



Changes in Land Use and Land Cover Along an Urban-Rural Gradient Influence Floral Resource Availability

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Abstract

Purpose of Review While several hundred thousand species of insects, mammals, and birds rely on flowers for food or reproduction, a surprising dearth of literature focuses specifically on floral resources. An understanding of floral resource availability is particularly necessary in urban areas, which have recently been proposed as important habitat for declining pollinator populations. In this study, we aim to synthesize existing information and provide new insights about the effects of land use and land cover (LULC) change and urbanization on the distribution, diversity, and abundance of floral resources.

Recent Findings Our results suggest that certain LULC types provide more floral resources than others. In particular, urban lands may have higher floral density than agricultural or natural lands. However, we also observed inconsistent findings between studies, and the relationship between urbanization and floral resource availability may vary by city, with this variation possibly due in part to city size, LULC composition, regional biome, and biases in sampling.

Summary It appears that cities have the potential to provide an important source of floral resources. However, a complete understanding of the effects of urbanization on floral resources requires that landscape composition and heterogeneity be taken into account. We recommend that more studies estimate floral resource availability at a landscape scale by combining data about LULC composition with data about floral resource availability within various LULC types. These studies should focus specifically on flower communities and be conducted along a full urban-rural gradient.

Keywords Flower abundance · Flower diversity · Urbanization · Resource availability · Pollinators · Urban biodiversity

Introduction

Flowers provide critical resources for a great diversity of animals. More than 350,000 arthropod species regularly use

flowers for food, reproduction, or other resources [1], and other taxonomic groups such as birds, bats, rodents, lizards, and even carnivorous mammals also feed on nectar and pollen [2, 3]. While a large body of literature documents the

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distribution and diversity of plants [4, 5], a surprising dearth of literature focuses specifically on the availability of floral resources.

Most of what is known about floral resources comes from pollinator studies conducted in rural areas. From these studies, in which floral resources are usually treated as a predictor variable, we know that floral resource availability varies with differences in land use and/or land cover (LULC). For example, in a Nigerian tropical rainforest ecosystem, secondary forests had higher floral abundance than agricultural land [6]. In rural and suburban landscapes of southeastern Canada, floral diversity was higher in residential gardens than in semi-natural ruderal grasslands, although a lower proportion of plant species in gardens were visited by bees [7]. Because floral resources differ with LULC type, and because LULC composition varies along an urban-rural gradient, urbanization is also likely to alter floral resource availability. From the limited number of urban studies that have been conducted, it is clear that floral resources can vary widely between urban LULC types [8, 9]. However, while urban areas have been proposed as refuges for pollinators [10], information about floral resources across the diversity of urban LULC types is still sparse. Therefore, more research on flower availability across a full urban-rural gradient is needed to understand the ability of urban landscapes to provide necessary resources to flower visitors.

Studies that do consider floral resource distribution along an urban-rural gradient often use a simplified urbanization gradient approach and do not consider the full range of LULC types present. For example, urbanization may be measured using proxies such as human population density (e.g., [11]), housing density (e.g., [12]), or impervious surface cover (e.g., [13]). However, considering the full complexity of the landscape may be especially important in urban areas, which are highly heterogeneous at a fine spatial scale [14]. Given this heterogeneity, we should not simply assume that floral resources would vary uniformly with a single proxy of urbanization. Of the studies that have examined floral resources in a way that incorporates this heterogeneity of LULC, none have done so across the full urban-rural gradient. Therefore, there is a need for an evaluation of floral resources that moves beyond a simplified urbanization gradient approach and incorporates the changes in LULC composition that occur with urbanization.

This more nuanced approach to assessing the effects of urbanization on floral resource availability is necessary to gain an accurate understanding of the ways in which urbanization impacts flower visitors. Most animals that use floral resources are highly mobile and thus can make use of complementary resources distributed across a heterogeneous landscape. For example, in a study of five bumble bee species in England, worker bees from three of the five species were estimated to

have travelled over two kilometers from their colony while foraging [15]. Therefore, local estimates of floral resources derived from small quadrats may not accurately represent the resources that are available, or the suitability of a landscape, to most foragers. However, most studies only measure floral resources at the local level and do not consider the full spectrum of LULC types available in the surrounding landscape.

Our goal in this paper is to synthesize existing information and provide new insights about the effects of urbanization on the distribution, diversity, and abundance of floral resources. To accomplish this, we first review published research that (1) examines local-level floral resources in a variety of LULC types that exist along an urban-rural gradient, (2) evaluates the effects of urbanization on floral resource availability using simplified proxies of urbanization such as impervious surface cover or housing density, or (3) incorporates landscape heterogeneity into estimates of landscape-scale floral resource availability by scaling up local-level estimates of floral resources in multiple LULC types. We then combine published information about local-level floral resource availability with published information about LULC changes across an urban-rural gradient to provide a novel estimate of how landscape-level floral resources might change along that gradient. In doing this, we aim to offer a new understanding of the potential of urban areas to provide floral resources for the many thousands of species that rely on nectar or pollen as sources of food.

Methods

Literature Search and Extraction of Information

We conducted a systematic literature search for studies that provide information either about the direct relationship between urbanization and floral resources or about floral resources within LULC types that exist on an urban-rural gradient. First, we searched for studies that included both a key term related to urbanization (e.g., “urban,” “suburban”; see Appendix 1, Table A1 for a full list of search terms) AND a key term related to floral resource availability (e.g., “flower abundance,” “floral diversity”). We then searched for studies that included a key term either related to LULC (e.g., “land use,” “land cover”) or indicating a specific LULC category (e.g. “vacant lot*,” “grassland*”) AND a key term related to floral resource availability. We restricted our search to studies published within the last five years, and all searches were conducted between February and April 2020 using the Web of Science database. If we encountered additional relevant studies cited in the articles returned by our search, we included these as well.

Studies identified by our literature search were then reviewed to determine whether they were relevant to our study. We categorized studies as relevant if they met the following criteria: (1) evaluated the relationship between proxies of urbanization (e.g., population density, percent impervious surface cover) and floral resource availability, (2) provided information about floral resource availability in one or more LULC types, or (3) estimated floral resource, nectar, or pollen availability on a landscape scale using a combination of local-scale estimates of floral resource availability and data about landscape composition. All other studies were removed from our list. Additionally, we did not generally consider studies of experimentally planted floral resources or studies that focused on a subset of flowering plants rather than the full community (e.g., flowers pollinated by hummingbirds). We encountered many studies that collected information about floral resource availability but did not report the floral resource measurements; we were unable to use these studies.

From each study categorized as relevant, we collected information including the location of the study, its position on an urban-rural gradient (urban, semi-urban, or rural), the measurements of floral resource availability that were used (e.g., abundance, diversity, percent flower cover), whether or not the study provided information about seasonal changes in floral resource availability, and the LULC types considered in the study. To classify the position of a study along an urban-rural gradient, we took our cues from the authors. If the authors defined their study sites as “urban” or “rural,” then we used the same classification. If they defined their study sites as “suburban,” “exurban,” or “small town,” we classified these as “semi-urban.” Many of the rural studies did not use the term “rural”; however, any study that took place in large-scale agricultural fields, or a national park or other large natural area far from urban development, was also considered “rural.” For the LULC classification, we assigned papers to one or more of the following categories based on their study site description: agriculture (crops), agriculture (orchard), agriculture (grazed land), agriculture (non-cultivated), timber stand, roadside or other right-of-way, forest, grassland, other natural land, residential, urban park, urban agriculture, and other urban (including green roofs, paved areas, cemeteries, schools, and unclassified urban areas). LULC categories are defined further in Appendix 1, Table A2.

When possible, we used information from the articles to extract flower density. We were able to do this only when the authors of the study provided either a direct estimate of flower density or a combination of flower abundance, sampling area, and the number of times each site was sampled. We excluded studies in which this information was included only in a figure and studies in which precise values of flower density or abundance separated by LULC type were not provided. To ensure that estimates of flower density were comparable between different studies, we calculated flower density only for studies

in which clusters of small flowers such as inflorescences, umbels, and racemes were each counted as a single floral unit. We did not calculate density for studies that counted each individual flower within an inflorescence, or for studies that counted the abundance of flowering plants rather than the flowers themselves. Additionally, when the same data were reported in multiple articles, we only collected information about flower density from one of those articles. See Appendix 2 for flower density and other information about each relevant article.

Each density measure was linked with one of the LULC types described previously. Because we were able to calculate density from only a small portion of the studies that we reviewed, and because of the variability in factors such as geographic location, climate, and season that existed within the dataset, we did not statistically compare density between different LULC types. However, we report summary statistics of flower density within each LULC type, and further summarize the floral density data in four condensed LULC categories (residential, urban mix, agricultural, and natural) to facilitate the landscape-level analysis described in the following section.

Scaling Up Floral Density to the Landscape Scale

To estimate differences in landscape-level floral resource availability along an urban-rural gradient, we combined the flower density information described above with information about how LULC composition changes from the center of a city to surrounding rural areas. We extracted information about LULC composition along an urban-rural gradient from three transect-based studies of different cities: New York City, USA [16], Phoenix, USA [17], and Xiamen City, China [18]. The three cities differ in population size, city structure, climate, global context, and LULC composition along the urban-rural gradient, and thus allow for some broader generalization across ecologically and socially diverse regions of the world. We provide some information about the population size, biome, and LULC composition of these three cities in Appendix 3.

Since the studies of each city used different LULC classification systems, we began by converting the LULC types in each paper into four categories that could be applied to all cities: residential land, urban mix (including all non-residential urban land), agricultural land, and natural land. Then, for each city separately, we used information about floral density within each of these four LULC types and the landscape composition in each city to estimate floral density along the urban-rural gradient. To do so, we first divided the urban-rural gradient into 10 or 20 km bands, with each band indicating the distance from city center. We used 10-km bands for the first 40 km from the city center, then switched to 20-km bands for distances beyond 40 km. In each band, we extracted

the approximate percent cover of each of the four LULC types described above. Then, we multiplied the floral density within each LULC type by the percent cover of that LULC type to estimate the total density of floral resources in each band.

Results and Discussion

Availability of Information

Our systematic literature search yielded a total of 789 studies, 135 of which were considered relevant to our review (Appendix 2). Of the relevant studies, 59 were conducted in Europe, 48 in North America, ten in South America, nine in Africa, six in Asia, and five in Australia (Fig. 1). Most of the relevant studies examined floral resources at only one location along the urban-rural gradient, but 17 considered either a full or partial urbanization gradient, allowing for direct comparisons between floral resources at different levels of urbanization. A total of 112 of the relevant studies provided information about floral resources in rural areas, 22 reported on urban areas, and 22 reported on semi-urban areas (these study categories are not mutually exclusive) (Fig. 2a). At the rural end of the gradient, a similar number of studies were available in both agricultural and natural LULC types. When considering specific LULC categories, the greatest number of studies were conducted in grasslands, followed by croplands and forests, with the smallest number of studies occurring in timber stands (Fig. 2b).

Relationship Between Proxies of Urbanization and Floral Resource Availability

While research on the effects of urbanization on pollinator communities has proliferated in recent years (e.g., [19, 20]), our search returned only eight studies published between 2016 and 2020 providing information about the relationship between urbanization and floral resource availability. These studies explored the relationship between measurements of urbanization—including population density [11], housing density [12], and impervious surface cover [13]—and flower abundance, diversity, or functional traits. The primary focus of most of these papers was the relationship between urbanization and pollinator communities, with the relationship between floral resource availability and urbanization often offered as a potential explanation for changes in pollinator abundance or diversity [21].

The inconsistent results of these eight studies emphasize the need for more research on the relationship between urbanization and floral resource availability. While one study found that building density had a positive effect on peak bloom abundance [12], another study reported a negative correlation between flower abundance and impervious surface [13]. Two studies found no effect of urbanization on flower abundance [7, 9]. Results describing the effects of urbanization on flower richness are similarly varied. Theodorou et al. [21] and Fitch [9] both found a positive effect of urbanization on flower richness. Conversely, Graves et al. [12] found that species richness decreased as building density increased. Two

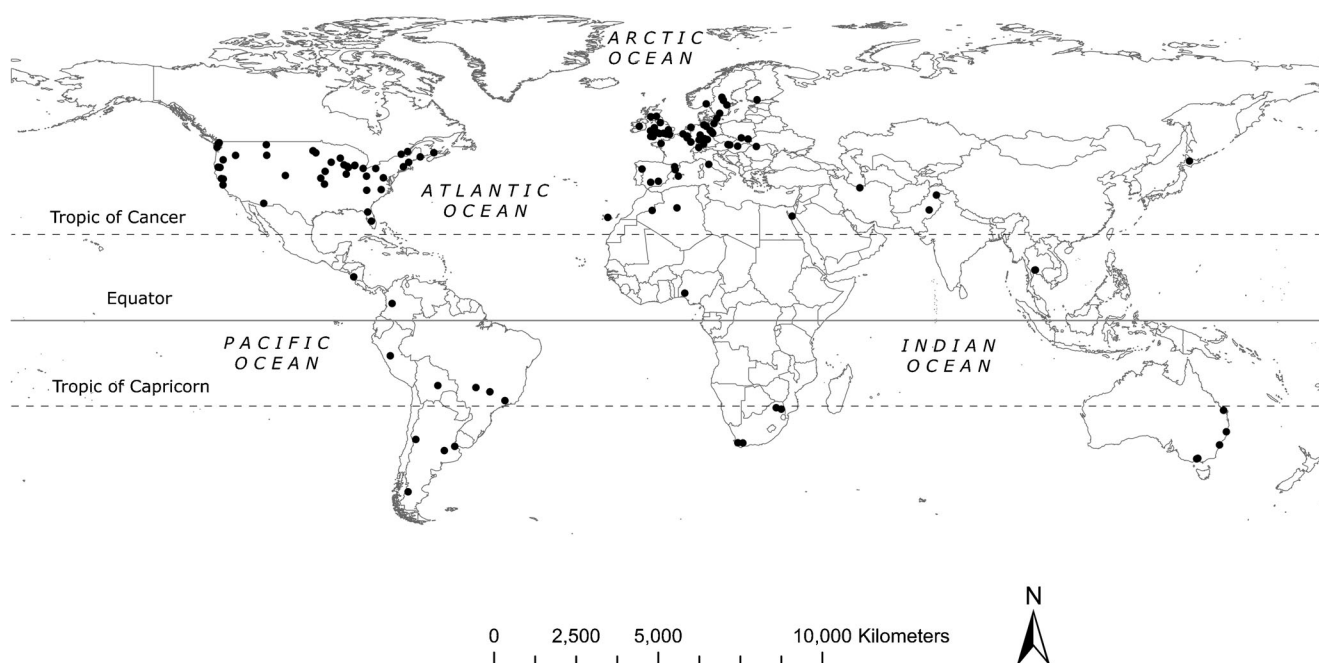


Fig. 1 Locations of studies that provide relevant information about floral resources

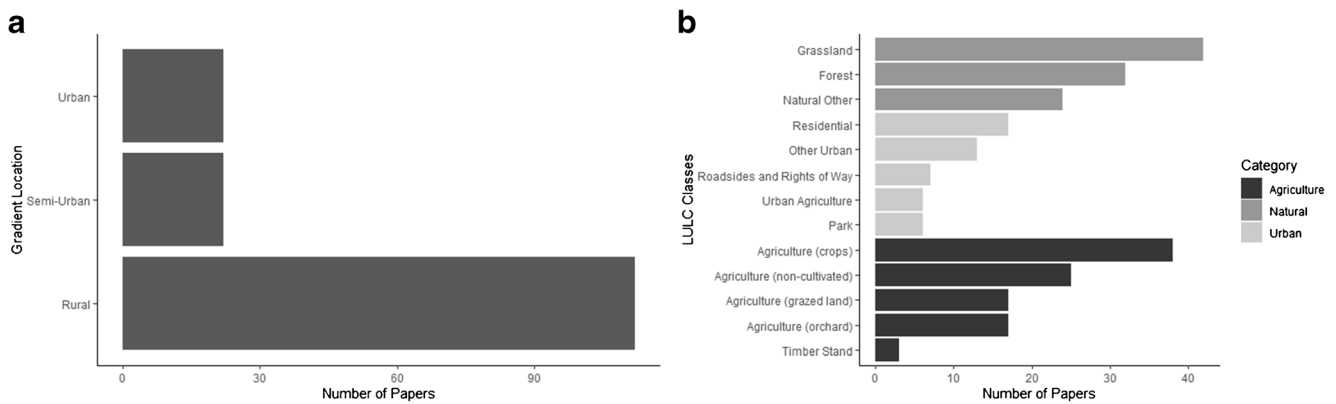


Fig. 2 The number of relevant studies identified by our review (**a**) at urban, semi-urban, and rural positions along an urban-rural gradient, and (**b**) within different LULC classes. Papers were counted more than

once in these figures if they provided information about floral resources at different locations along the urban-rural gradient or in different LULC categories

additional studies reported non-linear relationships between urbanization and floral resource availability: in residential areas of Chicago (USA), flower richness was found to peak at intermediate housing densities [11], while in Denver (USA), flower richness was found to be lowest in suburban areas, highest in rural areas, and intermediate in urban areas [19].

In addition to changes in flower abundance and richness that occur with urbanization, two studies also reported changes in the trait composition of floral resources. For example, in a small city in Pennsylvania (USA), flower communities in the city center included a greater percentage of introduced species than communities at rural field sites [20]. In residential neighborhoods of Chicago (USA), the richness of blooming annual species increased linearly with development intensity while the richness of perennial species peaked at an intermediate development intensity [11]. Floral abundance of ornamental species also peaked at an intermediate development intensity in Chicago, but floral abundance of weedy species was unrelated to urbanization [11].

The contradictory results among different studies could be caused by the use of different urbanization metrics, and by a failure of some studies to evaluate nonlinear models [11]. In addition, the effects of urbanization on floral resource availability are likely to vary in different contexts. For example, the relationship between urbanization and floral resource availability may depend on the size of the city and the portion of the urban-rural gradient in which the study is conducted. In dense downtown areas of large cities, residents often live in apartments without yards or gardens, and shade from high rise buildings inhibits flower growth [22]. As a result, studies conducted in these areas might be more likely to observe a negative effect of urbanization on floral resource availability. In contrast, studies evaluating neighborhoods with lower overall human population densities may be more likely to reveal a positive effect of urbanization on floral resource availability because increases in housing density lead to an increase in the number of home gardens present within an area, resulting in

greater floral diversity. Similarly, the relationship between urbanization and floral resource availability is likely to depend on the biome in which the city is located. For example, urban areas located in low-diversity biomes such as coniferous forests may have relatively higher floral diversity in comparison to their outlying rural areas, while urban areas located in high-diversity biomes may have relatively lower floral diversity in comparison.

Finally, different relationships between urbanization and floral resource availability may be observed in different LULC types, and some of the variation in patterns observed between studies may be related to the LULC categories in which these studies were conducted. For example, Theodorou et al. [21] found that flower richness was higher in urban than rural areas while Graves et al. [12] found that flower richness was lower in more densely populated areas. This difference could be due to the fact that the more rural study sites considered by Theodorou et al. [21] were composed largely of cropland while the study sites considered by Graves et al. [12] were located in forested areas, pastures, and hay fields. Overall, the studies relating proxies of urbanization to floral resource availability took place in a wide variety of LULC types, including urban parks, residential areas, urban agricultural sites, non-urban agricultural sites, natural and semi-natural habitats, and others. Individually, however, most studies focused on one to three LULC types. To gain a clearer understanding of the overall relationship between urbanization and floral resource availability, we need studies that consider all of the LULC types that exist along an urban-rural gradient and collect data across the entire urbanization gradient from the city center to surrounding rural areas.

While simplified proxies of urbanization may be useful in understanding broad patterns of change across an urban-rural gradient, and particularly for understanding change within a single LULC type, we suggest that simplified proxies are probably less useful for researchers who wish to compare results from different LULC types or understand floral

resource availability at the landscape scale. Instead, studies that take into account the heterogeneity of LULC types within urban landscapes are likely to provide a more accurate and nuanced picture of the complex relationships between urbanization and floral resource availability. More research would help illuminate the specific situations under which simplified proxies of urbanization can or should be used.

Variation in Floral Resource Availability Between LULC Types

Most studies in our review provided information about floral abundance, diversity, trait composition, and/or seasonality in only one or two LULC types. However, some studies included multiple LULC types, facilitating direct comparison. Two papers that stand out in this regard are Baldock et al. [8] and Baude et al. [23], both of which had very thorough coverage of numerous LULC types across Great Britain. Baldock et al. measured flower abundance and diversity within nine major urban LULC types in four British cities, and found that community gardens provide floral resource “hotspots” in urban areas [8]. Baude et al. compared nectar availability in all major *non*-urban LULC types and determined that calcareous grassland, broadleaved woodland, and neutral grassland produced the greatest amount of nectar per unit area from the most diverse sources, whereas arable land produced the least [23].

Other studies, with fewer LULC types, provide useful insights as well. For example, two different Canadian studies suggest that flower richness may be higher on residential lands compared to semi natural grasslands [7] or forested areas [24], possibly due to the diversity of ornamental species planted in gardens. Studies in rural Wisconsin (USA) [25] and Nigeria [6] both found lower flower abundance on agricultural land compared to forests or woodlands, aligning with patterns observed by Baude et al. [23]. Some studies compared provenance or conservation status of flowering plants in different LULC types. A study in a small Pennsylvania (USA) city observed the most native species in athletic field edges, followed by the city center, a college campus, and lastly home yards [20]. Undisturbed scrublands in Florida, USA, were found to have more endangered flowering species than pastures while non-native species were found only in pastures [26].

Seasonal patterns of floral resource availability were also found to vary between LULC types. In grasslands, floral resource availability tended to increase later in the flowering season [27–29]. In contrast, forests supported more resources earlier in the growing season [30, 31]. Like woodlands, orchards have more abundant flowers in spring that decline over time [25]. In other agricultural areas, including road verges and agro-environmental schemes, floral resources were greatest mid to late season [32, 33]. The length of the flowering period varies as well within different agricultural

LULC types. In one study, species in continuously grazed pastures had a longer flowering period compared to abandoned and restored pastures [34]. Another study found that hedgerows around agricultural fields had the highest phenological continuity of nectar production, while field edges had high nectar production but only for short periods of time [35]. Less research was available on the seasonality of floral resources in urban LULC types. However, one study found that flowering plant abundance declined throughout the growing season in urban residential areas [24], and another reported that flower availability was greatest mid-growing season in urban community gardens [36].

In our own comparison of floral density between LULC types, median flower density was highest in the “urban mix” LULC type and lowest in natural LULC types (Fig. 3a). This pattern could be due in part to the ways in which humans interact with floral resources in urban areas. For example, parks, which are part of the urban mix, often include flowerbeds with high densities of showy flowers. Furthermore, the urban mix includes community gardens, a LULC type with high densities of flowering plants by design that has been shown to provide exceptional resources to pollinators [8]. However, it is also important to note that the trends we observed may be partially due to sampling bias. Because many studies in urban areas are conducted in places with garden beds while very few are conducted on impervious surfaces, it is likely that we have overestimated flower density in cities. Floral density in agricultural areas may also have been overestimated due to the fact that sampling in crop fields is often intentionally conducted during peak bloom.

We also found that flower density varied within urban, agricultural, residential, and natural categories. For example, within agricultural LULC types, non-cultivated agricultural areas had higher floral densities than grazed lands, orchards, or crops (Fig. 3b), a result that is confirmed by several studies that directly compare these different LULC types [25, 37, 38] and is likely due to pollinator-friendly practices commonly used in non-cultivated areas such as the planting of flower strips. Among the urban mix LULC types, parks, roadsides, and other urban land uses had similar median floral densities ranging from 7.6 to 11.4 flowers/m², while studies in residential areas reported both the largest range of floral density values and the highest density value among all urban categories.

Landscape-Scale Floral Resource Availability

Our review uncovered 14 papers that estimated floral resources across landscapes. We identified two general approaches to scaling up local estimates of floral resources to larger areas. The first approach, taken by only a single paper, used generalized linear models to predict floral resources based on a suite of environmental predictor variables such as

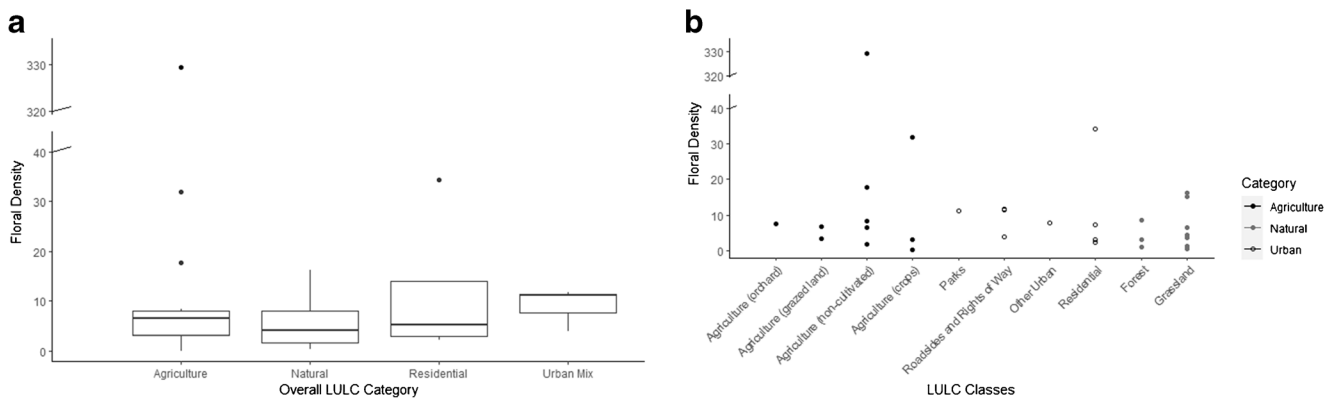


Fig. 3 Flower density within different LULC classes. Panel **a** shows flower density within the broader LULC categories that were used to estimate landscape-level floral resource availability, with median values

shown as horizontal lines inside each box. Panel **b** shows flower density within specific LULC classes. Each dot represents an individual study that was reviewed

topographic and soil characteristics [12]. These predictions were then mapped into geographic space using GIS software. The remaining papers all took a LULC-based approach to scaling up floral resources. In this second approach, floral resources are assumed to vary predictably with LULC class. Floral density (e.g., [16]), richness (e.g., [17]), nectar availability [23], or pollen availability [37] were measured or estimated in various LULC classes and then extrapolated across the landscape using LULC maps and GIS. The most thorough example of this second approach is Baude et al. [23], who estimated nectar availability for 260 plant species and combined this information with a historical, national-scale survey of plant community composition from 32 land classes across Great Britain (further condensed to 11 classes for landscape-scale extrapolation). Unfortunately, due to the design of the historical plant survey, urban areas were excluded from analysis. The LULC extrapolation approach has been formalized in the ecosystem service mapping software InVEST [39], which includes a pollination model adapted from Lonsdorf et al 2009 [40]. The InVEST pollination model is often parameterized based on expert opinion of floral resource availability rather than field data and combines estimates of floral resource availability with knowledge of pollinator nesting requirements and flight distances to predict pollination services. Although it was created for use in agricultural landscapes, it has been applied at least once in urban settings [41].

Studies varied in the scale at which they estimated floral resources. Some studies produced continuous, spatially explicit maps with pixel- or polygon-level estimates of *local* (i.e., within pixel or polygon) floral resources, with spatial extents ranging from 7330 km² [12] to the entirety of Great Britain (> 200,000 km²; 25) and spatial resolutions ranging from 30 m pixels [12] to LULC parcels of variable size [23]. Other studies used buffers of a defined radius to produce

pixel- or point-level estimates of *landscape-scale* (i.e., calculated over the entire buffer) floral resources. Buffer sizes were selected to represent foraging distances of focal organisms; in studies focused on bees, buffers were often one [42] or two kilometers [43] while a study focused on hoverflies tested several smaller buffers ranging from 100 to 1000 m [37].

Landscape-scale studies tended to focus on measures of landscape composition such as flower cover, abundance, or diversity. Among the studies we examined, only one explicitly measured the spatial arrangement of floral resources [12]. To understand wildflower viewing opportunities available to the public, Graves et al. [12] mapped hotspots of flower richness and abundance in the southern Appalachian Mountains (USA). They found that floral resources were spatially autocorrelated across the landscape, and that patch density and size varied with season. While this lack of focus on configuration of floral resources is not surprising given that landscape configuration is generally thought to be less important for pollinators than composition [44], a recent review on the effects of urbanization on pollinators has called for more research on configuration of the urban matrix [45].

Of the papers that examined floral resources across large spatial extents, only two focused on urban landscapes. The first paper, which did not empirically measure floral resources, used the InVEST pollination model to test the effects of different landscape modification scenarios on pollination services in community and residential food gardens in Chicago, USA [41]. The researchers found that converting 5% of lawn area to flower gardens could improve pollination services throughout the city, but the best spatial strategy differed depending on the desired outcome. In particular, if the objective was to enhance pollination for home gardeners, then creating flower gardens in a spatially distributed way across the city would be most beneficial. However, to enhance pollination at

existing urban farms and community gardens, the best strategy would be to concentrate the increased floral resources close to (within 250 m) the farms themselves. The second study took place in four cities in the UK [8]. The researchers conducted an empirical assessment of plants and pollinators in each city, comparing floral availability between nine major urban land uses and identifying the most important land uses for pollinator communities. By spatially extrapolating the results of their field surveys across each city, and using landscape modification scenarios, the researchers determined that increasing the area of allotment (i.e., community) gardens would be most likely to increase robustness of plant-pollinator networks. Neither of these studies compared floral resources inside cities to those outside cities.

At the rural end of the gradient, as with most papers we reviewed, landscape composition was the main focus. These studies suggest that open landscapes have a greater floral resource availability than forested landscapes [12], and landscapes with more natural LULC types may provide more floral resources than landscapes dominated by agricultural LULC types [23, 46]. Heterogeneous landscapes, with a mixture of LULC types, contain patches with different types and abundances of floral resources and are likely to provide a greater diversity and continuity of floral resources over the course of a year [12, 23, 25, 47]. Additionally, edge habitats such as hedgerows, field edges, and roadsides provide some of the highest densities of floral resources, suggesting that landscape configurations that alter edge habitat can also play an important role in landscape-scale floral resource availability [23, 37, 46].

To gain a more complete understanding of the effects of urbanization on floral resources, more studies should take the approach of Baldock et al. [8] and collect empirical field data from a wide range of urban LULC types. Furthermore, the data collection should be extended outside the city. Similar to Baldock et al. [8], sample sites should be geographically stratified to capture broad-scale variation in floral resources within individual LULC types. Below, we describe a landscape-scale approach in which we combine information about floral density in multiple LULC types with information about the distribution of LULC types along several urban-rural gradients to understand the relationship between floral resource availability and urbanization.

Scaling Up Floral Density to the Landscape Scale

By combining our estimates of flower density in various LULC types with information about landscape composition along an urban-rural gradient in three different cities, we were able to estimate how landscape-scale floral resource availability might change as you move from a city center to outlying rural lands. Our calculations suggest some variation between the three cities (Fig. 4) that is due to differences in landscape composition. While the three cities had fairly similar LULC in

the inner band (i.e., 0–10 km from the city center), with residential land as the most abundant LULC type in all cities, they began to diverge somewhat in the suburban areas. In particular, Xiamen City had a much higher proportion of ‘urban mix’ in the suburbs compared to the other two cities. Since urban mix had the highest floral density in our analysis, this produced an estimated peak in floral density in the suburbs for Xiamen City but an estimated slow decline in floral density when moving away from the center of the other two cities.

Our predicted patterns of floral resource availability along an urban-rural gradient are due to landscape composition along the same gradient, which in turn is determined by the socioeconomic and political processes guiding city growth. While cities are often assumed to grow in concentric rings, in reality, contemporary cities often grow in a more sprawling way resulting in embedded patches of agricultural and natural lands in suburban areas [48]. Because cities in different parts of the world often experience different growth patterns [49], we can also expect variation in patterns of floral resource availability. Of course, biome type and the LULC composition at the rural end of the urbanization gradient also impacts patterns of floral resource availability along an urban-rural gradient. For example, floral resources in a temperate forest are likely very different from floral resources in a tropical forest. However, because the density estimations that we used in these calculations are averages from multiple studies conducted around the world, they do not account for differences in floral density that are the result of local climatic conditions. Therefore, our estimates of landscape-level floral resources are not meant to be accurate for the specific regions we examined but instead are meant to represent very general trends across the globe.

Other Factors Affecting Floral Resource Availability on an Urban-Rural Gradient

While we have focused on the impacts of urbanization and associated changes in LULC composition on flower communities, a multitude of other factors also impact floral resource availability along an urban-rural gradient. In addition to current landscape patterns, land use legacies play an important role in shaping urban ecological communities [48]. In Phoenix AZ, residential yards that had previously been agricultural land contained more than twice as much organic matter, carbon, and nitrogen than yards converted from native desert [50], a change likely to be associated with differences in the composition of flower communities. Land use legacies also play an important role in shaping flower communities on the rural end of the urbanization gradient. For example, in arid grasslands of the Pacific Northwest, flower abundance was higher in remnant prairies than in prairie restorations [28].

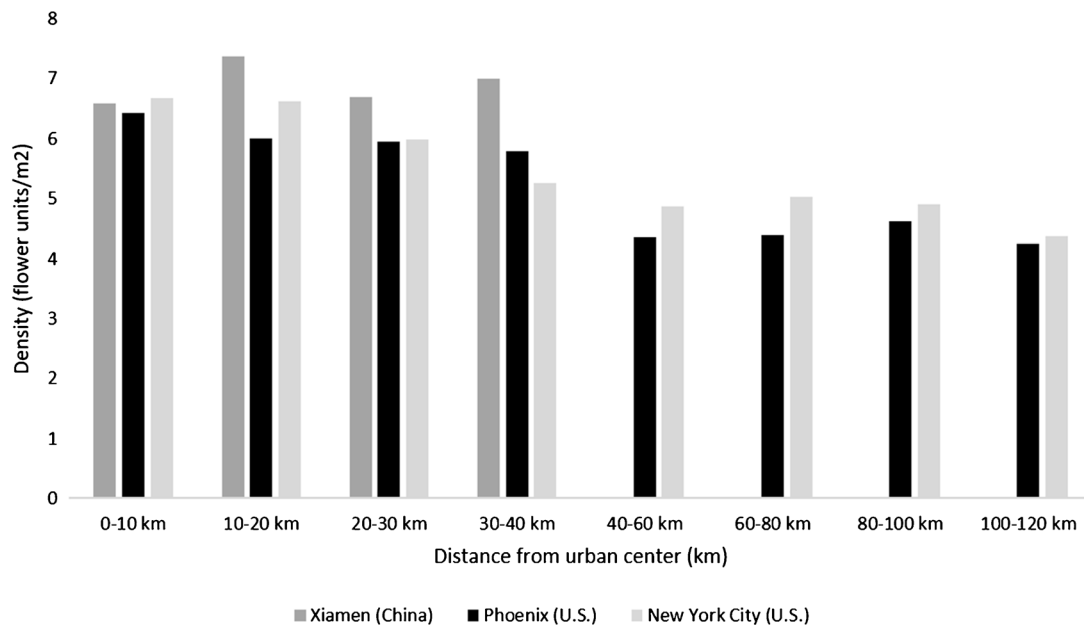


Fig. 4 Estimates of landscape-scale flower density across an urban-rural gradient in Xiamen (China), Phoenix (USA), and New York City (USA). These estimates were calculated by combining the flower density data

shown in Fig. 3a with published information regarding the LULC composition of each city. LULC information for Xiamen City was only available for the first four distance bands

Additionally, socioeconomic status has important effects on the availability of floral resources in cities. Several studies have found evidence that the “luxury effect”

impacts the composition of urban flower communities, with a greater abundance and diversity of flowers and flowering plants present in higher income areas [8, 51].

Table A1 Search terms for literature review

Urbanization	Land use / land cover		Floral resource availability
Urban*	Land Use	Crop*	Flower abundance
City	Land Cover	Grassland*	Flower availability
Cities	LULC	Pasture*	Flower diversity
Urban-Rural	Vacant lot*	Rights of Way*	Flower density
Rural-Urban	Yard*	Industrial	Flower species richness
Urban-Suburban	Lawn*	Wasteland*	Flower richness
Suburban-Urban	Garden*	Brownfield*	Flower resources
Urban-Exurban	Park*	Residential*	Flower bloom
Exurban-Urban	Cemetery*	Commercial*	Floral abundance
Suburb*	Forest*	Develop*	Floral availability
Exurb*	Prairie*	Green Space*	Floral diversity
	Habitat*	Farm*	Floral density
	Scrub*	Old Field*	Floral species richness
	Woodlands*	Natural Area*	Floral richness
	Savanna*	Green Infrastructure	Floral resources
	Desert*	Roadside*	Floral bloom
	Wetland*	Community garden*	
	School*	Orchard*	
	Rangeland*	Vineyard*	
	Agriculture*	Nursery*	

Management decisions enacted by city planners, homeowners, farmers, and natural resource managers also impact the abundance, diversity, and trait composition of flowers in cities, suburbs, and rural areas. For example, homeowners who spend more time gardening are able to increase the abundance and richness of flowering plants in their yards [51], and reducing the frequency of mowing has been shown to increase flower abundance in suburban lawns [52]. In agricultural landscapes, organic farming practices increase the availability of floral resources in both croplands [53] and cow pastures [54], and in natural areas, salvage logging implemented after severe wildfires has been shown to increase flower density [31].

Conclusions

Our results suggest that cities do have the potential to provide an important source of floral resources. In some cases, flower abundance and diversity appear to be higher in urban areas than in surrounding rural areas, possibly due to high floral density within certain LULC types that are common in cities such as yards and urban parks. This is important because it supports suggestions made recently (e.g., 8) that cities may be able to provide important habitat for pollinators and other flower visitors. Pollinator populations are in decline globally, due in large part to habitat loss in rural areas [55, 56], but the

recent research we have compiled here suggests that managing urban areas to provide resources to pollinators could play an important role in their conservation. Of course, a high abundance and diversity of floral resources alone does not ensure that flower visitors' needs will be met. For example, many pollinator species also require dead wood or loose bare soil for nesting sites [57].

While our results are encouraging, it is also important to note that they are inconsistent. It appears that the relationship between urbanization and floral resource availability may vary by city, with this variation possibly due in part to city size [22], LULC composition, and surrounding biome. Urban landscapes tend to be highly heterogeneous, and floral resource availability varies widely between LULC types. Furthermore, a single LULC type—such as residential land—could vary significantly in floral resource availability between the urban and rural ends of the gradient. Therefore, a complete understanding of the effects of urbanization on floral resource availability requires that landscape composition and heterogeneity be taken into account. We recommend more studies that model landscape-level floral resources by combining data about LULC composition with data about floral resource availability within various LULC types. These studies should focus specifically on understanding flower communities and be conducted along a full urban-rural gradient.

Appendix 1

Table A2 LULC categories used for classification of studies

LULC Category	Description
Agriculture (crops)	Any crop field that is not an orchard
Agriculture (orchard)	Agriculture that involves harvesting fruit from trees
Agriculture (grazed land)	Any form of agriculture that involves grazing animals (e.g. ranch, pasture, pastoral land)
Agriculture (non-cultivated)	Field edges, recently abandoned fields, hedgerows, fallows
Timber Stand	Areas used for timber extraction
Roadsides and Rights of Way	Roadsides, road verges, other rights of way
Forest	Primary forest, secondary forest, wild groves, rainforest, including forest edge and post-wildfire forests
Grassland	Prairies, meadows, old fields
Natural Other	Scrubland, shrubland, marshes, savanna, swamp, desert
Residential	Home gardens, lawns
Urban Parks	Urban parks and botanical gardens
Urban Agriculture	Community gardens and other agriculture occurring in urban settings
Other Urban	Green roofs, paved areas, commercial areas, cemeteries, schools, unclassified urban areas

Appendix 2

Full citation	Continent	Category 1 paper? ¹	Category 2 paper? ²	Category 3 paper? ³	Gradient location	LULC Types Considered	Flower Density (Floral Units/m ²)
Adedjoja, O., & Kehinde, T. 2018. Changes in interaction network topology and species composition of flower-visiting insects across three land use types. <i>AFRICAN JOURNAL OF ECOLOGY</i> , 56(4, SD), 964–971.	Africa	No	Yes	No	Urban, Semi-Urban, Rural	Agriculture (crops), Forest, Grassland	NA
Adhikari, S. L. A. Burkle, K. M. O. Neill, D. K. Weaver, C. M. Delphia, and F. D. Menalled. 2019. Dryland Organic Farming Partially Offsets Negative Effects of Highly Simplified Agricultural Landscapes on Forbs, Bees, and Bee-Flower Networks. <i>Environmental entomology</i> 48:826–835.	North America	No	Yes	No	Rural	Agriculture (crops)	NA
Adhikari, S., L. A. Burkle, K. M. O. Neill, D. K. Weaver, and F. D. Menalled. 2019. Agriculture , Ecosystems and Environment. Dryland organic farming increases floral resources and bee colony success in highly simplified agricultural landscapes. <i>Agriculture, Ecosystems and Environment</i> 270–271:9–18.	North America	No	Yes	No	Rural	Agriculture (orchard), Agriculture (non-cultivated)	NA
Alonso, C., Arceo-Gomez G., Meindl, G. A., Abdala-Roberts, L., Parra-Tabla, V., & Ashman, T.-L. 2017. Delimiting plant diversity that is functionally related via interactions with diurnal pollinators: An expanded use of rarefaction curves. <i>FLORA</i> , 232, 56–62.	Europe, North America	No	Yes	No	Rural	Grassland, Other Natural	NA
Amélie Y. Davis, Eric V. Lonsdorf, Cliff R. Shierk, Kevin C. Matteson, John R. Taylor, Sarah T. Lovell, Emily S. Minor. 2017. Enhancing pollination supply in an urban ecosystem through landscape modifications. <i>Landscape and Urban Planning</i> , Volume 162, 157–166	North America	No	No	Yes	Urban	Residential, Urban Parks, Urban Agriculture	NA
Babaei, M.-R., Fathi, S. A. A., Gilasian, E., & Varandi, H. B. 2018. Floral preferences of hoverflies (Diptera: Syrphidae) in response to the abundance and species richness of flowering plants. <i>ZOOLOGY IN THE MIDDLE EAST</i> , 64(3), 228–237.	Asia	No	Yes	No	Rural	Grassland	NA
Baldock, K. C. R., Goddard, M. A., Hicks, D. M., Kunin, W. E., Mitschunas, N., Morse, H., ... Memmott, J. 2019. A systems approach reveals urban pollinator hotspots and conservation opportunities. <i>NATURE ECOLOGY & EVOLUTION</i> , 3(3), 363+	Europe	No	Yes	Yes	Urban	Residential, Urban Parks, Other Urban, Roadsides	Residential: 34.36; Urban Parks: 11.21; Roadside: 11.43; Other Urban: 7.64
Balzan, M. V., Bocci, G., & Moonen, A.-C. 2016. Landscape complexity and field margin vegetation diversity enhance natural enemies and reduce herbivory by Lepidoptera pests on tomato crop. <i>BIOCONTROL</i> , 61(2), 141–154.	Europe	No	Yes	No	Rural	Agriculture (non-cultivated)	NA
Bartual, A. M., L. Sutter, G. Bocci, A. C. Moonen, J. Cresswell, M. Endling, B. Giffard, K. Jacot, P. Jeanneret, J.	Europe	No	Yes	No	Rural		NA

Holland, S. Pfister, O. Pintér, E. Veromann, K. Winkler, and M. Albrecht. 2019. The potential of different semi-natural habitats to sustain pollinators and natural enemies in European agricultural landscapes. <i>Agriculture, Ecosystems and Environment</i> 279:43–52	Europe	No	No	Yes	Rural	Agriculture (crops), Agriculture (orchard), Agriculture (non-cultivated)	NA
Baude, M., Kunin, W. E., Boatman, N. D., Conyers, S., Davies, N., Gillespie, M. A. K., ... Memmott, J. 2016. Historical nectar assessment reveals the fall and rise of floral resources in Britain. <i>NATURE</i> , 530(7588), 85+.	North America	No	Yes	No	Rural	Agriculture (crops), Agriculture (orchard), Forest, Grassland, Other Natural	NA
Bendel, C. R., Hovick, T. J., Limb, R. F., & Harmon, J. P. 2018. Variation in grazing management practices supports diverse butterfly communities across grassland working landscapes. <i>JOURNAL OF INSECT CONSERVATION</i> , 22(1), 99–111.	North America	No	Yes	No	Rural	Agriculture (grazed land), Grassland	NA
Bendel, C. R., Kral-O'Brien, K. C., Hovick, T. J., Limb, R. F., & Harmon, J. P. 2019. Plant-pollinator networks in grassland working landscapes reveal seasonal shifts in network structure and composition. <i>ECOSPHERE</i> , 10(1).	North America	No	Yes	No	Rural	Agriculture (grazed land)	NA
Berkley, N. A. J., Hanley, M. E., Boden, R., Owen, R. S., Holmes, J. H., Critchley, R. D., ... Parmesan, C. 2018. Influence of bioenergy crops on pollinator activity varies with crop type and distance. <i>GLOBAL CHANGE BIOLOGY</i> , 10(12), 960–971.	Europe	No	Yes	No	Rural	Agriculture (non-cultivated)	NA
Birdshire, K. R., Carper, A. L., & Briles, C. E. 2020. Bee community response to local and landscape factors along an urban-rural gradient. <i>URBAN ECOSYSTEMS</i> .	North America	Yes	Yes	No	Urban, Semi-Urban, Rural	Residential, Urban Park, Other Urban	NA
Bloom, E. H., Northfield, T. D., & Crowder, D. W. 2019. A novel application of the Price equation reveals that landscape diversity promotes the response of bees to regionally rare plant species. <i>ECOLOGY LETTERS</i> , 22(12), 2103–2110.	North America	No	Yes	No	Rural	Agriculture (crops)	NA
Buckles, B. J., & Harmon-Threatt, A. N. 2019. Bee diversity in tallgrass prairies affected by management and its effects on above- and below-ground resources. <i>JOURNAL OF APPLIED ECOLOGY</i> , 56(11), 2443–2453.	North America	No	Yes	No	Rural	Agriculture (grazed land), Grassland	NA
Burdine, J. D., & McCluney, K. E. 2019. Interactive effects of urbanization and local habitat characteristics influence bee communities and flower visitation rates. <i>OECOLOGIA</i> , 190(4), 715–723.	North America	Yes	No	No	Urban	Urban Agriculture, Other Urban	NA
Bushmann, S. L., & Drummond, F. A. 2015. Abundance and Diversity of Wild Bees (Hymenoptera: Apoidea) Found in Lowbush Blueberry Growing Regions of Downeast Maine. <i>ENVIRONMENTAL ENTOMOLOGY</i> , 44(4), 975–989.	North America	No	Yes	No	Rural	Agriculture (crops)	NA
Carlos, E. H., Weston, M. A., & Gibson, M. 2017. Avian responses to an emergent, wetland weed. <i>AUSTRAL ECOLOGY</i> , 42(3), 277–287.	Australia	No	Yes	No	Suburban	Other Natural	NA
Carman, K., & Jenkins, D. G. 2016. Comparing diversity to flower-bee interaction networks reveals unsuccessful	North America	No	Yes	No	Rural	Other Natural	NA

- foraging of native bees in disturbed habitats. *BIOLOGICAL CONSERVATION*, 202, 110–118.
- Carrie, R., Ekroos, J., & Smith, H. G. 2018. Organic farming supports spatiotemporal stability in species richness of bumblebees and butterflies. *BIOLOGICAL CONSERVATION*, 227, 48–55.
- Castro-Urgal, R., & Traveset, A. 2016. Contrasting Partners' Traits of Generalized and Specialized Species in Flower-Visitation Networks. *PLOS ONE*, 11(3).
- Choate, B. A., Hickman, P. L., & Moretti, E. A. 2018. Wild bee species abundance and richness across an urban-rural gradient. *JOURNAL OF INSECT CONSERVATION*, 22(3–4), 391–403.
- Cole, L. J., Brocklehurst, S., Robertson, D., Harrison, W., & McCracken, D. I. 2015. Riparian buffer strips: Their role in the conservation of insect pollinators in intensive grassland systems. *AGRICULTURE ECOSYSTEMS & ENVIRONMENT*, 211, 207–220.
- Colwell, M. J., Williams, G. R., Evans, R. C., & Shutler, D. 2017. Honey bee-collected pollen in agro-ecosystems reveals diet diversity, diet quality, and pesticide exposure. *ECOLOGY AND EVOLUTION*, 7(18), 7243–7253.
- Coulin, C., Aizen, M. A., & Garibaldi, L. A. 2019. Contrasting responses of plants and pollinators to woodland disturbance. *AUSTRAL ECOLOGY*, 44(6), 1040–1051.
- Crone, E. E., & Williams, N. M. 2016. Bumble bee colony dynamics: quantifying the importance of land use and floral resources for colony growth and queen production. *ECOLOGY LETTERS*, 19(4), 460–468.
- Dalmazzo, M., & Gerardo Vossler, F. 2015. Pollen host selection by a broadly polylectic halictid bee in relation to resource availability. *ARTHROPOD-PLANT INTERACTIONS*, 9(3), 253–262.
- Davidson, K. E., Fowler, M. S., Skov, M. W., Forman, D., Alison, J., Botham, M., ... Griffin, J. N. 2020. Grazing reduces bee abundance and diversity in saltmarshes by suppressing flowering of key plant species. *AGRICULTURE ECOSYSTEMS & ENVIRONMENT*, 291.
- de Deus, F. F., & Oliveira, P. E. 2016. Changes in floristic composition and pollination systems in a "Cerrado" community after 20 years of fire suppression. *BRAZILIAN JOURNAL OF BOTANY*, 39(4), 1051–1063.
- de Vere, N., Jones, L. E., Gilmore, T., Moscrop, J., Lowe, A., Smith, D., Hegarty, M. J., Creer, S., & Ford, C. R. 2017. Using DNA metabarcoding to investigate honey bee foraging reveals limited flower use despite high floral availability. *SCIENTIFIC REPORTS*, 7.

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| DeBano, S. J., Roof, S. M., Rowland, M. M., & Smith, L. A. 2016. Diet Overlap of Mammalian Herbivores and Native Bees: Implications for Managing Co-occurring Grazers and Pollinators. <i>NATURAL AREAS JOURNAL</i> , 36(4), 458–477. | North America | No | Yes | No | Rural | Agriculture (grazed land), Grassland | Agriculture (grazed land): 3.42; Grassland: 4.32 |
| Delaney, J. T., Jokela, K. J., & Debinski, D. M. 2015. Seasonal succession of pollinator floral resources in four types of grasslands. <i>ECOSPHERE</i> , 6(11). | North America | No | Yes | No | Rural | Grassland | NA |
| Demming, K. R., & Foster, B. L. 2018. Taxon-specific associations of tallgrass prairie flower visitors with site-scale forb communities and landscape composition and configuration. <i>BIOLOGICAL CONSERVATION</i> , 227, 74–81. | North America | No | Yes | No | Rural | Grassland | NA |
| Di'Carlo, L. A. S., DeBano, S. J., & Burrows, S. 2020. Arid grassland bee communities: associated environmental variables and responses to restoration. <i>RESTORATION ECOLOGY</i> . | | | | | | | |
| Djelloul, B. 2018. Understanding of the impact of the types of livestock on the steppe training systems. <i>UKRAINIAN JOURNAL OF ECOLOGY</i> , 8(4), 46–53. | Africa | No | Yes | No | Rural | Agriculture (grazed land) | NA |
| Dorado, J., & Vazquez, D. P. 2016. Flower diversity and bee reproduction in an arid ecosystem. <i>PEERJ</i> , 4. | South America | No | Yes | No | Rural | Other Natural | NA |
| Eeraerts, M., Smaghe, G., & Meeus, I. 2019. Pollinator diversity, floral resources and semi-natural habitat, instead of honey bees and intensive agriculture, enhance pollination service to sweet cherry. <i>AGRICULTURE ECOSYSTEMS & ENVIRONMENT</i> , 284. | Europe | No | Yes | No | Rural | Agriculture (orchard), Agriculture (non-cultivated), Roadside, Forest, Grassland | NA |
| Erenler, H. E., Orr, M. C., Gillman, M. P., Parkes, B. R. B., Rymer, H., & Maes, J.-M. 2016. Persistent nesting by <i>Anthophora latreillei</i> , 1803 (Hymenoptera: Apidae) bees in ash adjacent to an active volcano. <i>PAN-PACIFIC ENTOMOLOGIST</i> , 92(2), 67–78. | North America | No | Yes | No | Rural | Other Natural | NA |
| Fitch, G. M. 2017. Urbanization-mediated context dependence in the effect of floral neighborhood on pollinator visitation. <i>OECOLOGIA</i> , 185(4), 713–723. | North America | Yes | Yes | No | Urban, Semi-Urban, Rural | Urban Agriculture, Other Urban | NA |
| Flo, V., Bosch, J., Arnan, X., Primante, C., Martin Gonzalez, A. M., Barril-Graells, H., & Rodrigo, A. 2018. Yearly fluctuations of flower landscape in a Mediterranean scrubland: Consequences for floral resource availability. <i>PLOS ONE</i> , 13(1). | Europe | No | Yes | No | Rural | Other Natural | NA |
| Galbraith, S. M., Cane, J. H., Moldenke, A. R., & Rivers, J. W. 2019. Salvage logging reduces wild bee diversity, but not abundance, in severely burned mixed-conifer forest. <i>FOREST ECOLOGY AND MANAGEMENT</i> , 453. | North America | No | Yes | No | Rural | Forest | NA |
| Goldingay, R. L., & Ruegger, N. 2018. Elevation induced variation in the breeding traits of a nectar-feeding non-flying mammal. <i>ECOLOGICAL RESEARCH</i> , 33(5), 979–988. | Australia | No | Yes | No | Rural | Forest, Other Natural | NA |
| Gonzalez, O., & Loisele, B. A. 2016. Species interactions in an Andean bird-flowering plant network: phenology is more important than abundance or morphology. <i>PEERJ</i> , 4. | South America | No | Yes | No | Rural | Forest, Grassland | NA |

Graham, J. B., Nassauer, J. I., Currie, W. S., Ssegane, H., & Negri, M. C. 2017. Assessing wild bees in perennial bioenergy landscapes: effects of bioenergy crop composition, landscape configuration, and bioenergy crop area. <i>LANDSCAPE ECOLOGY</i> , 32(5), 1023–1037.	North America	No	No	Yes	Rural	Agriculture (crops)	NA
Grass, I., Albrecht, J., Jauker, F., Diekoetter, T., Warzecha, D., Wolters, V., & Farwig, N. 2016. Much more than bees-Wildflower plantings support highly diverse flower-visitor communities from complex to structurally simple agricultural landscapes. <i>AGRICULTURE ECOSYSTEMS & ENVIRONMENT</i> , 225, 45–53.	Europe	No	Yes	No	Rural	Agriculture (crops), Forest, Grassland	NA
Graves, R. A., Pearson, S. M., & Turner, M. G. 2017. Landscape dynamics of floral resources affect the supply of a biodiversity-dependent cultural ecosystem service. <i>LANDSCAPE ECOLOGY</i> , 32(2), 415–428.	North America	Yes	Yes	yes	Urban, Semi-Urban, Rural	Agriculture (grazed land), Forest	Agriculture (grazed land): 6.59; Forest: 0.84
Gutierrez-Chacon, C., Dorman, C. F., & Klein, A.-M. 2018. Forest-edge associated bees benefit from the proportion of tropical forest regardless of its edge length. <i>BIOLOGICAL CONSERVATION</i> , 220, 149–160.	South America	No	Yes	No	Rural	Agriculture (grazed land), Forest	NA
Halbritter, D. A., Daniels, J. C., Whitaker, D. C., & Huang, L. 2015. Reducing mowing frequency increases floral resource and butterfly (Lepidoptera: Hesperioidea and Papilionoidea) abundance in managed roadside margins. <i>FLORIDA ENTOMOLOGIST</i> , 98(4), 1081–1092.	North America	No	Yes	No	Urban	Roadside	11.76
Hamblin, A. L., Youngsteadt, E., & Frank, S. D. 2018. Wild bee abundance declines with urban warming, regardless of floral density. <i>URBAN ECOSYSTEMS</i> , 21(3), 419–428.	North America	No	Yes	No	Suburban	Residential, Grassland	NA
Hanley, M. E., Awbi, A. J., & Franco, M. 2014. Going native? Flower use by bumblebees in English urban gardens. <i>ANNALS OF BOTANY</i> , 113(5), 799–806.	Europe	No	Yes	No	Urban	Residential	NA
Hanson, T., & Ascher, J. S. 2018. An unusually large nesting aggregation of the digger bee <i>Anthophora bomboidea</i> Kirby, 1838 (Hymenoptera: Apidae) in the San Juan Islands, Washington State. <i>PAN-PACIFIC ENTOMOLOGIST</i> , 94(1), 4–16.	North America	No	Yes	No	Rural	Other Natural	NA
Happe, A.-K., Riesch, F., Roesch, V., Galle, R., Tschamtkke, T., & Batary, P. 2018. Small-scale agricultural landscapes and organic management support wild bee communities of cereal field boundaries. <i>AGRICULTURE ECOSYSTEMS & ENVIRONMENT</i> , 254, 92–98.	Europe	No	Yes	No	Rural	Agriculture (non-cultivated)	NA
Hardman, C. J., Norris, K., Nevard, T. D., Hughes, B., & Potts, S. G. 2016. Delivery of floral resources and pollination services on farmland under three different wildlife-friendly schemes. <i>AGRICULTURE ECOSYSTEMS & ENVIRONMENT</i> , 220, 142–151.	Europe	No	Yes	No	Rural	Agriculture (crops), Agriculture (grazed land)	NA
Hawkins, B. A., Thomson, J. R., & Mac Nally, R. 2018. Regional patterns of nectar availability in subtropical eastern Australia. <i>LANDSCAPE ECOLOGY</i> , 33(6), 999–1012.	Australia	No	Yes	No	Semi-Urban, Rural	Residential, Forest	NA

Heil, L. J., & Burkle, L. A. 2018. Recent post-wildfire salvage logging benefits local and landscape floral and bee communities. <i>FOREST ECOLOGY AND MANAGEMENT</i> , 424, 267–275	North America	No	Yes	No	Rural	Forest	8.56
Herbertson, L., Lindstrom, S. A. M., Rundlof, M., Bornmarco, R., & Smith, H. G. 2016. Competition between managed honeybees and wild bumblebees depends on landscape context. <i>BASIC AND APPLIED ECOLOGY</i> , 17(7), 609–616.	Europe	No	Yes	No	Rural	Agriculture (non-cultivated)	NA
Howell, A. D., Alarcon, R., & Minckley, R. L. 2017. Effects of Habitat Fragmentation on the Nesting Dynamics of Desert Bees. <i>ANNALS OF THE ENTOMOLOGICAL SOCIETY OF AMERICA</i> , 110(2), 233–243.	North America	No	Yes	No	Urban	Other urban	NA
Huelsmann, M., von Wehrden, H., Klein, A.-M., & Leonhardt, S. D. 2015. Plant diversity and composition compensate for negative effects of urbanization on foraging bumble bees. <i>APIDOLOGIE</i> , 46(6), 760–770.	Europe	Yes	No	No	Rural, Urban	Agriculture (crops), Grassland	NA
Johansen, L. q, Westin, A., Wehn, S., Iuga, A., Ivascu, C. M., Kallioniemi, E., & Lemarsson, T. 2019. Traditional semi-natural grassland management with heterogeneous moving times enhances flower resources for pollinators in agricultural landscapes. <i>GLOBAL ECOLOGY AND CONSERVATION</i> , 18.	Europe	No	Yes	No	Rural	Grassland	NA
Kallioniemi, E., Astrom, J., Rusch, G. M., Dahle, S., Astrom, S., & Gjershaug, J. O. 2017. Local resources, linear elements and mass-flowering crops determine bumblebee occurrences in moderately intensified farmlands. <i>AGRICULTURE ECOSYSTEMS & ENVIRONMENT</i> , 239, 90–100.	Europe	No	Yes	Yes	Rural	Agriculture (crops), Agriculture (orchard)	NA
Kaluza, B. F., Wallace, H. M., Heard, T. A., Minden, V., Klein, A., & Leonhardt, S. D. 2018. Social bees are fitter in more biodiverse environments. <i>SCIENTIFIC REPORTS</i> , 8.	Australia	No	Yes	No	Semi-Urban, Rural	Residential, Agriculture (orchard), Forest	NA
Khan, A. M., Qureshi, R., Arshad, M., & Mirza, S. N. 2018. CLIMATIC AND FLOWERING PHENOLOGICAL RELATIONSHIPS OF WESTERN HIMALAYAN FLORA OF MUZAFFARABAD DISTRICT, AZAD JAMMU AND KASHMIR, PAKISTAN. <i>PAKISTAN JOURNAL OF BOTANY</i> , 50(3), 1093–1112.	Asia	No	Yes	No	Urban, Semi-Urban, Rural	Residential, Other Urban, Agriculture (crops), Roadside, Forest, Grassland, Other Natural	NA
Knapp, J. L., Shaw, R. F., & Osborne, J. L. 2019. Pollinator visitation to mass-flowering courgette and co-flowering wild flowers: Implications for pollination and bee conservation on farms. <i>BASIC AND APPLIED ECOLOGY</i> , 34, 85–94.	Europe	No	Yes	No	Rural	Agriculture (crops), Agriculture (non-cultivated)	Agriculture (crops): 2.92; Agriculture (non-cultivated): 6.46
Korpela, E.-L., Hyvonen, T., & Kuussaari, M. 2015. Logging in boreal field-forest ecotones promotes flower-visiting insect diversity and modifies insect community composition. <i>INSECT CONSERVATION AND DIVERSITY</i> , 8(2), 152–162.	Europe	No	Yes	No	Rural	Timber Stand, Forest	NA
		No	Yes	No	Rural	Grassland	NA

Lucas, A., Bodger, O., Brosi, B. J., Ford, C. R., Forman, D. W., Greig, C., ... de Vere, N. 2018. Generalisation and specialisation in hoverfly (Syrphidae) grassland pollen transport networks revealed by DNA metabarcoding. <i>JOURNAL OF ANIMAL ECOLOGY</i> , 87(4, SI), 1008–1021.	Europe	No	Yes	No	Rural	Grassland	6.5
Lucas, A., Bull, J. C., de Vere, N., Neyland, P. J., & Forman, D. W. 2017. Flower resource and land management drives hoverfly communities and bee abundance in seminatural and agricultural grasslands. <i>ECOLOGY AND EVOLUTION</i> , 7(19), 8073–8086.	Europe	No	Yes	No	Rural	Grassland, Agriculture (non-cultivated)	Agriculture (non-cultivated): 1.74; Grassland: 3.69
Malfi, R. L., Walter, J. A., Roulston, T. H., Stuligross, C., McIntosh, S., & Bauer, L. 2018. The influence of conopid flies on bumble bee colony productivity under different food resource conditions. <i>ECOLOGICAL MONOGRAPHS</i> , 88(4), 653–671.	North America	No	Yes	No	Rural	Grassland	NA
Mallinger, R. E., Gibbs, J., & Gratton, C. 2016. Diverse landscapes have a higher abundance and species richness of spring wild bees by providing complementary floral resources over bees' foraging periods. <i>LANDSCAPE ECOLOGY</i> , 31(7), 1523–1535.	North America	No	Yes	No	Rural	Agriculture (crops)	Agriculture (crops): 0.0275; Agriculture (orchard): 7.63; Forest: 2.93; Grassland: 0.42
Martins, K. T., Albert, C. H., Lechowicz, M. J., & Gonzalez, A. 2018. Complementary crops and landscape features sustain wild bee communities. <i>ECOLOGICAL APPLICATIONS</i> , 28(4), 1093–1105.	North America	No	No	Yes	Urban, Semi-Urban, Rural	Agriculture (orchard)	NA
Martins, K. T., Gonzalez, A., & Lechowicz, M. J. 2017. Patterns of pollinator turnover and increasing diversity associated with urban habitats. <i>URBAN ECOSYSTEMS</i> , 20(6), 1359–1371.	North America	Yes	Yes	No	Semi-Urban, Rural	Residential, Grassland	NA
Melin, A., Rouget, M., Colville, J. F., Midgley, J. J., & Donaldson, J. S. 2018. Assessing the role of dispersed floral resources for managed bees in providing supporting ecosystem services for crop pollination. <i>PEERJ</i> , 6.	Africa	No	No	Yes	Rural	Residential, Other Urban, Agriculture (crops), Grassland	NA
Milam, J. C., Litvatis, J. A., Warren, A., Keirstead, D., & King, D. I. 2018. Bee Assemblages in Managed Early-successional Habitats in Southeastern New Hampshire. <i>NORTHEASTERN NATURALIST</i> , 25(3), 437–459.	North America	No	Yes	No	Exurban	Grassland, Forest	NA
Mizunaga, Y., & Kudo, G. 2017. A linkage between flowering phenology and fruit-set success of alpine plant communities with reference to the seasonality and pollination effectiveness of bees and flies. <i>OECOLOGIA</i> , 185(3), 453–464.	Asia	No	Yes	No	Rural	Other Natural	NA
Morales, H., Ferguson, B. G., Marin, L. E., Navarrete Gutierrez, D., Bichier, P., & Philpott, S. M. 2018. Agroecological Pest Management in the City: Experiences from California and Chiapas. <i>SUSTAINABILITY</i> , 10(6).	North America	No	Yes	No	Urban	Urban Agriculture	NA
Moron, D., Skorka, P., & Lenda, M. 2019. Disappearing edge: the flowering period changes the distribution of insect	Europe	No	Yes	No	Rural	Agriculture (non-cultivated), Grassland	NA

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Morrison, J., Izquierdo, J., Hernandez Plaza, E., & Gonzalez-Andujar, J. L. 2017. The role of field margins in supporting wild bees in Mediterranean cereal agroecosystems: Which biotic and abiotic factors are important? AGRICULTURE ECOSYSTEMS & ENVIRONMENT, 247, 216–224.	Africa	No	Yes	No	Rural	Agriculture (orchard)	NA
Nel, L., Pryke, J. S., Carvalheiro, L. G., Thebault, E., van Veen, F. J. F., & Seymour, C. L. 2017. Exotic plants growing in crop field margins provide little support to mango crop flower visitors. AGRICULTURE ECOSYSTEMS & ENVIRONMENT, 250, 72–80.	South America	No	Yes	No	Rural	Forest	NA
Nery, L. S., Takata, J. T., Camargo, B. B., Chaves, A. M., Ferreira, P. A., & Boscolo, D. 2018. Bee diversity responses to forest and open areas in heterogeneous Atlantic Forest. SOCIOBIOLOGY, 65(4, SI), 686–695.	Europe	No	Yes	No	Rural	Other Natural	NA
Nery, L. S., Takata, J. T., Camargo, B. B., Chaves, A. M., Ferreira, P. A., & Boscolo, D. 2018. Bee diversity responses to forest and open areas in heterogeneous Atlantic Forest. SOCIOBIOLOGY, 65(4, SI), 686–695.	Africa	No	Yes	No	Rural	Agriculture (orchard)	NA
Norfolk, O., Eichhorn, M. P., & Gilbert, F. 2016. Flowering ground vegetation benefits wild pollinators and fruit set of almond within arid smallholder orchards. INSECT CONSERVATION AND DIVERSITY, 9(3), 236–243.	Europe	No	Yes	Yes	Semi-Urban, Rural	Other Urban, Agriculture (crops), Agriculture (orchard), Agriculture (non-cultivated), Timber Stand, Roadside, Forest, Grassland	NA
Nuemberger, F., Haertel, S., & Steffan-Dewenter, I. 2019. Seasonal timing in honey bee colonies: phenology shifts affect honey stores and varroa infestation levels. OECOLOGIA, 189(4), 1121–1131.	Europe	No	No	Yes	Rural	Agriculture (crops)	NA
Nuemberger, F., Keller, A., Haertel, S., & Steffan-Dewenter, I. 2019. Honey bee waggle dance communication increases diversity of pollen diets in intensively managed agricultural landscapes. MOLECULAR ECOLOGY, 28(15), 3602–3611.	Europe	No	Yes	Yes	Urban, Semi-Urban, Rural	Agriculture (crops), Agriculture (orchard), Agriculture (non-cultivated), Grassland	NA
Ouvrard, P., & Jacquemart, A.-L. 2018. Agri-environment schemes targeting farmland bird populations also provide food for pollinating insects. AGRICULTURAL AND FOREST ENTOMOLOGY, 20(4), 558–574.	Europe	No	Yes	No	Rural	Agriculture (non-cultivated)	17.76
Pane, A. M., & Harmon-Threatt, A. N. 2017. AN ASSESSMENT OF THE EFFICACY AND PEAK CATCH RATES OF EMERGENCE TENTS FOR MEASURING BEE NESTING. APPLICATIONS IN PLANT SCIENCES, 5(6).	North America	No	Yes	No	Rural	Grassland	NA
Pfeiffer, V., Silbernagel, J., Guedot, C., & Zalapa, J. 2019. Woodland and floral richness boost bumble bee density in	North America	No	Yes	No	Rural	Agriculture (crops), Forest, Grassland, Other Natural	NA

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- Simba, L. D., Foord, S. H., Thebault, E., van Veen, F. J. F., Joseph, G. S., & Seymour, C. L. 2018. Indirect interactions between crops and natural vegetation through flower visitors: the importance of temporal as well as spatial spillover. *AGRICULTURE ECOSYSTEMS & ENVIRONMENT*, 253, 148–156.
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Yes	No	Yes	No	Rural	Agriculture (crops), Agriculture (non-cultivated)	NA
Yes	No	Yes	No	Urban, Rural	Agriculture (non-cultivated)	NA
Yes	No	Yes	No	Rural	Forest, Other Natural	NA
Yes	No	Yes	No	Rural, Semi-Urban	Agriculture (crops), Agriculture (orchard), Forest, Other Natural	NA
Yes	No	Yes	No	Urban	Urban Parks, Other Urban	NA
Yes	No	Yes	No	Rural	Grassland	NA
Yes	No	Yes	No	Rural	Grassland	NA
Yes	No	Yes	No	Urban, Semi-Urban, Rural	Agriculture (orchard)	NA
No	Yes	No	No	Urban, Semi-Urban, Rural	Other Urban, Agriculture (crops)	NA
Yes	No	Yes	No	Urban, Semi-Urban, Rural	Other Urban, Agriculture (crops), Agriculture (orchard), Roadside, Other Natural	NA

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¹ Category 1 papers discuss relationship between proxies of urbanization and flower availability

² Category 2 papers provide measurements of flower availability in one or more LULC type

³ Category 3 papers estimate flower availability at a landscape scale

Appendix 3

Description of Three Cities Used to Scale Floral Density Up to the Landscape Scale

New York City is a city of 18 million people in the temperate forest biome of the northeastern United States. It was established in 1624. In the Medley et al. [16] study, the rural portion of the 140 km urban-rural transect is dominated by deciduous forests and has less than 20% agricultural land use in most places. Phoenix is a city of 1.7 million people in the Sonoran Desert of the southwestern United States. It was established in 1881. In the urban-rural transect in this city, agricultural land cover peaks at approximately 40 km from the urban center, but desert becomes the dominant land cover at farther distances [17]. Xiamen City is a city of 3.5 million people located on the subtropical southeastern coast of China and was established in 1394. In the study by Lin et al. [18], the urban-rural transect is shorter than the other two papers and only extends 40 km from the city center. The far suburbs (30–40 km from the city center) are dominated by residential and urban land covers but have approximately 20% and 16% of forest and agricultural land cover, respectively.

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Author Contribution LL and EM conceived of the presented idea. LL, MK, NB, AD, KS, PJ, and EM read and summarized the papers about floral resources; LL, NB, AD, KS, and PJ extracted and calculated floral density values from the papers. MG identified, read, and summarized the papers about LULC change along an urban-rural gradient, and calculated the landscape-level floral resources along that gradient. PJ and MG created the figures. All authors discussed the results and contributed to the final manuscript.

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Declarations

Conflict of Interest On behalf of the authors, the corresponding author states that there is no conflict of interest.

Human and Animal Rights and Informed Consent This article does not contain any studies with human or animal subjects performed by any of the authors.

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