non-native, solitary insect pollinators have been little studied, yet they may be especially common in urban areas because of higher propagule pressure. A large-scale survey of urban bee communities found that 19% of the bee species in New York City were non-native species, which is surprisingly high compared to the 2% of the bee species in nearby rural New Jersey, which were non-native (Matteson 2008). Furthermore, 90% of the urban non-native species were solitary (Matteson 2008). Large cities may thus provide an opportunity for testing the effects of non-native pollinators as a global change driver, as opposed to effects driven by the few exceptionally invasive species. Further surveys are needed to determine the prevalence of non-native pollinators in other cities and global regions.

While non-native social pollinators may exert strong competitive effects on other bees by monopolizing floral resources (Winfree 2010), concerns about non-native solitary pollinators centre around their competition for nesting resources with ecologically similar native species. For example, *Megachile sculpturalis*, a recent introduction to North America, has been observed attacking and usurping nest tunnels excavated by the similarly sized, native *Xylocopa virginica* (Roulston & Malfi 2012). The effects of non-native solitary pollinators on urban plant–pollinator interactions are unknown, but we consider strong negative effects unlikely, due to the high generalism of plant–pollinator interactions (Memmott, Waser & Price 2004).

Urban warming and climate change

Cities experience different climates from surrounding rural areas, and temperate cities in particular experience higher temperatures from surrounding environments (Pickett *et al.* 2011). Urban warming may affect plant–pollinator interactions through community filtering mechanisms acting on species' physiological tolerances, through phenological shifts that may affect the ability of plants and pollinators to find one another in time. Despite the potential for urban warming studies to have broad relevance for climate change research, the use of urban study systems for testing temperature effects on plant–pollinator interactions is currently rare.

There is good evidence that warmer urban temperatures act as a direct filter on plant communities by selecting for thermophilic native plants and by enabling the establishment of non-native plants from warmer regions (Williams, Hahs & Vesik 2014). It is possible that urban warming similarly filters bee communities. In response to warm winter temperature treatments, spring-emerging bee species overwintering as adults lost more weight before emergence than summer-emerging bees overwintering as larva, likely because of higher metabolic activity in response to warmth (Fründ, Zieger & Tschardt 2013). Spring-emerging bees are negatively impacted by urbanization, although loss of habitat and spring foraging resources are currently considered the likely drivers (Matteson 2008; Wray, Neame & Elle 2014). Further research is needed to determine what,

if any, impact this physiological pathway has on urban pollinator communities and plant–pollinator interactions.

Recent studies of plant–pollinator interactions and climate warming are motivated by concerns that plant and pollinator phenology will respond to warming at different rates or to different phenological cues and will therefore be temporally separated from one another. In aggregate, plants and pollinators respond similarly to climate warming (Bartomeus *et al.* 2011), thereby suggesting that warming will not drive mutualism collapse through plant–pollinator phenology mismatch. However, individual species may have variable phenological responses to climate warming, producing considerable shifts in species overlap and potential interaction partners, necessitating the development of novel interaction networks (CaraDonna, Iler & Inouye 2014). Urban warming tends to advance plant flowering phenology, although species responses are heterogeneous and may be driven by correlated factors such as photoperiod, moisture and CO₂ concentrations (Neil & Wu 2006). Future studies comparing temporal overlap between plants and pollinators occurring in both rural and urban habitats will provide information on whether urban warming, or other sources of intraspecific phenological variation, is causing synchronous shifts in plant and pollinator phenology or driving different patterns of association between plants and pollinators. Species found only in rural or urban habitats would be unsuitable to include in such an analysis, since they would likely introduce large interspecific phenological variation due to other factors (as discussed in the previous section on non-native and ornamental plants).

Cities provide replicated natural experiments in which to test the effects of climate change on plant–pollinator interactions at large spatial scales. Covarying climatic factors may be controlled experimentally, as done in a study of potted brittlebush (*Encelia farinosa*) that found urban-located plants bloomed later and longer than desert-located plants regardless of watering treatment (Neil *et al.* 2014). Another approach is to use historical records to validate space-for-time substitution study designs for studying climate change. One such study combined herbarium records with contemporary surveys to determine that a plant–herbivore interaction responds positively to temperature increases occurring both between urban and rural habitats and over long-term climate trends within each habitat (Youngsteadt *et al.* 2014). A potential third approach is to compare plant–pollinator responses to warming among urban areas experiencing different intensities of heat island effects. This study design has the advantage of partially controlling for other urban drivers, such as non-native and ornamental species, that likely have strong independent effects on phenological responses but are present in most urban areas. Finally, future research on urban climates as drivers of plant–pollinator interactions should take particular care to acknowledge temperate research bias, since urbanization may have different effects on tropical or arid climate variables. For example, in

Phoenix in the arid south-western United States, irrigation of ornamental plants causes cooler daytime temperatures through increased evaporation and transpiration, although night-time temperatures are warmer than in surrounding desert (Brazel *et al.* 2000).

Environmental contaminants

Environmental contaminants are important ecological functions in urban landscapes (Pickett *et al.* 2011) and have been the focus of a number of experimental studies of plant–pollinator interactions especially in laboratory settings. We discuss the effects of soil nitrogen deposition and soil pollution on plant–pollinator interactions in some depth, before briefly addressing contaminants that have been studied less often in the context of plant–pollinator interactions.

NITROGEN DEPOSITION

Urban soils are characterized by eutrophication caused primarily by atmospheric nitrogen compounds produced by industrial or transportation combustion and deposited in water and soil as nitrate (Pickett *et al.* 2011). Plant species vary in their ability to take advantage of nitrogen additions, resulting in shifting competitive dynamics that can change relative abundances of pollinator host plants. For example, high levels of nitrogen addition reduced plant–pollinator interactions by shifting plant composition from flowering forbs to grasses, which do not interact with pollinators (Burkle & Irwin 2010). Evidence for similar community filtering is found in north-western European grasslands, where higher atmospheric nitrogen deposition is correlated with community shifts away from insect-pollinated forbs and towards grasses and other clonal and wind-pollinated plants (Helsen *et al.* 2013). In the case of urban grassland fragments, the nitrogen-induced reduction in pollinator-attractive plants may be mediated by compensating increases in urban-associated plants within either the natural fragments or the nearby urban matrix, since urban-associated plants also tend to prefer high-nutrient soil (Williams, Hahs & Vesik 2014).

Nitrogen deposition has been shown to alter plant–pollinator interactions through several non-filtering mechanisms, including plant reproductive investment and quality of mutualistic reward. For example, low levels of nitrogen addition increased forb growth and flower number, size and nectar production in two plant species, although these changes did not result in higher per-flower visitation (Burkle & Irwin 2010). In another alpine system, adding both fertilizer and pollen to plants non-additively increased seed production, suggesting that nitrogen addition can increase per-visit effectiveness by removing bottom-up limitation on plant reproduction (Brookes, Jesson & Burd 2008). From the pollinator perspective, increases in nectar and pollen quantity or quality could improve foraging efficiency and ultimately reproduction, as shown by an experiment in

which female butterflies raised on poor larval diet produced more eggs when fed amino acid-fortified nectar as adults (Mevi-Schütz & Erhardt 2005). However, demonstrations of trophic transfer of nitrogen from soil to floral rewards to pollinators are currently rare and exhibit complex dynamics. For example, soil nitrogen additions did not change amino acid profiles in *Cucurbita* nectar, but did alter ratios of fructose to glucose sugars (Hoover *et al.* 2012). Bumblebee workers (*Bombus terrestris*) consumed more of the altered nectar, but subsequently suffered reduced longevity. Furthermore, intraspecific nitrogen addition effects tend to be highly context dependent, as demonstrated by different effects of nitrogen treatment levels (Burkle & Irwin 2010) or interactions between nitrogen treatments and pollen availability (Brookes, Jesson & Burd 2008), pollinator larval nutrition (Mevi-Schütz & Erhardt 2005), and warming and CO₂ treatments (Hoover *et al.* 2012). These context-dependent and non-additive effects highlight a need for future studies to consider interactive effects between nitrogen deposition and other urban drivers.

SOIL POLLUTION

Soil pollutants may affect plant–pollinator interactions through pollutant accumulation in plant nectar and pollen. Several studies have looked for effects on pollinator foraging choices in a laboratory setting. Adding nickel to nectar reduced *Bombus* visit duration in jewelweed (Meindl & Ashman 2013). Other metal pollutants such as selenium were not shown to affect pollinator behaviour at flowers (Hladun *et al.* 2013), which may have negative effects on plant–pollinator interactions if metal toxicity reduces bee fitness or pollinator availability to plants.

A study in Europe tested landscape-scale effects of heavy metal pollution along long (*c.* 20 km) gradients surrounding industrial smelters, (Moroń *et al.* 2012). They found that soil pollution was correlated with high levels of cadmium, lead and zinc pollution in trap nest pollen stores, demonstrating that bees use contaminated plants in the field. Pollen pollution correlated with mortality before emergence. The diversity and abundance of bees using trap nests declined sharply at the most polluted site, suggesting either negative long-term demographic effects or an ability of dispersing females to detect and avoid polluted habitat, as hinted in the previously discussed laboratory *Bombus* studies.

OTHER ENVIRONMENTAL CONTAMINANTS

The effects of pesticides, air pollution, light pollution, and human noise and traffic have all received brief consideration as drivers of plant–pollinator interactions via pollinator behaviour. Although they are associated with agricultural land use, pesticides are applied regularly and at high concentrations in residential areas to maintain lawns and gardens. One study found that neonicotinoid

lawn treatment negatively impacted bumblebee colonies, but the effect was removed if flowers exposed to direct application were mowed directly after (Larson, Redmond & Potter 2013). Common urban air pollutants such as diesel exhaust break down some floral volatiles in a laboratory setting, which reduces recognition by trained honeybees and may interfere with honeybees locating rewarding flowers by smell (Girling *et al.* 2013). Nocturnal plant–pollinator interactions may also be sensitive to light pollution, which attracts night-flying insect pollinators like moths (Fox 2013). The effects of light on pollination by nocturnal vertebrates are unknown, but are likely affected by light-avoidance behaviours, as demonstrated in seed-dispersing bats (Lewanzik & Voigt 2014). Finally, human noise and traffic may impact plant–pollinator interactions by frightening animals. An unusual example is from Argentina, where European house sparrows (*Passer domesticus*) forage nectivoresly on South African ornamental aloe (*Aloe arborescens*). Sparrow visitation to aloe plants and movement between plant patches decreased on weekends, apparently in response to higher traffic and pedestrian activity (Leveau 2008).

Future directions

Studies that explicitly attempt to link specific urban drivers with changes in community composition and consequences for partner reproduction or nutrition are needed to understand the roles of key plant–pollinator traits, such as phenology, body size and mutualist specialization. Thus far, studies have identified sensitive traits in plants or pollinators that do not have readily interpretable meaning vis-à-vis plant–pollinator interactions, such as nesting habitat and seed size (Hernandez, Frankie & Thorp 2009; Williams, Hahs & Vesik 2014). Even when relevant sensitive traits are identified, such as lower proportions of specialist pollinators in urban habitats (Hernandez, Frankie & Thorp 2009), few studies attempt to determine whether partner species experience any consequences. Alternatively, traits like pollinator body size may have demonstrated consequences for partner species (Geslin *et al.* 2013), but researchers have yet to identify consistent responses to specific urban drivers. Additionally, both the studies we review here and the literature overall are heavily biased towards insect and especially bee pollinators. Flies were rarely represented, despite evidence from agricultural and natural systems that flies are frequent flower visitors and passive pollen carriers (Winfree, Bartomeus & Cariveau 2011; Orford, Vaughan & Memmott 2015). Further research is needed to determine the extent to which the mechanistic pathways presented here function similarly in systems dominated by non-bee pollinators, for example in regions where vertebrate pollination is common.

As discussed in the urban climate section, the current literature on urban plant–pollinator interactions is heavily biased towards temperate cities in Europe and North America. Cities share many abiotic and biotic features, but

vary widely in how those features differ from the regional natural habitats they are superimposed upon (Pickett *et al.* 2011). Therefore, similar urban drivers may filter plant–pollinator traits differently in different biogeographic regions. We expect large collaborative studies that achieve replication across cities will continue to contribute important insights into such regional contexts (e.g. La Sorte *et al.* 2014). Expanding current understanding to include cities in Africa and Asia is particularly important since these continents will experience the great majority of global urban expansion in coming decades (Seto, Güneralp & Hutyra 2012).

Finally, environmental heterogeneity exists within as well as between cities (Pickett *et al.* 2011). For example, higher bee abundance was associated with urban areas of higher human population density, likely mediated through higher abundance of flowers (Lowenstein *et al.* 2014). Within urban areas, neighbourhood income level is an important driver of plant community properties such as richness and proportion of non-native ornamentals (e.g. Hope *et al.* 2003), and we expect that these effects of socio-economics extend to pollinators and plant–pollinator interactions, although this was unsupported by studies in New York City (Matteson, Grace & Minor 2013) and Chicago (Lowenstein *et al.* 2014). Despite high within-urban heterogeneity, we expect that the broad drivers we discuss here are fairly universal to urban landscapes and that the mechanisms documented in the literature can be expected to occur in many contexts albeit with widely differing strengths and outcomes. A key challenge is understanding the extent to which variation in surrounding environmental variables, such as soil moisture, species identity, management and landscape configuration, modifies the effect of the main drivers identified in this review.

Conclusions

Many studies reviewed here demonstrate the benefits of urban environments as a study system for understanding the mechanistic effects of different global change drivers on plant–pollinator interactions. For example, urban habitat fragmentation has provided a tractable system in which to study pollinator foraging movement and behaviour as mechanisms driving fragmentation effects on plant pollination and reproduction. Urban research has also contributed to understanding the role of pollinator foraging preference in plant–plant competition, by making use of the high concentration of non-native plants in urban environments. We expect that urban areas additionally provide a uniquely powerful system for researching effects of large community-level shifts in bloom phenology, driven by non-native plants and management practices such as selection of long-blooming cultivars and irrigation, as well as intraspecific phenology shifts driven by urban warming. Because large urban areas provide more extreme temperature conditions than can be observed in regional temperature trends across time, urban warming may provide a

useful proxy system for studying the effects of climate warming on plant–pollinator interactions. Urban environments also provide gradients in many different environmental contaminants, such as soil nitrogen and heavy metal pollution, which are valuable for extending the results of small-scale mechanistic studies to landscape scales. Future studies are needed to address knowledge gaps such as the role of traits in community filtering mechanisms, and to correct research biases towards temperate European–American regions and bee pollinators.

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Data Accessibility

This review does not use data and therefore is not associated with archived data.

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