



REVIEW

Plant–pollinator interactions in urban ecosystems worldwide: A comprehensive review including research funding and policy actions

Jéssica Luiza S. Silva , Marcela Tomaz Pontes de Oliveira , Oswaldo Cruz-Neto ,
Marcelo Tabarelli , Ariadna Valentina Lopes 

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Abstract Urbanization has rapidly increased in recent decades and the negative effects on biodiversity have been widely reported. Urban green areas can contribute to improving human well-being, maintaining biodiversity, and ecosystem services (e.g. pollination). Here we examine the evolution of studies on plant–pollinator interactions in urban ecosystems worldwide, reviewing also research funding and policy actions. We documented a significant increase in the scientific production on the theme in recent years, especially in the temperate region; tropical urban ecosystems are still neglected. Plant–pollinator interactions are threatened by urbanization in complex ways, depending on the studied group (plant or pollinator [generalist or specialist]) and landscape characteristics. Several research opportunities emerge from our review. Research funding and policy actions to pollination/pollinator in urban ecosystems are still scarce and concentrated in developed countries/temperate regions. To make urban green spaces contribute to the maintenance of biodiversity and the provision of ecosystem services, transdisciplinary approaches (ecological–social–economic–cultural) are needed.

Keywords Ecosystem service · Pollination · Scientometrics · Urban ecology · Urban green areas · Urbanization

INTRODUCTION

Pollination is directly related to the persistence and maintenance of biodiversity for both plant and associated animals, thus representing an important ecosystem function (e.g. Potts et al. 2010; Ollerton et al. 2011; IPBES 2016). In addition, pollination is a key ecosystem service for agricultural production, as about 35% of world crops rely on animal pollination (IPBES 2016; Potts et al. 2016), and about three-quarters of major food crops in the world depend to some extent on animal pollination services, either to ensure volume or quality of production (Klein et al. 2007; IPBES 2016).

Currently, cities are growing about twice as fast as the urban population itself (Seto et al. 2013). This growth may be due to four synergistic factors: natural growth, migration from rural to urban areas, migration due to extreme events (e.g. drought) and redefinition of administrative boundaries (Seto et al. 2013). Many cities around the world are usually surrounded by a green belt, with varying lengths, retaining agricultural or wild lands. Urbanization has negatively influenced biodiversity (McKinney 2002, 2006, 2008), through the fragmentation and destruction of natural habitats, introduction of non-native species, modification of natural events and changes in ecosystem processes (Müller et al. 2013). These effects occur due to rapid changes in landcover which lead to the functional impoverishment of the ecosystem (Tratalos et al. 2006). On the other hand, cities create social, economic and biological conservation opportunities, and promote the development of culture, art and education (e.g. McKinney 2002; Müller et al. 2013). When managed properly, urban green areas offer, thus, opportunities for maintaining biodiversity and act, therefore, as source areas for ecosystem services.

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Urbanization has altered the dynamics of interactions between plants and pollinators around the world (Verboven et al. 2012; Harrison and Winfree 2015). While some studies in urban green areas document decreases in pollinator richness and abundance (e.g. Bergerot et al. 2010; Bates et al. 2011; Hamblin et al. 2018), others indicate beneficial effects of urbanization, such as contributing to increase in richness of plant and animal species (e.g. McKinney 2008; Baldock et al. 2015; Hall et al. 2016). This increase in pollinator richness has been reported exclusively for urban green spaces in temperate regions and is directly associated with the use of non-native plant species and species in which the flowering period overlaps in urban green spaces, especially in gardens and green roofs (e.g. Fetridge et al. 2008; Tonietto et al. 2011). However, even in temperate regions, urbanization can negatively affect plant–pollinator interactions by decreasing: (a) the number and diversity of interactions, (b) the frequency of visits by specialist pollinators, such as coleopterans, Sirphidae (Geslin et al. 2013) and solitary bees (Tonietto et al. 2011), (c) and consequently, the reproductive success of plant species (Verboven et al. 2012; Geslin et al. 2013). Thus, it is possible that the effects of urbanization on plant communities and pollinators may differ between regions and climates and depend on local species composition.

Urban green areas/spaces consist of any type of vegetation (public or private) inserted in an urban matrix and comprise a range of formats and sizes including squares, parks, public walkways, green roofs, and gardens (Kabisch and Haase 2012; Boulton et al. 2018). Urban green areas can contribute to human well-being (Cox et al. 2018), benefiting quality of life (e.g. air quality improvement, temperature reduction, humidity regulation, which contribute to reduction of diseases) (e.g. Zhang et al. 2017) and improve biodiversity, since they can act as ecological corridors by connecting natural vegetation remnants (e.g. Peng et al. 2017). In this context, urban ecosystems can sustain plant and animal populations (e.g. Barton and Pretty 2010; Elmqvist et al. 2015), representing a source of resources for pollinators (Aleixo et al. 2014; Baldock et al. 2015; Siemaszko and Zych 2017), frugivores (Pufal and Klein 2015), herbivores (e.g. Morón et al. 2017), scavengers (Bonnington et al. 2013) and omnivores (François et al. 2008). In addition, these areas also help in the educational process, through the understanding of nature (Cox et al. 2018). Thus, considering the rapid expansion of cities, urban green areas are elements that can, to a certain extent, mitigate the effects of the conversion of natural ecosystems to human modified landscapes, and therefore have great importance as a source area for the provision of ecosystem services (Wang et al. 2019) and global biodiversity conservation (e.g. Frankie et al. 2005).

Much of what urban green spaces provide is mainly due to trees that offer environmental, economic, social, and cultural benefits. These benefits involve: support climate change mitigation and adaptation (they can reduce local air temperature by between 2 and 8 °C), filter for urban pollutants, help protect water sources and contribute to the treatment of wastewater, play an important role in local biodiversity conservation, by providing habitat to plants and animals (environmental benefits), contribute to food and nutrition security, mainly due to urban agriculture, increase cities' resilience to severe weather events, alleviate poverty (e.g. creating job opportunities such as in gardening, agriculture), increase property value by 20% and attract tourists (economic and livelihood benefits), create recreational, cultural and social opportunities, and positively impact physical and mental health (social and cultural benefits) (FAO 2014, 2018).

Plant–pollinator interactions in urban ecosystems was theme of only three literature reviews, which discusses the strengths and weaknesses of garden plant lists (in the United Kingdom, North America and Western Europe) to help pollinators (Garbuzov and Ratnieks 2014), review the mechanistic pathways through which urban drivers modify plant–pollinator interactions, basically in the temperate regions (Harrison and Winfree 2015) and, more recently, review how urbanization is driving insect pollinator diversity and pollination (Wenzel et al. 2020). These three reviews are distinct but none of them addresses: (1) a robust analysis of the evolution of the topic (scientometrics); (2) plant–pollinator interactions as ecological process, (3) in which type of urban green spaces the plants and pollinators are found, (4) other pollinator group than insects, (5) research funding/grants and (6) policy documents on the topic.

Here we examine the evolution of studies on plant–pollinator interactions in urban ecosystems worldwide, present the state of the art, knowledge gaps, opportunities and future directions, as well as the research funding/grants and policy documents related to plant–pollinator interactions in urban green spaces. In synthesis, we evaluate the main impacts of urbanization on plant–pollinator interactions and emphasize how urban green spaces act as opportunities for conservation/maintenance of biodiversity, seeking to answer some key questions: What is the global status of studies on plant–pollinator interactions in urban ecosystems? Which is the most studied region (temperate or tropical)? What are the most studied pollination vectors? What are the effects of urbanization on the studied organisms? What do we know about plant–pollinator interactions in tropical urban ecosystems? What is the global status of research funding and what are the policy actions on plant–pollinator interactions to urban ecosystems?

METHODS

Scientometrics of studies on plant–pollinator interactions in urban ecosystems

A bibliographical search was carried out in the ISI Web of Science—Science Citation Index Expanded platform (www.webofknowledge.com) (last accessed on February 28, 2020) with the following search argument: “*urban** and *pollinat**” appearing in the title, keywords and/or abstract. After searching and sorting, we kept articles dealing with plant–pollinator interactions in urban ecosystems, including diverse urban green spaces in temperate and tropical regions, such as: pollinators and plants they visited, frequency of pollinator visits to flowers, functional diversity of plants and pollinators, reproductive success of plants following biotic pollination, and plant–pollinator network (see Fig. 1 for details). We excluded from our database articles that dealt exclusively with subjects or aspects indirectly associated with pollination, such as: (a) genetic and/or physiological approaches, (b) other interactions such as herbivory, dispersion, ant protection, parasitism, (c) pollen-related allergy, (d) pollen “rain”,

(e) nesting sites, (f) plant lists, (g) animal lists (even if it was a checklist of bees or other pollinator agent), (h) phenology of plants or animals, (i) not conducted in urban areas and (j) conducted in natural forest remnants located in the urban perimeter (see Fig. 1 for details). Figure 1 is based on The PRISMA Statement: Preferred Reporting Items for Systematic Reviews and Meta-Analyses (sensu Moher et al. 2009; www.prisma-statement.org).

Our final database included 13 scientometric categories to evaluate the progress of the topic. These categories refer to different items in each article, such as: publication year, authors, journal, methodology, effects of urbanization, further detailed in Table 1. The scientometric analyses were summarized in graphs to identify the global scientific development of the theme and trends in publications.

Review of studies on plant–pollinator interactions in urban ecosystems

The focus of the review was to evaluate the influence of urbanization on the pollination of plant species (i.e. plant–pollinator interactions) occurring in urban green areas. Urban green areas were classified in: university campus,

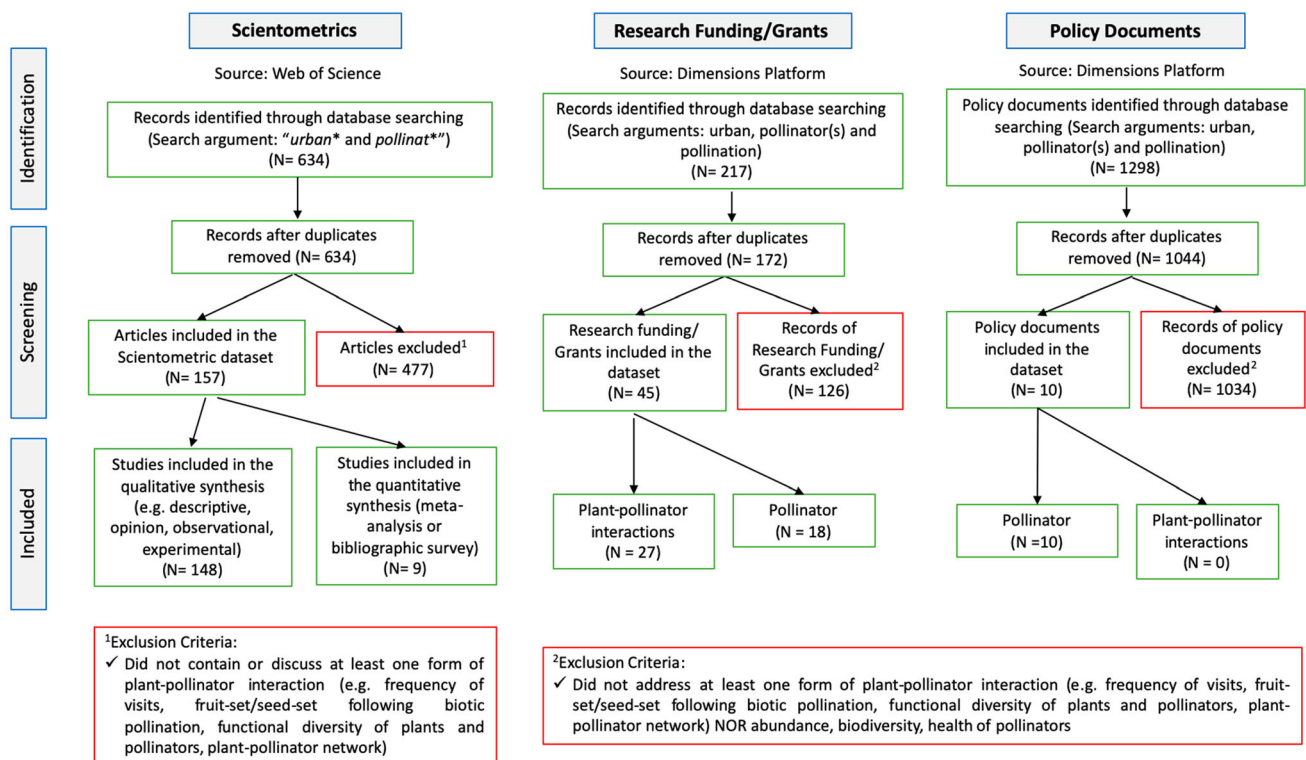


Fig. 1 Flow diagram representing the body of literature reviewed, research funding/grants and policy documents on plant–pollinator interactions in urban ecosystems, which were considered in this study (including counts of sources and exclusion criteria used to filter the body of literature, research funding/grants and policy documents into the final dataset reviewed). Search argument for the scientometric analysis in the Web of Science: “*urban** and *pollinat**”; search arguments for Dimensions Platform: urban, pollinator(s) and pollination. This diagram is based on The PRISMA Statement: Preferred Reporting Items for Systematic Reviews and Meta-Analyses (sensu Moher et al. 2009; www.prisma-statement.org.)

Table 1 Information and categories selected for the scientometric analysis (Adapted from Viana et al. 2012)

Items for analysis	Categories
1. Publication year	–
2. Corresponding author name	–
3. Corresponding author country	–
4. Co-author names	–
5. Article title	–
6. Journal title	–
7. Country of the study area	–
8. Ecoregion/Climatic zone where the study was carried out	1. tropical, 2. subtropical, 3. temperate, 4. Mediterranean, 5. not applicable
9. Nature of the method	1. descriptive, 2. review, 3. observational (sampling), 4. experimental, 5. meta-analysis, 6. opinion
10. Type of urban green space	1. park, 2. garden (public and/or private), 3. road and/or sidewalk and/or flowerbed, 4. green roof, 5. university campus, 6. cemetery, 7. more than one category, 8. urbanization gradient, 9. others
11. Plant origin	1. native, 2. exotic, 3. invasive, 4. endemic, 5. not specified
12. Pollination vector	1. bees, 2. other insects, 3. bats, 4. birds, 5. several groups of pollinators, 6. not specified
13. Effect of urbanization	1. positive, 2. negative, 3. neutral, 4. more than one effect*, 5. not applicable

Articles were surveyed in the ISI Web of Science—Science Citation Index Expanded platform (www.webofknowledge.com) with the following search argument: “*urban** and *pollinat**” appearing in the title, keywords and/or abstract

*For example: an increase in pollinator visits to flowers, but a decrease in reproductive success (fruit-set), in a plant species with genetic self-incompatibility

gardens (public and/or private), parks, green roofs, and roads and/or public walkways (Table 1). In addition, information on the study focus (plant, pollinator or plant–pollinator interactions), plant origin (when reported in the study), pollination vector and effect of urbanization (see Table 1 for more information) were verified.

Research funding/grants and policy documents related to plant–pollinator interactions or to pollination and pollinators in urban ecosystems

In order to review research funding and policy documents related to plant–pollinator interactions or to pollination and pollinators in urban ecosystem worldwide, we used a database provided by Dimensions Platform (<https://www.dimensions.ai/>). The Dimensions platform is an inter-linked research information system provided by Digital Science, which focuses on the broader set of use cases, that goes beyond the standard publication-citation (research articles and their citations, books). This platform includes publication (more than 106 million), alternative metrics, grants, patents, clinical trials and policy documents with a standard set of research classifications via machine-learning techniques (Hook et al. 2018). Dimensions has gathered, cleaned and rendered unambiguous a global database, which check all sources on grant data for new data monthly.

Data on research funding/grants and policy documents were searched by combining the keywords: pollinator and urban, pollination and urban. The search was conducted in

March 2020 and included all research funded and policy documents available in the platform (from 1962 for policy documents and from 1994 for research funding). All research funding records and policy documents were individually checked for duplicates. We expanded the inclusion criteria and considered research funding and policy documents that addressed pollinator (e.g. abundance, diversity and pollinator health) and plant–pollinator interactions (including pollination process as proxy to interaction) in urban ecosystems as the main subject of the funded project. For policy documents we considered documents that addressed conservation, maintenance and improvement of plant–pollinator interactions or pollinator in urban ecosystems (see Fig. 1 for details). The inclusion and exclusion criteria are described in Fig. 1. For the construction of maps with scientific publications, research funding and policy documents we grouped these data into two categories represented by countries with developed and developing economies according to the United Nations (2019).

RESULTS AND DISCUSSION

Scientometrics of studies on plant–pollinator interactions in urban ecosystems

Our initial bibliographical search returned 634 articles, published from January 1945 to February 2020, of which 157 were selected for analyzing the scientometrics of

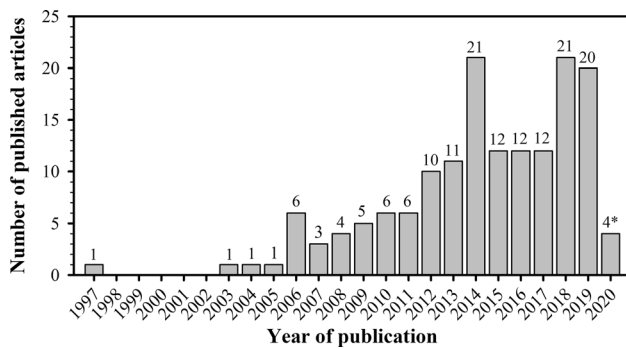


Fig. 2 Growth of research effort through time on plant–pollinator interactions in urban ecosystems. Search was carried out in the Web of Science with the argument “urban* and pollinat*”, returning 634 articles, 157 of which were related to this topic and included in our database. *Number of articles for 2020 refers only to January and February

studies on plant–pollinator interactions in urban ecosystems (Supplementary Material Table S1). After sorting and excluding studies that were not directly related to the topic of our study, we observed that the first article investigating plant–pollinator interactions in urban areas was published in 1997. Articles on this topic were published in 19 of the 24 years since then, with a five-year gap without any publications (1998–2002) consecutive to the first publication. In total, 75.8% of the analyzed articles were published between 2012 and 2019, indicating a recent increase trend in publications on this topic worldwide. This increase contains three peaks of publications, in 2014, 2018 and 2019, in which 21, 21 and 20 articles were published, respectively. In the period between 1997 and 2011, we observed an average of 3.5 published articles/year (Fig. 2).

During these 24 years, articles documenting plant–pollinator interactions in urban ecosystems worldwide were published in 79 scientific journals (Supplementary Material Table S1); 53 of these scientific journals published only one article related to the topic, these journals are not restricted to urban ecology (Supplementary Material Table S2). The scientific journals that published more on plant–pollinator interactions in urban ecosystems were *Urban Ecosystems* (15 articles), *Landscape and Urban Planning* and *Biological Conservation* (10 articles each) (Fig. S1). However, only the journals *Urban Ecosystems* and *Landscape and Urban Planning* focus exclusively on urban green spaces dynamics and together accounted for 31.6% ($N = 25$) of the registered articles. These findings reveal that scientific production on plant–pollinator interactions in urban ecosystems is recent and still largely neglected. This pattern is reinforced by the fact that most scientific publications are published in journals not primarily focused in urban ecology.

The three most cited articles on plant–pollinator interactions ecology in urban ecosystem [1. Winfree et al.

(2007), published in *Conservation Biology*, 2. Parker (1997), *Ecology*, and 3. McFrederick and LeBuhn (2006), *Biological Conservation*; Supplementary Material Table S1] investigated several aspects of plant–pollinator interactions, all of them in temperate urban ecosystems, such as pollination outcomes, pollinator behavior and the role of temperate urban green spaces in maintaining species of plants and pollinators. These articles also reveal the main branches on which the current knowledge on plant–pollinator interactions in urban systems has been developed, as discussed below.

The authors of the 157 selected publications are affiliated to institutions in 26 countries. These authors are mainly affiliated with institutions in the United States (45 articles), United Kingdom (17 articles), France (16 articles) and Brazil (13) that together authored 59.8% of the selected articles (Figs. 3 and S2A). Similarly, studies developed in these countries account for 59.2% of the published articles (Figs. 3 and S2B).

Regarding climatic regions, 77.7% of the analyzed articles were conducted in temperate regions, followed by tropical regions (14.6%). The subtropical and Mediterranean regions represented less than 3.2% of the articles each (Fig. 4a). Our data revealed that the number of published articles carried out in temperate urban ecosystems is disproportionately high when compared to the amount conducted in tropical ecosystems, a fact corroborated by the nationality of the corresponding authors. Research on urban ecology in the tropics is limited by lack of investments (Anderson et al. 2013; Pauchard and Barbosa 2013), which is quite worrying. The tropical region is recognized for its high species richness, diversity and endemism (e.g. Brown 2014), and is where most biodiversity hotspots are located (Myers et al. 2000). In addition, these regions have cities that are growing at an alarming rate.

Observational articles represented 84.0% of our sampling, followed by experimental articles (8.9%) and meta-analyses (3.9%), respectively. Literature reviews, descriptive and opinion articles were the least represented, with less than 1.3% each (Fig. 4b). Observational approaches were mostly local and/or regional, therefore making data collection less complex and costly.

From the two literature reviews that returned from our bibliographical search, one discusses the strengths and weaknesses of lists of garden plants to help pollinators, documenting that although the choice of species used in urban green spaces in the United Kingdom, North America and Western Europe was mostly based on non-empirical information, those lists were considered useful and a starting point for future research (Garbuzov and Ratnieks 2014). The second article reviews the mechanistic pathways through which urban drivers modify plant–pollinator interactions and concludes there are knowledge gaps,

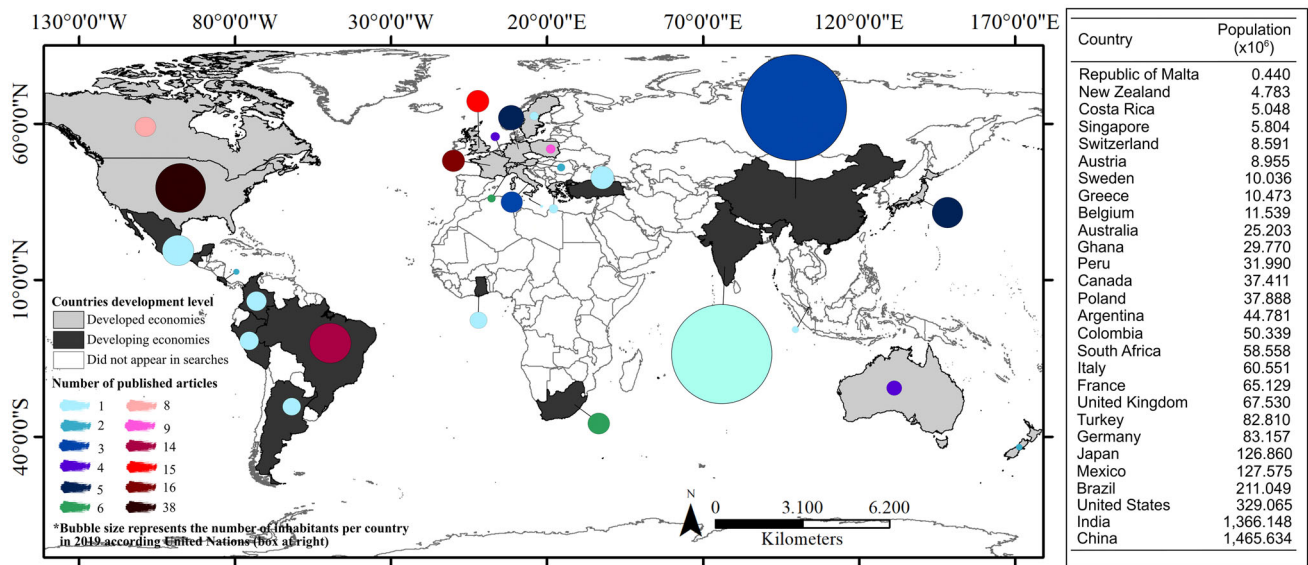


Fig. 3 Distribution of articles related to plant–pollinator interactions in urban ecosystems in countries with developed (light grey) (80.89%; $N = 127$) and developing economies (19.11%, $N = 30$) (dark grey). For the inclusion and exclusion criteria when searching articles at Web of Science (2020) (www.webofknowledge.com), please see the Flow diagram in Fig. 1. Bubble color represents the number of published articles; Bubble size represents the number of inhabitants (population) in each country, which are informed in the box at right (Data source: The United Nations 2019)

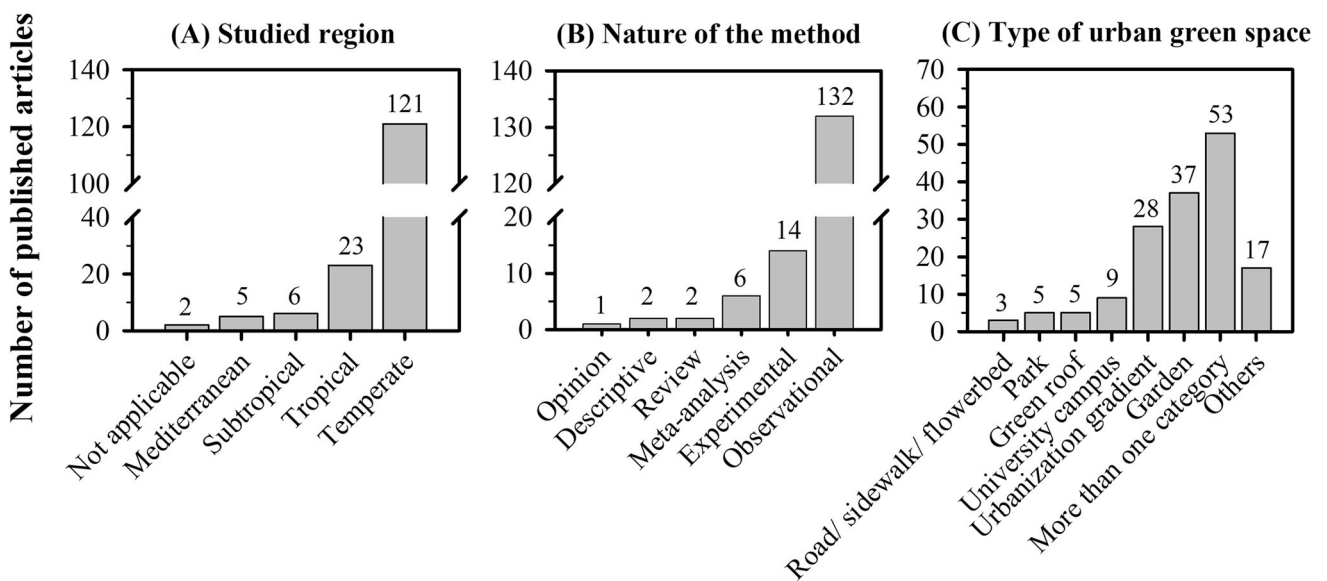


Fig. 4 Number of articles on plant–pollinator interactions **a** per the climatic zones: tropical, subtropical, temperate, Mediterranean, of the country of the study; **b** categories of nature of the study method; and **c** type of urban green space where the studies were developed: park, garden (public and/or private), road and/or public walkways and/or flowerbed, green roofs, university campus, cemetery, more than one category, urbanization gradient and others. Our search in the Web of Science with the argument “urban* and pollinat*” returned 634 articles, 157 of which were related to this topic and included in our database

including understanding the effects of plant and pollinator trait filtering on plant–pollinator interactions and the need for more studies on temperate European-American regions and bee pollinators (Harrison and Winfree 2015).

Considering the low representativeness of literature reviews (only two articles, Fig. 4b) and the approach chosen by the authors, it is notorious that plant–pollinator interactions in urban ecosystems is still poorly explored in

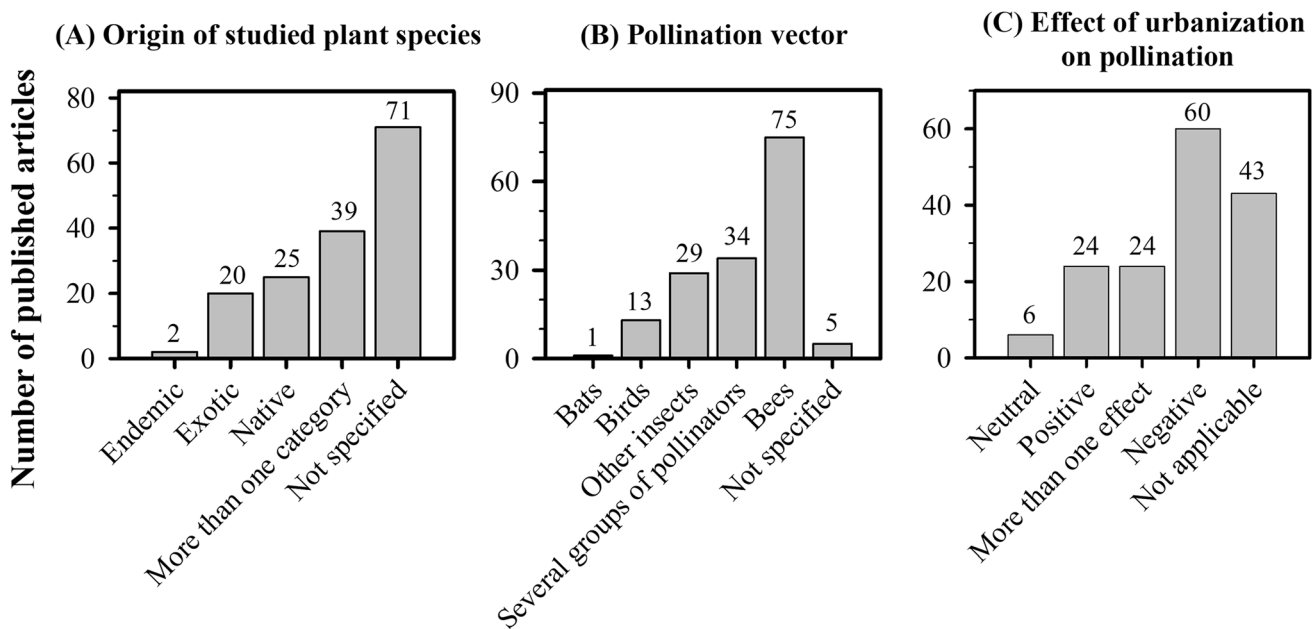


Fig. 5 Number of articles on plant–pollinator interactions in urban ecosystems regarding the **a** origin of the plant(s) involved in the interaction with the study site; **b** pollination vector; and **c** categories of urbanization effect: neutral, positive, more than one effect, negative and not applicable in studies on this topic Our search in the Web of Science with the argument “urban*” and pollinar*” returned 634 articles, 157 of which were related to this theme and included in our database

both temperate and tropical regions. A third review on the topic, not yet indexed in the ISI Web of Science until the end of February 2020, Wenzel et al. (2020), aimed to present a systematic review of literature to identify drivers of urban pollinator populations and pollination, but they reviewed publications on insect pollination exclusively. The authors did not mention the existence of studies with other groups of pollinators, such as vertebrates (see for example French et al. 2005; Mendonça and Anjos 2006; Arizmendi et al. 2007; Pauw and Louw 2012; Previatto et al. 2012; Coetzee et al. 2018, for birds and Kobayashi et al. 2018 for bats) or the neglect of studies with these vectors as urban pollinators. In our review we found that studies involving vertebrate pollinating vectors accounted for almost 10% of the articles (Fig. 5b; Supplementary Material Table S1) on the plant pollinator interactions in urban ecosystems as will be detailed below.

In total, at least six types of urban green spaces were mentioned in the 157 analyzed articles (Fig. 4c). Studies carried out exclusively in gardens represented 23.5% of our sampling. These studies were followed by articles conducted across urbanization gradients or in university campi, which account for 17.8% and 5.7% respectively. Articles investigating urban plant–pollinator interactions exclusively in parks, green roofs, and roads and/or public walkways are scarce, representing less than 3.3% each. Despite these differences, articles carried out in more than one type of urban green space are dominant and accounted for 33.7% of all articles. In urban ecosystems, parks can

have similar species composition to surrounding natural forest remnants (EIP Associates 2002), at least in cities in temperate regions. Due to native biodiversity, urban parks may favor migration and gene flow across urban green areas, increasing the connection of these areas with natural forests remnants close to cities (Florgard 2007). Thus, we emphasize that parks seem to represent a great opportunity to understand changes in pollination mechanisms caused by the intensification of urbanization in both temperate and tropical regions.

Surprisingly, we have identified only two articles dealing with plant–pollinator interactions and urban agriculture (Frankie et al. 2009; Potter and Lebuhn 2015). In both papers residential gardens are used for the development of urban agriculture. Urban agriculture can be defined as the plant cultivation and/or raising of animals in/or around cities for subsistence and/or commercialization, practiced in any type of urban green space (e.g. Smit et al. 1996; van Veenhuizen 2006). This activity has grown impressively in the world (Orsini et al. 2013), and is strongly practiced by low-income population of developed and developing economies (e.g. van Veenhuizen 2006; de Zeeuw et al. 2011; Orsini et al. 2013). Urban agriculture can provide a variety of ecosystem services, including pollination (Potter and Lebuhn 2015; Aerts et al. 2016; Zhao et al. 2019). However, little is known about pollination services for urban agriculture (Matteson and Langellotto 2009). Nonetheless, some studies indicate that urban agriculture in residential gardens can play a fundamental role in

maintaining pollinators, especially wild bees, regardless of landscape context (garden size, proximity to a natural area, surface permeability) (Smith et al. 2006; Frankie et al. 2009; Potter and Lebuhn 2015; Bennett and Lovell 2019; Zhao et al. 2019). Although the provision of pollination services for urban agriculture has been investigated only for some groups of insects, especially bees (e.g. Smith et al. 2006; Frankie et al. 2009; Potter and Lebuhn 2015; Bennett and Lovell 2019; Zhao et al. 2019), urban agriculture has the potential to promote richness, abundance and diversity of other pollinator groups in urban ecosystems.

Unexpectedly, a total of 45.2% of the studies did not inform the origin of the plants. Among the ones that reported origin, 16% studied pollination of native plants, 12.7% evaluated exotic plants and only 1.3% mentioned investigation of endemic plants (Fig. 5a). The occurrence, and in some instances, predominance of exotic plants in urban ecosystems, mainly those located in tropical regions, is due to the ornamental function associated to urban green areas (Moro et al. 2014; Moro and Castro 2015; Silva et al. 2020). These urban green spaces dominated by exotic plants may be detrimental to the maintenance of local biodiversity (McKinney 2002, 2006). On the other hand, native plant species may improve the ecological quality of urban green spaces by supporting the native plant and animal community (Moro and Castro 2015) and are strongly recommended for future urban forestry initiatives (Courtney et al. 2014; Silva et al. 2020).

Regarding pollination vectors, bees were the most studied, representing 47.8% of the analyzed articles, followed by studies that included several groups of pollinators, which represented 21.6% of the articles. Articles focusing on other insect groups, birds and bats accounted for 18.5% (25 articles), 8.3% (13) and 0.6% (2), respectively (Fig. 5b). In Wenzel et al. (2020), which only address pollinating insects, bees also appear as the main vector in urban green areas. Indeed, bees are the most common biotic pollinator and are associated with the maintenance of most plant species in many communities, both in temperate and tropical regions, and in urban and natural ecosystems as well (e.g. Potts et al. 2010; Hennig and Ghazoul 2011; Aleixo et al. 2014; IPBES 2016, and this study). Additionally, bees are the main pollinators of agricultural crops, pollinating about 90% of the crops for which the degree of dependence on pollinators has already been estimated (Klein et al. 2007). Bees are critical to ensure not only increased production (e.g. Gallai and Vaissière 2009), but also the quality of the fruit produced (Garratt et al. 2014; Klatt et al. 2014). Finally, the ease of data collection (observation and specimen collection) also drives researchers to study bees.

Alternatively, based on our findings, other pollinator groups, mainly vertebrates, seem to be neglected in studies

on plant–pollinator interactions of urban ecosystem. Vertebrate pollinators (e.g. birds, bats, rodents and lizards) are also essential for crops of economic interest (see IPBES 2016; Ratto et al. 2018). As the dependence on pollination by vertebrates is higher in the tropics than in temperate regions [since the exclusion of vertebrate pollinators negatively affects up to 71% the reproductive success of plant species and caused a reduction in seed set of almost 58% in the tropics (Ratto et al. 2018)], it is expected that these groups may be also relevant in tropical urban ecosystems. Analyzing bats separately, which are considered the most specialized vertebrates, the decline of pollinating bats may result in reduced fruit and seed formation of 83% of bat pollinated plants worldwide (Ratto et al. 2018). This is also relevant to urban ecosystems, as bats commonly occur in urban green spaces (Jung and Threfall 2015; Russo and Ancillotto 2015). Due to the sensitivity of specialist and vertebrate pollinators to the effects of urbanization (Melles et al. 2003; Pauw and Louw 2012; Jung and Threfall 2015), the occurrence of these groups can act as bioindicators of the integrity of ecological functions and services in urban green spaces (e.g. Russo and Ancillotto 2015).

Main impacts of urbanization on plant–pollinator interactions

The effect of urbanization on plant–pollinator interactions was mentioned in 114 (72.6%) of the 157 analyzed articles. Among the 114 studies that mentioned an effect of urbanization on plant–pollinator interactions, 52.6% reported negative effects, 21.05% registered positive effects, and 5.3% did not detect any impact of urbanization on plant–pollinator interactions (neutral); urbanization may also have distinct and complex effects (more than one effect) on plant–pollinator interactions, which have been observed in 21.05% of the analyzed articles (Fig. 5c). An example of a complex effect would be an increase in pollinator visits to flowers, but a decrease in reproductive success (fruit-set), in a plant species with genetic self-incompatibility. The impacts of urbanization on plant–pollinator interactions are mainly related to the maintenance of plant and pollinator species, to pollinator behavior, and to plant reproductive success in urban green spaces.

Plants and pollinators in urban green areas were investigated in isolation or in combination with other aspects of plant–pollinator interactions in 82 out of the 157 analyzed articles. In general, urban ecosystems in both temperate and tropical regions fail in preserving the whole diversity of plant species and functional traits (e.g. Bergerot et al. 2010; Geslin et al. 2013; Matteson et al. 2013; Anderson et al. 2014; Garbuzov and Ratnieks 2014; Desaegher et al. 2019). The diversity of pollinators, specifically those with

specialized functional traits (e.g. Bergerot et al. 2010), is also reduced in urban green spaces in temperate regions (e.g. Basteri and Benvenuti 2010; Bates et al. 2011; Matteson and Langelotto 2011; Tonietto et al. 2011; Glaum et al. 2017). Similarly, reductions in the diversity of bees, wasps and beetles (e.g. Guenat et al. 2018; Oliveira et al. 2019a), butterflies (e.g. Jain et al. 2016), and specialized birds (e.g. Coetzee et al. 2017; Maruyama et al. 2019) were documented in tropical urban green spaces associated to urbanization or to natural areas. Articles comparing the diversity of species of other pollinator groups, such as hawkmoths, bats and non-flying mammals between natural areas and urban green spaces in tropical regions were not present in our database, indicating that the impacts of urbanization on specialized plant–pollinator interactions in the tropics are still poorly known.

In temperate regions, the distribution of the reduced diversity of plant and pollinators retained in urban green areas seems to follow the characteristics of the surrounding habitat. The proximity of temperate urban green spaces to forest remnants and agricultural areas, together with an increased diversity of flowering plants and floral resources, are positively related to the diversity of bees, flies, hoverflies, butterflies, beetles and wasps among other insect pollinators (e.g. Winfree et al. 2007; Sattler et al. 2010; Bates et al. 2011; Tonietto et al. 2011; Pellissier et al. 2013; Shwartz et al. 2013; Pardee and Philpott 2014; Kratschmer et al. 2018; Luder et al. 2018). This biodiversity is also mainly positively correlated with the proximity to gardens and allotments (e.g. Foster et al. 2016; Baldock et al. 2019). In the tropics, in addition to these aspects, urban green spaces that present a high number of plant species that continuously offer floral resources may represent a refuge to many groups of pollinators, mainly bees (e.g. Aleixo et al. 2014). Independently of habitat characteristics, plants and pollinators with generalist functional traits tend to benefit from urban ecosystems in both temperate (Hamblin et al. 2018; Kratschmer et al. 2018; Desaegher et al. 2019) and tropical regions (Zotarelli et al. 2014; Coetzee et al. 2018; Guenat et al. 2018).

The impacts of urbanization in pollinator behavior were mentioned, separately or in combination with other aspects of plant–pollinator interactions, in 92 out of the 157 analyzed articles. In general, urbanization has complex effects on pollinator behavior, mainly by changing foraging routes, frequency and duration of floral visits, and by promoting changes in floral resource selection. Reduced number of visits and interactions among flowers and pollinators are frequently observed in urban green areas in temperate regions (e.g. Liu and Koptur 2003; Andrieu et al. 2009; Geslin et al. 2013; Matteson et al. 2013) and in the few studies carried out in the tropics (e.g. Maruyama et al. 2019; Oliveira et al. 2019a). Despite the reduction in

visitation rate, increase in the number of flowers, larger floral displays and higher production of pollen and nectar had positive effects on floral visits by bees (e.g. Leveau 2008; Hennig and Ghazoul 2011; Coetzee et al. 2017; Irwin et al. 2018; Jusselme et al. 2019) and by hummingbirds (Calviño-Cancela 2006) in temperate urban green spaces. In addition, pollinators may preferably visit native (e.g. French et al. 2005) or exotic plant species depending on the intensity of urban stressors (Buchholz and Kowarik 2019).

Increased intensity of anthropogenic disturbances such as habitat loss, fragmentation, heat island and soil pollution, can act as filters and pave the way for the introduction and even invasion of exotic plant species in urban green areas (e.g. Harrison and Winfree 2015). Exotic species can offer a greater amount of resources in places where native plants are absent or with reduced abundance. However, exotic plants can (a) represent a risk to the health of pollinators (since the floral resources offered may not have nutritional values similar to those of native plants) (Stout and Morales 2009; (b) compete with native plants for native pollinators, (Totland et al. 2006; see references cited in Kovács-Hostyánski et al. 2016); in addition to (c) facilitating the invasion of non-native floral visitors (Morales and Aizen 2002, 2006; Traveset et al. 2013). Consequently, the frequency of pollinator visits to exotic species can be increased (Totland et al. 2006), as well as the reproductive success (Silva et al. 2020). Silva et al. (2020) analyzed tree fruiting in 19 urban green spaces (parks and squares) in a tropical city (Recife), northeastern Brazil, and documented that all exotic species (which represents ~ 50% of the total) set fruits. It is worth mentioning that, from a landscape perspective, the introduction of exotic plant species in urban areas can threaten urban and peri-urban/peri-rural agriculture in both temperate and tropical countries by changing pollinator foraging route in those areas. Thus, food crops that depend on animal pollinators (about 35%) to guarantee the volume or quality of production (Klein et al. 2007) may have their production threatened due to pollinator decline. Reductions in visitation rates in urban green spaces may be related to the combination of reduced pollinator diversity, reduction in area of foraging routes, as previously observed for Euglossini bees in tropical regions (Lopez-Urbe et al. 2008), disruption of plant–pollinator networks (Lowenstein et al. 2019), and exclusion of less competitive pollinator groups (Brizola-Bonacina et al. 2012) in many urban green areas. Regarding the duration of floral visits and foraging routes, they may be increased in urban ecosystems, as observed for butterflies in temperate regions (Andrieu et al. 2009) and for hummingbirds in the Neotropical region (Calviño-Cancela 2006). We emphasize that, as floral resources are more sparsely distributed and scarce in urban green spaces (Bergerot et al. 2010; Desaegher et al. 2019), pollinators may travel longer

distances and spend more time collecting floral resources to supply their energy demands.

Impacts of urbanization on plant phenology and reproductive success were mentioned, in isolation or in combination with other aspects of plant–pollinator interactions, in 40 of the 157 analyzed articles. In total, seven articles informed the flowering period of the plants, three studies carried out in tropical regions, three in temperate regions and one in areas in both climatic zones. In temperate urban green areas, mass flowering and production of floral resources are positively associated with attraction of numerous insects, such as bumblebees and honeybees, flies, moths, and butterflies (Denisow et al. 2013; Benvenuti 2014; Wray and Elle 2015). Similarly, continuous flowering may provide pollen, nectar and oil that support bee communities in tropical urban ecosystems (Aleixo et al. 2014). Alternatively, urbanization can be associated with increased flowering duration in tropical urban green spaces, contrasting with shorter flowering (3–4 months) in forest remnants, as observed for a legume tree (e.g. Oliveira et al. 2019a, b). Articles investigating the flowering phenology of plants pollinated by nocturnal animals in temperate and tropical regions were not registered in our database.

Among the articles investigating the relationship between urbanization and plant reproductive success, 21 analyzed the female component, six the male component and five both. Female reproductive success was measured as the proportion of flowers that originated viable fruits and number of seeds per fruit in most of the analyzed articles, while male reproductive success was mainly measured by pollen load observed in pollinators and pollen dispersion. In general, both male and female components of plant reproductive success are negatively affected by urbanization processes in temperate areas (e.g. Parker 1997; Jędrzejewska-Szmek and Zych 2013; Leong et al. 2014; Bennet et al. 2018; Hou et al. 2019) and in the few studies in the tropics (Oliveira et al. 2019a, b).

In the case of female reproductive success, distinct levels of fruit- (Parker 1997; Pellissier et al. 2012; Pellegrino and Bellusci 2014; Oliveira et al. 2019a) and seed-set decreases have been extensively documented in urban green areas, sometimes reaching up to 80% (e.g. Cheptou and Andevano 2006). Female reproductive success may also change across distinct types of urban green spaces in temperate regions (e.g. Pellissier et al. 2013), in which green roofs may have higher levels of seed set in comparison to plants on the ground level (e.g. Ksiazek et al. 2012). Reductions in female plant reproductive success may be strongly affected by the quality and quantity of pollen grains deposited in the flower stigma. Besides bees, flies, butterflies and moths also collect pollen from very diverse plant groups in temperate urban ecosystems, and

may contribute to dispersion of pollen grains over short distances (e.g. Jędrzejewska-Szmek and Zych 2013; Bennet et al. 2018). We emphasize that limitations in pollen movement and pollen deposition in receptive stigmas may be directly related to reductions in the reproductive output of plants in urban green spaces worldwide. Studies investigating other aspects of reproductive success, such as pollen removal by pollinators in both temperate and tropical regions were not observed in our database.

There are countless factors (landscape, local, abiotic, and social) responsible for driving plant–pollinator interaction in urban ecosystems. The reviews by Harrison and Winfree (2015) and Wenzel et al. (2020) highlight landscape, local, and abiotic factors. The landscape factors considered are the composition of the landscape, which includes the proportion of impervious surface, and the configuration of landscape, such as the spatial distribution and size of urban green spaces (resulting from fragmentation and habitat loss), in addition drives related to connectivity between urban areas and urban areas and natural or semi-natural areas. The local drives include temporal distribution of floral resources, referring to the beginning and duration of flowering and nesting sites, for example. Abiotic factors, on the other hand, are related to establishment of heat islands (higher temperature in cities than in the surrounding areas), which has been amplified due to climate change; air pollution, through the high emission of greenhouse gases and soil pollution, where pollutants can be concentrated in the nectar and pollen produced by plants; use of pesticides for weed control, for example; and the presence of native and exotic species of plants and animals, which may have been managed or not (Harrison and Winfree 2015; Wenzel et al. 2020). In addition to these main and well-discussed factors, we must emphasize some social factors that can also act on the plant–pollinator interaction in urban green areas, such as the level of education, income and lifestyle of the population (including ethnicity/culture). These factors are capable of influencing the management of domestic gardens, parks, flower beds and green roofs, for example, changing the local floristic composition (through the planting of non-native plant species) and consequently the supply of resources to pollinators (Kendal et al. 2012). This is particularly important for the management of urban agriculture in the different types of green spaces (Zhao et al. 2019).

In synthesis, we identified a pattern of impairment or disruption of plant–pollinator interactions in urban ecosystems worldwide, although there are conflicting evidences suggesting that cities could retain high diversity of pollinators (Tommasi et al. 2004; Sattler et al. 2010) thus adequately contributing to plant reproductive success (e.g. Rossum 2010). Plant–pollinator interactions in urban green areas may be negatively impacted in distinct levels. Firstly,

reduced diversity of flowering plants and nesting sites in urban green spaces may impair the establishment of pollinators. Indeed, many groups of pollinators, such as bees, flies, hoverflies, wasps, birds and hummingbirds, had reduced diversity of species or functional traits in urban green areas according to our review. In a second level, urbanization is associated with negative changes in pollinator behavior, such as decreases in foraging routes (e.g. Lopes-Uribe et al. 2008), which may be particularly detrimental for plant–pollinator interactions involving sparsely distributed urban green spaces. Specifically, many plant species in urban green areas are not visited by pollinators (Lowenstein et al. 2019), as a response to limitation in foraging routes, scattered distribution and impervious surfaces surrounding urban ecosystems. Finally, by reducing pollinator movement, the frequency of floral visits and the quantity of pollen grains that may be deposited in the flower stigmas are decreased, thus harming the female reproductive success of many plants in urban ecosystems.

Research funding/grants and policy documents related to pollination and pollinators in urban ecosystem

Our initial search returned 217 research funding/grants, published from 1994 to 2020. After sorting and excluding duplicates, 172 records remained; of which 45 were

selected because they were destined to researches that addressed pollination, pollinator or plant–pollinator interactions in urban ecosystems; 27 of these 45 were directed to plant–pollinator interactions in urban ecosystems (Supplementary Material Table S3). The first research funding/grant on the theme occurred only in 2005 (Supplementary Material Table S3). Developed economies concentrated practically all funding (97.8%) related to plant–pollinator interactions or pollinators in urban ecosystems, while only a single research funding was granted and applied in a country with developing economy (2.2%) (Fig. 6). The United States, Canada and the United Kingdom accounted, together, for 89% of the research funding/grants; while countries such as Brazil, Belgium, Germany, Norway and Sweden had only one research funding/grant on the topic (Supplementary Material Table S3). Research funding on plant–pollinator interactions or pollinators in urban ecosystems was only approximately US\$7.1 million in the 25 years since the first funding. It is worth mentioning that: (1) 62% of the research funding/grants were addressed to researches on pollinating insects, and of these 85.7% were specifically for bees; (2) 29% had some information at the website to which the project was linked but failed to inform the pollinator group of the study; (3) 4.5% focused on birds and bats (2 research funding/grants only); (4) 4.5% of the research funding/grants did not have any information at the

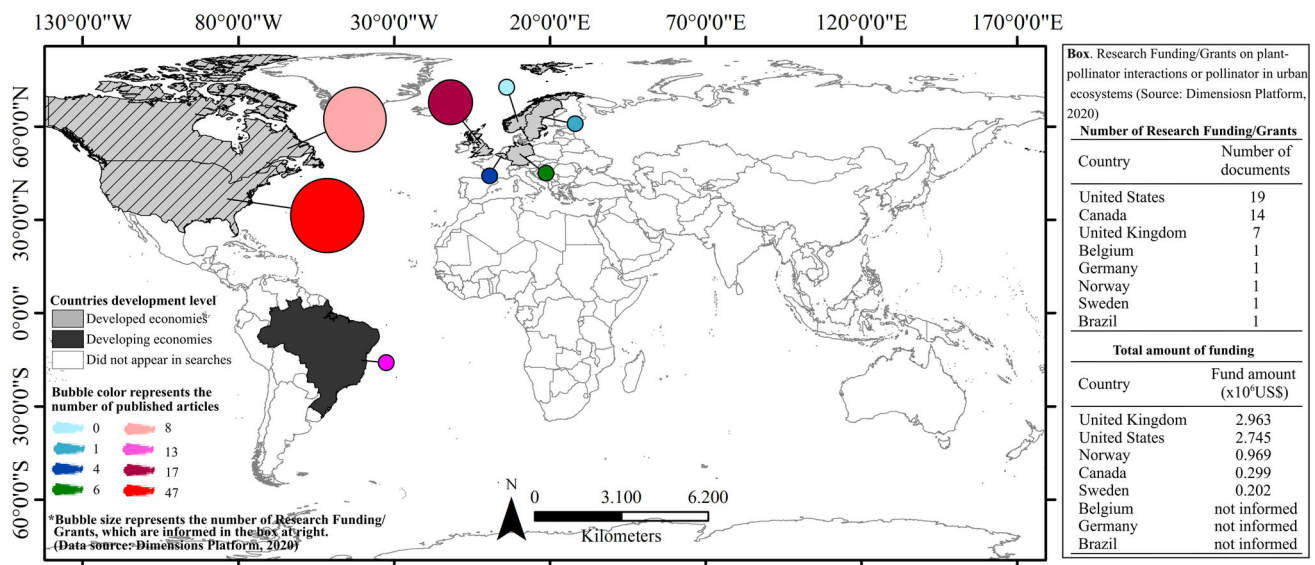


Fig. 6 Research Funding/Grants for projects related to plant–pollinator interactions or to pollinator (e.g. abundance, diversity, healthy) in urban ecosystems in countries with developed (light grey) (97.78%; $N = 44$) and developing economies (2.22%, $N = 1$) (dark grey). In light grey and hatch pattern Grants/Research Funding for Canada (US\$ 299,370.00 million), the United States (US\$ 2,745,636.00) and the United Kingdom (US\$ 2,963,526.00)—together they accounted for 83.67% of the investments ($N = 40$). For the inclusion and exclusion criteria when searching Research Funding/Grants at Dimensions Platform (2020), please see the Flow diagram in Fig. 1. Bubble color represents the number of published articles; Bubble size represents the number of Research Funding/Grants, which are informed in the box at right. This box also details the total amount of funding per country (Data source: Dimensions Platform 2020; <https://www.dimensions.ai/>)

website to which the project was linked (Supplementary Material, Table S3 for details).

We did not find any policy documents related to plant–pollinator interactions in urban ecosystem. However, 10 policy documents addressed, in general, the conservation, maintenance and improvement of pollinators in the United Kingdom ($N = 8$), Italy ($N = 1$) and Australia ($N = 1$). None of the policy documents are specific to urban ecosystems, although they mention urban green areas. All these policy documents were established by government agencies of developed countries (Supplementary Material Table S4).

In the last decade, there has been a growing concern about the decline of pollinators worldwide (e.g. Potts et al. 2010, 2016; Dicks et al. 2016). But the alerts and efforts to protect and conserve pollinators are mainly related to food production and security (e.g. Gallai et al. 2009; Bauer and Wing 2010; Novais et al. 2016; Sluijs and Vaage 2016). In a recent review, for instance, Hall and Steiner (2019) examined relevant policies for insect pollinators in the United States, and reported 109 laws related to agriculture, pesticide use, habitat improvement and awareness. Despite this, our findings clearly indicate that research funding and the development of government policies aimed at plant–pollinator interactions or pollinators in urban ecosystems are still insufficient and/or scarce, especially in countries with developing economy. Pollination in urban green spaces represents an ecosystem service that contributes to human well-being (e.g. Cox et al. 2018). Therefore, we must pay attention to the need for greater technical and scientific funding, local recommendations, particularities of each location, and public awareness, aiming to protect plants and pollinators in urban green areas to promote healthier urban ecosystems. In particular, public initiatives are needed to encourage and support the development of urban agriculture, with the establishment of clear recommendations and with planning and management techniques that maximize biodiversity. Thus, urban green spaces, in turn, may help in the maintenance of biodiversity, ecosystem services and improve the quality of life of humans in cities.

CONCLUSIONS

Our scientometric approach reveals that plant–pollinator interactions in urban ecosystems is a recent research field that is mainly explored in temperate regions by researchers affiliated to institutions in the United States, United Kingdom and France. Plant–pollinator interactions in tropical urban ecosystems is still neglected. The most studied pollination vectors are insects, mainly bees, in both tropical and temperate regions. In general, urbanization

may exert negative and complex effects on plant–pollinator interactions. Generalist plants and pollinators predominate in urban ecosystems. Despite the recent increase in the number of published articles, several research opportunities emerge from our review. Specifically, studies investigating more detailed aspects of pollen removal by distinct groups of pollinators were not registered in our database. Similarly, studies investigating the pollination of nocturnal plants and maintenance and behavior of nocturnal vectors in urban areas, such as bats, are scarce or even nonexistent, when considering other nocturnal pollinators, such as non-flying mammals, lizards and hawkmoths. These studies would be particularly relevant for the tropics, which harbor the most biodiverse and populated regions of the world, but where plant–pollinator interactions in urban ecosystem is still neglected. Additionally, research funding and policy actions for pollination and pollinators in urban ecosystems are still scarce and concentrated in developed economy countries and in temperate region. To make urban green areas contribute to the maintenance of biodiversity and provision of ecosystem services, transdisciplinary approaches that integrates ecological, social, economic and cultural factors are needed.

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AUTHOR BIOGRAPHIES

Jéssica Luiza S. Silva is a postdoc at the Department of Botany of the Universidade Federal de Pernambuco. Her research interests include plant ecology and pollination biology in urban and natural ecosystems.

Address: Departamento de Botânica, Centro de Biociências, Universidade Federal de Pernambuco, Recife, Pernambuco 50670-901, Brazil.
e-mail: jessicaluizassilva@gmail.com

Marcela Tomaz Pontes de Oliveira has got her PhD at the Department of Botany of the Universidade Federal de Pernambuco. Her research interests include pollination in urban ecosystems. *Address:* Programa de Pós-Graduação Em Biologia Vegetal, Centro de Biociências, Universidade Federal de Pernambuco, Recife, Pernambuco 50670-901, Brazil.
e-mail: marcelatomaz@gmail.com

Oswaldo Cruz-Neto is a postdoc at the Department of Botany of the Federal University of Pernambuco. His research interests include plant ecology, with an emphasis on tropical pollination ecology. *Address:* Departamento de Botânica, Centro de Biociências, Universidade Federal de Pernambuco, Recife, Pernambuco 50670-901, Brazil.
e-mail: ocruznt@gmail.com

Marcelo Tabarelli is a Professor at the Universidade Federal de Pernambuco (UFPE). His research work includes diverse aspects of tropical environmental degradation and conservation ecology. MT is a leading Brazilian ecologist who recently won an award from The Humboldt Foundation for his scientific contribution to tropical ecology and conservation. He has coordinated and collaborated in diverse projects funded by the Brazilian Government. *Address:* Departamento de Botânica, Centro de Biociências, Universidade Federal de Pernambuco, Recife, Pernambuco 50670-901, Brazil.
e-mail: mtrelli@ufpe.br

Ariadna Valentina Lopes (✉) is a Professor at the Universidade Federal de Pernambuco. AVL is Member and Leading Author of the IPBES (Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services) Thematic assessment on pollinators, pollination and food production. Her recent research includes analyses of how the diversity of plant reproductive strategies influences the diversity of biological communities; landscape ecology; effects of human disturbance on the reproduction of tropical plants; pollination service. She is a leading Brazilian author who has coordinated and collaborated in diverse projects funded by the Brazilian Government. *Address:* Departamento de Botânica, Centro de Biociências, Universidade Federal de Pernambuco, Recife, Pernambuco 50670-901, Brazil.
e-mail: avflopes@ufpe.br