



# Urbanization driving changes in plant species and communities – A global view

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## ABSTRACT

The urban landscape is becoming the environment most familiar to most of humanity, which has consequences for society, the environment, and biodiversity. Here, we present a systematic review of current research integrating several areas of urban ecology to evaluate how plants are responding to urbanization. We found that most studies were conducted in Europe and North America. The most represented biome was that of Temperate Broadleaf and Mixed Forests. The majority of studies reported negative consequences of urbanization. The Urban Drivers most commonly cited as responsible for changes in plant species and communities were Land Cover Change and Biotic Invasion. In general, urbanization reduces the richness of plant species and pollinators' availability. It also homogenizes the environment, promotes the invasion of non-native species, causes changes in phenological events, and presents difficulties for plant growth. However, some species show evidence of adaptation to these adversities through their phenotypic plasticity and the evolution of traits that make individuals resilient to the urban environment. Although it has been established that urbanization imposes novel selective pressures resulting in unique adaptations to city life, patterns of changes in biodiversity in response to urbanization can vary by region, biomes, city history, and the taxa studied. The Urban Drivers responsible for floristic responses work simultaneously by modifying the environment. Therefore, it is challenging to predict response patterns of plants under urban growth. It is necessary to outline strategies for continuous monitoring to document the progress of species in perpetuating themselves in the face of urbanization.

## 1. Introduction

Urbanization is a complex socio-economic process with numerous consequences for different levels of society, the environment, and biodiversity (United Nations, 2018). The urban landscape is becoming the most familiar environment for most of humanity, despite covering a small proportion of the Earth's surface (Niemelä, 2011). More than half of the world's people currently live in urban areas, with 55 % of the world's population residing in urban areas in 2018, compared with 30 % in 1950, reflecting a shift in the spatial distribution of populations from rural to urban areas (Parris, 2016; United Nations, 2018). Urban population growth is expected to continue, such that the world's urban population will reach five billion in 2028 and six billion in 2041 (United Nations, 2018).

Urbanization leads to primary (e.g., removal of existing vegetation and construction of urban infrastructure) and secondary (e.g.,

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habitat loss, fragmentation and isolation, climatic changes, pollution of air, water, and soil) processes that represent many challenges to the persistence of non-human species (Parris, 2016). Cities have distinctive characteristics due to the changes that happen to the land in urban areas. All ecosystems are affected by the same broad suite of state factors (Chapin et al., 2002), such as climate, substrate, resident organisms, relief, and the system's history. The urban ecosystem is no different. However, urban biotic communities are also highly influenced by anthropogenic impacts. Natural areas, agriculture, and forests are primarily replaced by predominantly built-up surfaces, changing cities' environment, which significantly impacts the physical environment, ecosystem processes, and ecology of organisms that live in cities (Grimm et al., 2008; McDonnell and MacGregor-Fors, 2016).

Biological introductions and human disturbance, combined with primary and secondary urbanization processes, impact species' births, deaths, immigration, and emigration rates. These combined factors lead to population growth or decline, which in turn may further alter intra- and interspecific interactions in different groups of organisms (Parris, 2016). Understanding the relative roles of abiotic, biotic, and anthropogenic filters that shape local communities provides a deeper understanding of community assembly, leading to practices that ensure the future of sustainable and biodiverse cities (Aronson et al., 2016).

The impacts of urbanization on biodiversity and ecosystems, especially on a global scale, are insufficiently understood. Previous work has established that urban areas impose novel selective pressures resulting in unique adaptations to city life (Niemelä, 2011). Although generalizations about the effect of urban areas on biodiversity are often made, actual patterns can vary by region, biomes, and city history (Müller et al., 2013; Niemelä, 2011). Furthermore, understanding which species are likely to benefit and which are likely to be detrimentally impacted will be important for biodiversity conservation and ecosystem services in an increasingly urbanized world (Williams et al., 2015). To improve our understanding of ecology in urban ecosystems, there is a need for comparative research worldwide (McPhearson et al., 2016).

The discipline of urban ecology has provided increasing evidence of how environmental changes affect species' population ecology, community structure, and ecosystem processes (Donihue and Lambert, 2015). Specific trends of living organisms' responses to urban stressors have been predicted based on prior knowledge of ecology and evolution (Johnson et al., 2015). Most of the recent studies in urban evolutionary ecology have focused on animals, particularly mammals, arthropods, and birds, and fewer studies have examined the effects of urbanization on plant evolution (Aronson et al., 2014; Johnson et al., 2015; Rivkin et al., 2019). Previous reviews on the topic of urban ecology have specified issues regarding the possible responses of plants to the biotic and abiotic changes that occur in urban areas (e.g., Alberti et al., 2017; Aronson et al., 2016; Cadotte et al., 2017; Eckert et al., 2010; Harrison and Winfree, 2015; Jochner and Menzel, 2015; Johnson et al., 2015; Rai, 2016; Williams et al., 2015, 2009). However, how the impacts of urbanization drive the evolution of living organisms in cities remains poorly understood (Donihue and Lambert, 2015; Johnson and Munshi-South, 2017; Rivkin et al., 2019).

Most studies examine only a few populations in one city (Johnson and Munshi-South, 2017). However, cities worldwide have different development histories and urbanization varies in intensity. Moreover, cities are inserted in different biomes and climates that can lead to a variety of responses in local biodiversity. The different contexts in which cities have developed their histories provide an excellent opportunity to understand the repeatability and pace of evolution in response to human activity. Considering this, we still need to understand more deeply the effects that this inevitable increase in urbanization will bring to the environment to facilitate the establishment of resilient and sustainable urban ecosystems (Johnson and Munshi-South, 2017; Niemelä, 2011).

In this article, we do a comprehensive systematic review of what has been found in the last eleven years of publications in urban ecology, focusing on plant species and communities worldwide. Our goals were to (1) summarize how urbanization drives plant changes in species and communities worldwide, (2) to understand whether plants respond to urban environments via phenotypical plasticity or through adaptation, (3) and to analyze whether Urban Drivers generate different responses based on the biome and urban density in plant species and communities. We also aimed to integrate several areas that fall under urban ecology to evaluate species plant and communities' structure changes in response to Urban Drivers.

## 2. Methods

We undertook a broad systematic review of peer-reviewed articles reporting data about the effects of urbanization in two ecological levels (species and communities) in vascular plants worldwide. We focused on studies and observations made completely in the field, comparing the results obtained between urban and non-urban areas (e.g., natural, agricultural, and green areas). We also included studies reporting comparisons between different time points in the history of increasing urbanization in various cities. We did not include studies exclusively performed with urban environment simulations in laboratory/greenhouse or those that evaluated flora that did not occur spontaneously in the study area.

From June 2020 to January 2022, we searched the literature in the Web of Science (WoS) database. The related search keywords were "urban plants" AND "species richness" OR "ecology" OR "genetic" OR "evolution" OR "adaptation" OR "pollinators" OR "reproduction" OR "dispersion" OR "physiology." We considered the matches to our search terms within the topic, title, keywords, and abstract. Studies meeting the inclusion criteria were: i) published in a peer-reviewed journal, ii) written in English, iii) reporting observational or experimental field data about effects of urbanization in plants, iv) published between 2010 and 2021. We recorded the studies in a spreadsheet, and relevant information was extracted and allocated into categories to summarize the methodologies used in the articles and the obtained results.

We classified the studies' methods according to the designed approach: urban–non-urban gradient, urban vs. non-urban (spatial comparison between urban and non-urban habitats), or temporal (changes over years of urbanization). We also recorded locations globally, considering the 14 terrestrial biomes of the world according to Dinerstein et al. (2017) (updated version of the Terrestrial Ecoregions of the World from Olson et al., 2001). When the city of the study was provided, we classified them as "megacity" if they have

more than 1 million inhabitants, in keeping with the United Nations' World Economic Situation and Prospects (United Nations, Department of Economic and Social Affairs, 2018), or as "small cities" if they have fewer than 1 million inhabitants. We also recorded the variables analyzed in each study. We categorized them into major areas to overview the main variables studied over the past eleven years. The variables allowed us to identify the following principal major areas reviewed: "community traits" (e.g., species richness and abundance, vegetation cover, demography, non-native species richness, herbivory, species conservation status), "physical environment" (e.g., land use, temperature, precipitation, evapotranspiration, soil properties, air and soil pollution, habitat type, percentage of impervious surfaces, carbon dioxide [CO<sub>2</sub>] concentrations), "morphological traits" (e.g., diameter at breast height, leaf area, shape, number of leaves, size), "physio-chemical traits" (e.g., leaf content [carbon and nitrogen], biomass, photosynthesis, stomatal conductance, thermal and shade tolerance, gas exchange measurements), and "reproductive biology" (e.g., phenology [flowering], flower morphology, pollination, reproductive success, seed dispersal, germination, and fruiting).

The responses of plant species and communities to urbanization were categorized according to the following Urban Drivers: biotic invasion, climate, human activities, land cover change, and pollution (Alberti et al., 2017; Aronson et al., 2016; Piana et al., 2019; Pickett et al., 2011). Biotic invasion represents the introduction of non-native species in the habitat. Climate refers to climate changes in urban areas, especially warming. Human activities are how humans directly act on urban biodiversity (e.g., through gardening practices). Land cover change refers to fragmentation and land conversion, and pollution is attributed to environmental contamination through soil and air pollutants. These responses were classified as negative (urban habitats negatively affect fitness), neutral (when species' and communities' responses do not differ between urban/rural habitats), or positive (species and communities are successful in the urban environment, maintaining the ecological balance). If a study found several responses, we considered each one individually according to the abovementioned criteria.

### 3. Results

The number of studies evaluating plant responses to urbanization has increased over the past ten years (Fig. 1). We found 171 studies that fit our selection criteria. Most of the studies were carried out in temperate biomes (113), with Temperate Broadleaf and Mixed Forests most represented with 102 studies (Fig. 2). Most studies took place in Europe and North America (60 and 43, respectively). Forty studies were conducted in Asia, 14 in South America, eight in Africa, and only seven in Oceania (Fig. 2).

Most of the studies (89) used the urban–non-urban gradient to describe how urbanization drives changes in species and communities. Forty-two studies used a simple comparison between urban and non-urban habitats, and eighteen used the temporal approach to explain how urbanization is changing species and communities over the years. In addition, 22 studies used combinations of these approaches. Most of the studies (103) were conducted with comparisons in different plant communities, and 68 studies analyzed specific species. Thus, analyses involving general community traits are among the most studied. Further details on the methodologies used in the studies to determine plants' responses to urbanization are found in Supplementary Table 1.

The most commonly cited Urban Drivers responsible for changes in plants in the reviewed literature (Fig. 3) were land cover change (129) and biotic invasion (56). Pollution was the least cited (Fig. 3). Overall, the studies identified varied responses in plants, often showing the same species or community demonstrating beneficial, neutral, or harmful responses, depending on which major areas were analyzed (Supplementary Table 2). However, most studies (133) reported negative responses (Supplementary Table 2). Table 1 summarizes how plants are responding to urbanization.

### 4. Discussion

#### 4.1. Urbanization and urban drivers

The responses of plants to urbanization can be complex and varied (Table 1; Supplementary Table 2). More than one Urban Driver may be responsible for some community and plant traits changes, or several different changes may result from one driver. The

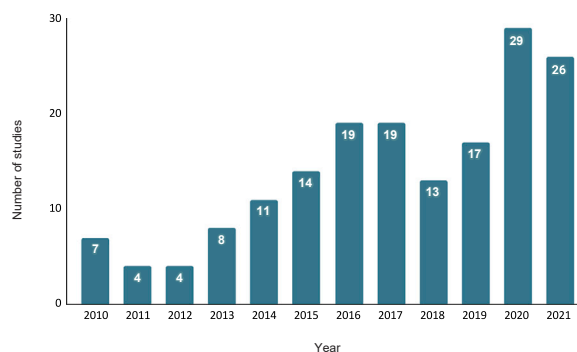
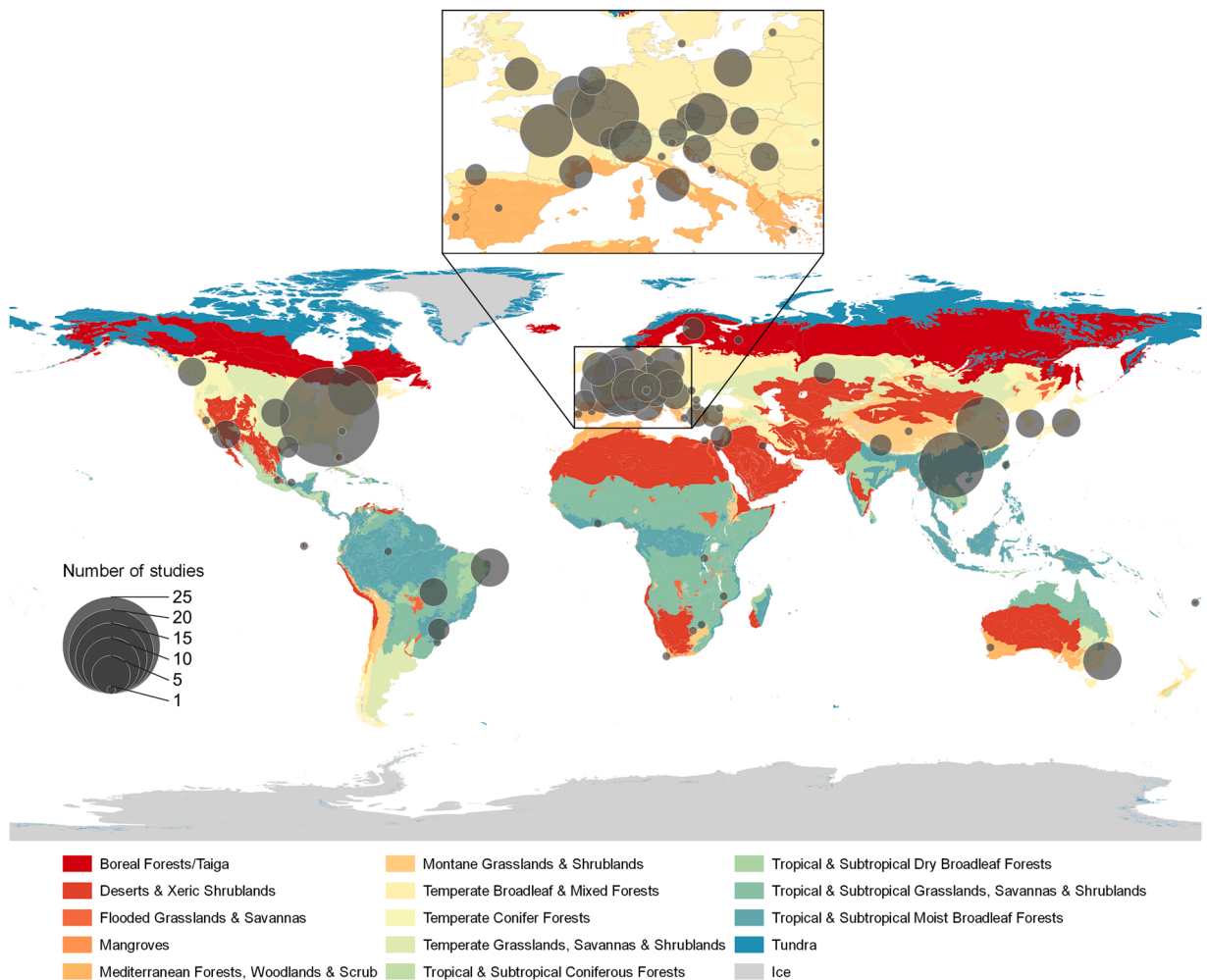
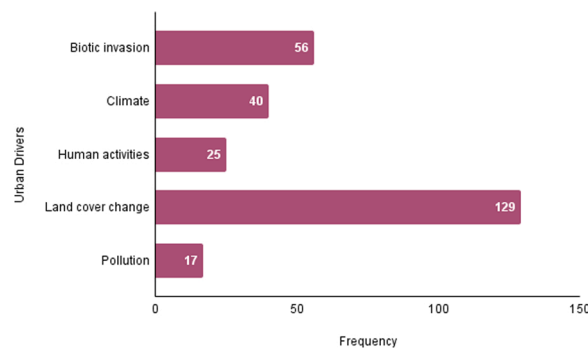


Fig. 1. Number of studies relating changes in plant species and communities in response to urbanization between 2010 and 2021.



**Fig. 2.** Number of studies relating changes in plant species and communities in response to urbanization within their locations on biomes according to [Dinerstein et al. \(2017\)](#) (updated version of the Terrestrial Ecoregions of the World from [Olson et al., 2001](#)).



**Fig. 3.** The frequency at which Urban Drivers are held responsible for changes in plant species and communities based on the literature review from the last eleven years.

consequences are a network of responses connected to various drivers, making systematic cause-and-effect classification through frameworks in urban environments difficult ([Aronson et al., 2016](#); [Williams et al., 2015](#)). We found that urbanization mainly negatively affects plants compared with neutral and positive responses, both in megacities and small cities. They result from a single driver or by combination among different Urban Drivers.

**Table 1**

Negative, neutral, and positive examples of responses of plants to six Urban Drivers. The data was compiled based on a literature review from the last eleven years of publications of the effects of urbanization on plant species and communities.

Urban Drivers	Negative	Neutral	Positive
<i>Land cover change</i>	Lower plant cover; prevalence of abiotic pollination and dispersal; lower ability to reproduce sexually; reduction of dispersal ability between fragments; lower reproductive success; higher proportions of non-native, generalist, and disturbance-tolerant species	Species richness remains stable; reproduction modes did not change in response to urbanization	Urbanization of grasslands areas keep high nature conservation value through the favoring of insect-pollinated species; adaptations to attract more pollinators; reproduction modes changes in response to urbanization; biotic differentiation
<i>Climate</i>	Higher abundance of non-native species adapted to warmer conditions; phenological events start earlier; asynchrony between the phenology of plants and pollinators; decrease in species richness; changes in photosynthetic rates; lower water use efficiency	No changes in the timing of phenological events	Thriving of native thermophilous species; urban areas as a refuge for endangered species with affinities for hot and dry surfaces
<i>Pollution</i>	Decrease in species richness; delays in phenology; higher leaf nitrogen concentration; lower content of chlorophyll-a; associated arthropod biota affected through the reduction in palatability; higher weed coverage	Inconsistent changes in leaf morphology	More species with higher affinities to nutrient soil content
<i>Human activities</i>	Facilitation of the spread of non-native plant species by roads and railways; increase in ornamental non-native species in urban gardens, with lower functional richness; beneficial of human dispersed plants; higher abundance of species with lower conservation value; decrease in species richness	–	Human preferences for showy flowers may are good for pollinators in urban areas, favoring animal-pollinated plants
<i>Biotic Invasion</i>	Loss of species richness by the colonization of non-native species phylogenetically similar to the resident species; reduction in the diversity of native species; evolution of non-native species to compete with natives; pollinators preference for non-native species; species turnover;	Native species keeping fitness front invasion of non-native species	Increase of total plant species richness

## 4.2. Urban Drivers and their effects on plant species and communities

### 4.2.1. Land cover change

When it comes to urbanization, fragmentation due to land cover change is the central axis of biodiversity loss. A considerable amount of the reviewed literature described decreased species richness in plant communities related to land cover change (Abd El-Wahab, 2016; Albrecht and Haider, 2013; Anderson et al., 2020; de Araújo et al., 2021; Aronson et al., 2015; Bigirimana et al., 2011; Cochard et al., 2017; Deák et al., 2016; Dolan et al., 2011; Fekete et al., 2020; Glišić et al., 2021; Güler, 2020; Heneidy et al., 2021; Kalusová et al., 2019; Kolbe et al., 2016; Kummli et al., 2021; Lopez et al., 2018; Lowry et al., 2020; Melliger et al., 2018; Nero, 2019; Peng et al., 2019; Planchuelo et al., 2020a; Salgado et al., 2021; Silva-Junior et al., 2018; Tian et al., 2015; du Toit et al., 2020; Vakhlamova et al., 2014; Vallet et al., 2010a; Wang et al., 2020a; Wang et al., 2020b; Wu et al., 2013; Yan et al., 2019; Zhang et al., 2016) - Supplementary Table 2). The disturbance created by land cover changes, fragmenting landscapes from native vegetation to areas covered by impervious surfaces, homogenizes the physical environment. In consequence, the urbanization process creates similar environments that select identical traits and life histories in both native and non-native species, causing a reduction in species richness and shifts in the community's composition (species turnover) (Aronson et al., 2016; Brice et al., 2017, 2016; Dolan et al., 2017; Freitas et al., 2020; McKinney, 2006; Paquin et al., 2020).

Studies with functional-trait approaches have demonstrated specific features of plants selected by the urban environment leading to habitat homogenization since low functional-trait diversity in communities was detected in several cases (Anderson et al., 2020; Concepción et al., 2017; Melliger et al., 2018; Milanović et al., 2021; Nock et al., 2013; Ribeiro et al., 2019; Trentanovi et al., 2013). Some of the responses to habitat homogenization were a higher presence of generalist and disturbance-tolerant species (Everingham et al., 2019; Huang et al., 2013; Mccune and Vellend, 2013; Oliveira et al., 2020; Yang et al., 2021), ruderal species (Bigirimana et al., 2011; Wang et al., 2020a, 2020b; Zhang et al., 2020), and pioneers (Concepción et al., 2015; Nero, 2019; Pennington et al., 2010) as well as a decline in phylogenetic richness (Cui et al., 2019; El-Barougy et al., 2021; Knapp et al., 2017; Lopez et al., 2018; Silva-Junior et al., 2018). In these studies, we found a convergence of selected traits in urban habitats related to loss of animal-related characteristics (e.g., shifts to self- and wind-pollination and dispersal), fast growth rates (e.g., short stature and small seeds), long flowering periods, and demanding resource-use strategy (e.g., softer wood, larger leaves, lower leaf mass per area). Reductions in the number of functional groups of organisms decrease the efficiency by which whole communities capture biologically essential resources, which is



acknowledged as critical for community stability and functioning (Cardinale et al., 2012). These findings raise that analyzing functional traits in plants is more potent in capturing species' response to environmental filtering driven by urbanization (Anderson et al., 2020; Dolan et al., 2017) beyond just tabulating changes in species richness.

At the same time, some studies revealed that native plant communities could be resilient to fragmentation, keeping their diversity (Fekete et al., 2020; Hahs and McDonnell, 2013; Landis and Leopold, 2014; Lechuga-Lago et al., 2017; Santos et al., 2016; Schwoertzig et al., 2016). The persistence of native species in urban areas shows us that we have alternatives to face the consequences of urbanization. The city's structures can provide favorable and heterogeneous environments for stress-adapted native species and even endangered species (Dallimer et al., 2012; Fekete et al., 2020; Heneidy et al., 2021; Paquin et al., 2020; Planchuelo et al., 2020b; Qian et al., 2020; Schmidt et al., 2014; Schmiedel et al., 2015; Sonti et al., 2021; Trammell et al., 2020). Investigating the functional traits and ecological strategies of native species adapted to fragmented environments can help establish conservation priorities, using local native adapted species for urban greening purposes. Also, forests and protected areas close to urban environments have been essential in maintaining and sending propagules of native species to fragmented areas (Blood et al., 2016; Davis et al., 2015; Gulezian and Nyberg, 2010).

Because of low habitat fragment connectivity in urban environments, insect-pollinated species can experience a lower quality of pollinator services in terms of decreased visitation rate and the lowered ability of pollinators to carry pollen between fragmented populations (Bartlewicz et al., 2015; Geslin et al., 2013), bringing different consequences for populations and communities. In most cases, both self-compatible and self-incompatible plants showed a decrease in reproductive success due to the reduction of the variety of pollinators, their low effectiveness, and low visit frequency, often reducing the seed set (Hou et al., 2019; Irwin et al., 2018; Leong et al., 2014; Lhotte et al., 2014; Oliveira et al., 2019). *Teucrium pseudochamaepitys*, an endangered species in Southern France, experienced low reproductive success, despite effective pollination in urban habitats (Lhotte et al., 2014). Lhotte et al. (2014) showed a lower diversity of pollinators, with *Apis mellifera* ensuring 97 % of pollination. They demonstrate that changes in land use threaten the short-term persistence of populations due to competition.

However, other studies suggested that pollinators may also be mobile between urban fragments (Filiz et al., 2015; Kobayashi et al., 2018; Van Rossum, 2010; Verboven et al., 2014). Verboven et al. (2014) analyzed the pollinator frequency in *Trifolium repens*, a species pollinated mainly by generalist bumblebees. Generalist species with large foraging ranges were previously found not to be strongly affected by urban land use (Bates et al., 2011). This finding reinforces that plant species that are not supported by these generalist pollinators are not the most suitable species for conservation efforts in cities.

Species that do not depend on pollinators for reproduction can maintain their reproductive success when performing selfing under conditions of lower pollinator availability (Ushimaru et al., 2014). The ability to tolerate fragmentation with traits that allow reproduction by selfing has also been identified by analyzing genetic diversity in *Viola grypoceras* in Kyoto, Japan (Toma et al., 2015). This study found no significant difference in allelic richness between the urban fragmented and suburban forests.

Genetic studies can be valuable for describing how plant populations have responded to habitat fragmentation due to land cover change. Molecular markers described limited gene flow between urban and rural populations (Bartlewicz et al., 2015; Emel et al., 2021; Wodkiewicz and Gruszczyńska, 2014) detected through high genetic structure between populations. On the other hand, there can be a failure to detect a genetic response to habitat fragmentation due to insufficient time having elapsed since fragmentation, as seen by Delnevo et al. (2021). Despite the current intense fragmentation, they found similar levels of genetic diversity across populations and a weak spatial genetic structure in *Conospermum undulatum* in Western Australia, highlighting the importance of considering the historical habitat dynamics when investigating fragmentation consequences in long-lived plants (Delnevo et al., 2021). These authors related that the currently fragmented populations of *C. undulatum* were part of a continuous population 70 years ago, resulting in the present weak genetic structure.

Knowing the reproductive system of a species and how populations respond to fragmentation through genetic studies is an effective way of evaluating the success of a species in the face of urbanization. Studying plant species with alternatives to biotic pollination and species pollinated by animals that can move between fragments is essential to establish which species are suitable for creating green areas. Above that, maintaining protected forest areas close to cities would be a more effective way to maintain more specific plant-pollinator relationships, maximizing species richness and ecosystem stability.

#### 4.2.2. Climate

Fragmentation only is often insufficient to explain plant species' distributions in urban landscapes (Williams et al., 2009). Fragmentation in urban habitats includes the introduction of materials that are not biologically active covering the soils in urban habitats, allowing additional drivers to be responsible, on a smaller or larger scale, for decreasing the number of species (Grimm et al., 2008; McKinney, 2002). These drivers include climate (which increases the phenomenon of the Urban Heat Island [UHI]) and soil and air pollution (Pickett et al., 2011). These particularities associated with urban areas significantly impact species in anthropogenic habitats (Williams et al., 2009). Indeed, increased temperatures in cities were related to reduced species richness by filtering out species not adapted to warmer habitats (Albrecht and Haider, 2013; Chen et al., 2014; Concepción et al., 2017; Yu et al., 2021). For example, Chen et al. (2014) demonstrated that the increase in mean annual temperature over the past half-century in Harbin, China, caused a decrease in temperate species and increased in tropical species over the years.

One of the best bioindicators for anthropogenic climate change is phenology. Studies on urban phenology helped to detect UHIs. There is a strong relationship between changes in the timing of natural events, such as leaf unfolding, flowering, fruit ripening, or leaf coloring and fall and changes in regional temperatures (Jochner and Menzel, 2015). Studies at a spatial scale detected advanced and more extended phenological events (Cochard et al., 2019; Davis et al., 2016; Fisogni et al., 2020; Kondratyeva et al., 2020; Massetti et al., 2015; Oliveira et al., 2019; Su et al., 2019; Yakub and Tiffin, 2017). Long-term studies that focused on more prolonged periods of

observations (Fitchett and Raik, 2021; Lee, 2017; Lindh et al., 2018; Neil et al., 2010; van Vliet et al., 2014; Xingyuan et al., 2016), as well as those that combined both temporal and spatial analyses also detected earlier phenology events (Comber and Brunsdon, 2015; Jeong et al., 2011; Li et al., 2017; Qiu et al., 2017). Analyses involving a large time scale associated with data between urban and non-urban populations can be useful for comparing the period in which there were changes in phenology and the events of expansion of urbanization in cities.

In contrast, some studies did not find significant changes in phenology in urban gradients (Jochner et al., 2013, 2012; Zipper et al., 2016). The authors suggest that other specific characteristics of the regions where the cities are located, such as altitude, humidity and vegetation type, can influence climatic conditions, making it difficult to analyze and interpret urban phenology. Santangelo et al. (2020a) reported later phenology in *Trifolium repens*. However, they suggest that changes in the biotic community (e.g., insects) or other components of the abiotic environment (e.g., soil moisture) were responsible for this observed pattern. Other factors that interact with temperature changes can make it challenging to analyze results. Therefore, detailed investigations of the system studied are needed to fully understand the effect of urban environmental conditions on plant phenology (Jochner and Menzel, 2015).

Little is known regarding vegetation changes in phenology affecting plant-animal interactions. Changes in flowering phenology lead to a mismatch between the flowering period and pollinators' activity (Fisogni et al., 2020), leading to a possible reduction of pollination services in urban areas and a reduction in reproductive success. Plants may respond differently from pollinators to climatic conditions; therefore, it is suggested that phenological studies focusing on specific species should consider the behavior of pollinators and how they respond to climate change. On the other side, Davis et al. (2016) described increased flower productivity in *Angophora costata*, *Eucalyptus pilularis*, and *Corymbia gummifera* within urban landscapes due to more extended flowering periods, leading to a higher abundance of nectarivorous parrots in Sydney, Australia. More extended periods of phenological events in urban vegetation result in more food resources for associated animals in the form of nectar and pollen (Jochner and Menzel, 2015). This shows that cities can maintain species that have good productivity in warmer habitats, providing resources that attract local animals and increasing the productivity of the habitat.

In addition to higher temperatures attributable to UHI, climate change can lead to increased carbon dioxide and ozone levels in urban areas and greater drought stress experienced by plants (Barradas and Esperon-Rodriguez, 2021; Calfapietra et al., 2015). Zipper et al. (2017) demonstrated that UHIs significantly increase evapotranspiration demand associated with variability in impervious cover, with consistent relationships from year to year in Madison, United States. Lahr et al., (2018, 2015) demonstrated direct negative effects of temperature and water availability on photosynthesis.

Conversely, Searle et al. (2012) did not find changes in the photosynthetic capacity of foliage in *Quercus rubra* driven by urbanization in New York, United States. Climate change is a constant threat to biodiversity, increasing species' vulnerability. Knowing the vulnerabilities of species can help decision-makers plan conservation actions that minimize the effects of global warming on plant productivity.

#### 4.2.3. Pollution

High levels of soil and atmospheric pollution have potentially adverse impacts on the growth and development of plants (Rai, 2016). Different consequences were found when analyzing the effects of pollution in urban areas. Contaminated soils also have been described as the cause of reduced species richness and structural injuries (Bouraoui et al., 2019; Huang et al., 2013; King and Hovick, 2020). The high concentration of soil contaminants (Cadmium, Copper, and Zinc) and salts presented in the cited studies above are detrimental to plant development, causing a reduction in growth by accumulating in roots, stems, and leaves (Kabata-Pendias, 2004). Air pollution was associated with a decrease in the quality of seeds (Turmukhametova and Shadrina, 2020) and affected plant growth, seen through changes in the size and shape of the plant parts studied by Su et al. (2021) and Vujić et al. (2015). Jochner et al. (2015) found an association between delays in phenology and the presence of air pollutants. The authors indicate that this association might be attributable to other environmental conditions statistically correlated with pollution. Because they excluded the influence of air temperature in their analyses, other factors altered by pollution in urban areas, such as radiation and soil nutrients, may be related to the delay in phenology (Jochner et al., 2015).

Chlorophyll measurement is an important tool for evaluating the effect of air pollutants on plants, as it plays an essential role in plant metabolism. Reductions in chlorophyll concentration are usually associated with air pollution (Rai, 2016). Molnár et al. (2018) demonstrated lower chlorophyll-a content in *Celtis occidentalis* leaves, proving that this species is an effective indicator of anthropogenic emission of air pollutants. In the same line, Xiao et al. (2021) showed decreased photosynthetic rate and total chlorophyll contents in the canopies in Guangzhou, China. Still, herbs and shrubs responded with an increase to the same parameter (Xiao et al., 2021).

Roadside plantations are expected to combat air pollution since trees can act as a sink for CO<sub>2</sub> by fixing carbon during photosynthesis (Singh, 2021). The deposition of particulate matter on the leaves interrupted stomatal leaf exchanges by.

reduced CO<sub>2</sub> assimilation rate (photosynthesis) and the exchange of water (transpiration) in *Alstonia scholaris*, *Grevillea robusta*, and *Mangifera indica* (Singh, 2021; Singh et al., 2020). However, these species presented modulations in physiological and biochemical processes for acclimatizing or adapting to the altered environment, contributing to future species selection to combat air pollution in cities (Singh et al., 2020).

Pollution was the least cited urban driver among the studies evaluated. The rapid growth of cities has dramatically increased emissions of pollutants with heavy metals in the soil and toxic gases in the air, decreasing the quality of habitat in urban centers. More studies need to be carried out using pollution as one of the parameters of comparison between communities and plant species, since pollution is very present in cities, especially those in developing countries.

#### 4.2.4. Biotic invasion

Apart from the higher similarity in native species composition among cities, seen through the reduction of species richness, studies described a spread of non-native species in urban habitats (Bigirimana et al., 2011; Blouin et al., 2019; Knapp et al., 2017; Lososová et al., 2016; Oliveira et al., 2020). This process of replacing localized native species with increasingly widespread non-native species promotes biotic homogenization, beyond habitat homogenization. Non-native species may enrich local biodiversity, but global diversity is decreased by the extinction of local species that are lost to the global species pool (McKinney, 2006).

The invasion of non-native species into new regions provokes researchers' concern because of perceived threats to agricultural productivity, native biodiversity and ecosystem functioning, and human aesthetics and wellbeing. Cadotte et al. (2017) observed that the alterations of the physical environment in urban habitats offer unique opportunities for these invasions. They create a unique combination of environmental conditions that do not exist in unmodified landscapes. Here, we found that land cover change is one of the most significant opportunities for the gain of non-native species, as seen through their increase in proximity of urban centers (Atasoy et al., 2018; Blood et al., 2016; Chimaimba et al., 2020; Dallimer et al., 2012; Fornal-Pieniak et al., 2020; Greene and Blossey, 2014; Kalusová et al., 2019; Kühn et al., 2017; Landis and Leopold, 2014; Malkinson et al., 2018; Paquin et al., 2020; Park et al., 2021; Pellegrini et al., 2021; Pennington et al., 2010; Schmiedel et al., 2015; Tew et al., 2021; Tordoni et al., 2017; Vakhlamova et al., 2014; Yan et al., 2019), and with the urbanization process over the years (Celesti-Grapow and Ricotta, 2021; Kopel et al., 2015; Wirth et al., 2020; Yu et al., 2021). Furthermore, climate change is crucial for establishing non-native thermophilic species favored by warm conditions typical of urban habitats (Géron et al., 2021; Schmidt et al., 2014; Sołtysiak, 2020). Similarly, soil modification by higher quantities of nutrients and pollutants was related to an increase of non-native species (Grella et al., 2018; Lopez et al., 2018).

Cadotte et al. (2017) also infer that cities are islands of reduced competition or offer an escape from natural enemies. Moreover, other authors describe higher competitive skills in non-native species depending on their inserted context (Fukano et al., 2020). Ruderal species that use the competitive ruderal (CR) strategy allocate most of their nutrient supply to growth and reproduction to better compete for space and achieve wide distribution (Chen et al., 2014). Disturbed surfaces support the establishment of non-native species because other species have low competitive ability (Deák et al., 2016). Nitrophilic species have a more remarkable competitive ability due to the high presence of nitrogen in urban soils and thus can exclude less nitrophilic species (King and Hovick, 2020). Zeeman et al. (2017) demonstrated a significant shift in the composition of urban grasslands towards taller plants within non-native species, which is correlated with competitive vigor. In a temporal analysis, Cui et al. (2019) suggest that similar ecological niches between native and invasive species lead to a decrease in the competitive power of native species due to the lack of natural enemies for invasives in the local urban ecosystem.

Furthermore, Cadotte et al. (2017) observe that high immigration rates of non-native species are facilitated by humans (see Section 4.2.5). For example, *Carpobrotus edulis*, a succulent plant native to South Africa, has been intentionally introduced globally as an ornamental to prevent soil erosion in coastal areas in Galicia, Spain. The higher presence of *C. edulis* in urban coastal dunes increases soil impacts, allowing for the establishment of the native but ruderal, *Scolymus hispanicus*, which is not adapted to the typically limiting conditions of coastal dunes (Lechuga-Lago et al., 2017).

The performance of these non-native species in the novel habitats will define their persistence in becoming invasive species. They need to deal with a suite of biotic interactions beyond just competition. In particular, they must interact with consumers, pathogens, and mutualists (Cadotte et al., 2017); therefore, we should pay attention to possible changes in the communities' dynamics in urban habitats. For example, in Florida, *Ficus microcarpa* trees were planted as ornamentals as early as 1912. Today, adults are seed sources for fig-eating birds that disperse this invasive species and make it difficult to control the species' abundance (Caughlin et al., 2012). Non-native trees in urban habitats shelter fewer invertebrates, being a possible stronger driver of invertebrate declines in urban areas in Sweden (Jensen et al., 2021). The invasive shrub *Cytisus scoparius* (Scotch broom) is under natural selection by pollinators for increased flower size, but only in urban populations, in Lacey-Olympia, United States. This natural selection by pollinators could result in an invading species' adaptive evolution into a new pollination niche (Bode and Tong, 2018).

We can see the biotic invasion as an urban driver by itself, but it is strongly influenced by the other drivers described. The adverse conditions provided by the urban habitat are very favorable for the spread of non-native species and are one of the greatest threats to local biodiversity. This makes biotic invasion one of the priorities for continuously monitoring populations of exotic species already present in cities and efforts to reduce the spread of new exotic species.

#### 4.2.5. Human activities

Human-assisted "intentional" migration is a major conduit for non-native species that become invasive, and the impact of invaders on native biodiversity remains an area of intense research (Van Kleunen et al., 2015). People move among cities and introduce organisms for a variety of reasons. During the European colonization of Burundi and Brazil, for example, many European and tropical ornamental species of different biomes from local species were introduced for landscaping purposes (Bigirimana et al., 2011; Oliveira et al., 2020). In the contemporary world, the use of species for horticultural interest (Dolan et al., 2011; Greene and Blossey, 2014) and ornamental and gardening practices (Dolan et al., 2017; dos Santos et al., 2020; Gaggini et al., 2017; Löki et al., 2019; Ranta and Viljanen, 2011) are other forms of human activities that introduce exotic species. Human activities facilitate dispersion by roads and railways (Concepción et al., 2016; Gaggini et al., 2017; Rivkin et al., 2021; Skultety and Matthews, 2017; Štajerová et al., 2017; Vakhlamova et al., 2016). Vehicles are an important vector for plant dispersal; thus, rails, roads, rivers, or canals can play as corridors for the spread of plants, resulting in high propagule pressure of exotic species (Ricotta et al., 2014).

Environmental education works involving the dissemination of knowledge of local species should be implemented to prevent the entry of new exotic ornamental species. In addition, encouraging the use of native species for ornamentation is important to restore the productivity of the local ecosystem, increasing resources for the animal community associated with plant species.



#### 4.3. Does urbanization lead to phenotypic plasticity or adaptation in plants?

The drivers that impact fitness in plant communities can be challenging to discern. Urbanization includes environmental change along multiple interacting dimensions that can dramatically increase the complexity of environments to which populations must adapt. Understanding how traits may diverge with urbanization in response to Urban Drivers is necessary to understand the evolution of organisms in urban environments (Rivkin et al., 2019; Santangelo et al., 2022). Here, we have demonstrated that the number of studies describing how Urban Drivers are responsible for changes in plant species and communities has increased in recent years.

Species have evolved phenotypic traits in their historic ranges that might confer an ecological advantage allowing for colonization and establishment in urban environments (Rivkin et al., 2019). For example, five of the six studies with graminoid communities showed positive responses to urban environments. These studies confirmed that this group of plants might be highly adapted to this habitat type. Graminoids have assured insect pollination and can persist in disturbed soils by producing small, durable seeds (Albrecht and Haider, 2013; Beal-Neves et al., 2020; Cochard et al., 2017). Other traits, such as the capacity to grow taller individuals and increase vegetative reproduction, facilitate access to more resources and allow a species to spread (Cochard et al., 2019; Zeeman et al., 2017). Grassland ecosystems are evolutionarily related to disturbance regimes that maintain the high species richness of these systems under appropriate intensity and frequency (Overbeck et al., 2005). Another group that can take advantage of urbanization's new conditions, as Duffy and Chown (2016) observe, are the C<sub>4</sub> plants. Because C<sub>4</sub> plants are organisms adapted to warm environments, through the increase of photosynthetic activity, it is possible that native plants of this group will not be harmed by the global phenomenon of Urban Heat Islands.

Environmental changes induced by urbanization often select plants with specific traits that enhance plant persistence, competition, or resource retention (Ilyas et al., 2021; Murray-Stoker and Johnson, 2021; Song et al., 2019; Vallet et al., 2010b). These authors reported that plants in the urban forests presented an acquisitive strategy through a higher specific leaf area. Higher leaf nitrogen was also related to urban plants (Nikula et al., 2010; Song et al., 2019). Vasconcellos et al. (2019) demonstrated through dendrochronological characteristics of *Ceiba speciosa* growing in urban areas of Rio de Janeiro, Brazil, that this species is plastic and stress-tolerant under polluted conditions. Pollutant levels are lower during the rainy season, and microclimatic conditions may influence radial growth relationships. The authors showed that urban trees have a more immediate growth response to rain than rural ones.

Little is known about the phenotypic changes induced by pollinator and mate limitations on reproductive traits in disturbed urban plant populations (Eckert et al., 2010). For example, *Commelina communis*, an annual species in the metropolitan area of Osaka-Kobe, Japan, showed increased reductions in traits promoting outcrossing under pollen-limited conditions induced by urbanization (Ushimaru et al., 2014). The authors argue that the observed floral diversity across the urbanization gradient may not be driven by urbanization itself but by urbanization-induced pollinator-limited conditions. Larger flowers were described by Santangelo et al. (2020a) in *Trifolium repens*, associated with near-complete turnover of pollinator morphological groups along the urbanization gradient in Toronto, Canada. Hou et al. (2019) described shifts in flower structures in *Gentiana dahurica*, which demonstrated plasticity in producing longer flowers as urbanization intensified. These shifts may have enhanced the floral display and pollinator attraction to ensure reproductive success. However, pollinator visits to the urban area were insufficient to ensure species' reproductive success. Irwin et al. (2018) showed that pollination was associated with the selection for larger floral display sizes in *Gelsemium sempervirens*. However, there is little difference in phenotypes between urban and non-urban sites. Together, these results provide important insights into the possible adaptive evolution of reproductive traits in response to pollinators' limitations in urban areas.

Rivkin et al. (2021) showed how urbanization has the potential to lead to novel selection pressures on ecological interactions by analyzing Darwin's finches and its essential food resource, *Tribulus cistoides*, in the Galápagos Islands. *T. cistoides* presents a mericarp defended by sharp spines with variations in their morphology. Rivkin et al. (2021) found that urbanization imposes phenotypic selection against small mericarps, potentially leading to the evolution of larger fruits.

A recent study has used the globally distributed plant white clover (*Trifolium repens*) as a model for examining evolutionary responses to urbanization (Santangelo et al., 2020b). This species exhibits a Mendelian polymorphism that produces hydrogen cyanide (HCN), an antiherbivore defense trait. This trait has been shown to exhibit adaptive evolution to winter temperature gradients (Santangelo et al., 2020b; Thompson et al., 2016), selecting against cyanogenesis due to reduced snow cover in cities. Thompson et al. (2016) showed no evidence that herbivory is likely to explain the observed urban-rural clines in cyanogenesis. Johnson et al. (2018) also demonstrated that populations did not exhibit changes in genetic diversity with increasing urbanization, indicating that genetic drift is unlikely to explain urban-rural clines in HCN frequency. Analyzing changes in the frequency of genotypes that produce HCN and the frequency of the alleles at genes that epistatically interact to produce HCN, Santangelo et al. (2020b) demonstrated that urban environments often select for similar phenotypes. However, different selective agents and targets underlie the evolutionary response in different cities.

Another model species that has received attention with descriptions of different patterns of natural selection is *Crepis sancta*, a common ruderal winter annual in southern France. The species can produce both dispersing and non-dispersing seeds (Imbert, 1999). Dubois and Cheptou (2017) demonstrated that fragmented urban populations of *C. sancta* that occur in small patches surrounded by an unsuitable matrix, such as asphalt and concrete, produce a higher fraction of non-dispersing seeds. This selection pattern had been observed previously (Cheptou et al., 2008) and is consistent with the higher cost of dispersing seeds in more fragmented habitats. Through neutral microsatellite markers, Dubois and Cheptou (2017) accessed the levels of genetic diversity among populations and traits related to plant size. They observed that the substantial quantitative variation among populations for size was independent of fragmentation and urbanization, reflecting the patterns of neutral genetic variation or the role of other selective agents.

Another interesting trait that may be passing through natural selection in *C. sancta* is the pattern of flowering phenology. Delayed phenology was observed by Dubois and Cheptou (2017) and Lambrecht et al. (2016). Both studies suggest that natural selection in

urban habitats selects delayed flowering, allowing slower-growing plants to gain enough energy to reproduce or reflect the lower diversity of flowering plants in fragmented urban habitats. Lambrecht et al. (2016) also observed increased plant size in the urban habitat. They suggest that *Crepis* plants may benefit from growing and developing leaves over a more extended period, accumulating more carbon before the onset of reproductive resource demands, or increased respiration during warmer nights. In contrast, species demonstrated relaxation of selection on reproductive traits linked to attractiveness (Dubois and Cheptou, 2017).

Despite these promising results, clear examples of the effects of urban environments on evolution by natural selection exist in few urban systems. More studies that compare genetically based phenotypic divergence and local adaptation between urban and non-urban areas are needed to build a mechanistic understanding of how natural selection operates in urban systems (Rivkin et al., 2019). For example, genomic data have revealed that urban populations were more closely related to individuals from other urban populations than to geographically proximate rural areas (Yakub and Tiffin, 2017). This result suggests that selection in urban environments favors specific traits that can drive adaptation and shape population structure.

Human beings have appeared as the major selective agent in the process of evolution in urban environments, either indirectly through the expansion and development of cities leading to habitat fragmentation and further consequences, as well as directly through agriculture and gardening practices. It is necessary to list more model species for these studies on a global scale, involving genomic analyses and functional, physiological, and reproductive traits. The integration of this information can provide feedback to help slow the degradation of biodiversity in cities and to understand how urbanization drives evolutionary diversification in plants.

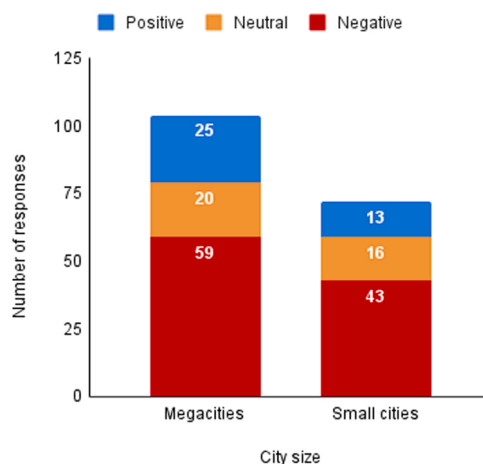
#### 4.4. The role of regional particularities and urbanization in floras worldwide

It is evident that urbanization has many negative consequences for plants and that the environmental changes caused by urbanization are the same worldwide (Niemelä, 2011). Still, the intensity with which organisms suffer from these changes can vary and depend on the context in which cities are inserted. Cities are embedded in varied biogeographical regions and landscape settings. A global viewpoint is necessary to understand the processes that shape urban biodiversity (Werner, 2011).

Megacities are more vulnerable to natural and man-made disasters due to their higher concentrations of people (Kraas, 2008). We found that seven of the nine studies that evaluated how pollution drives changes in plants in megacities showed negative results. In smaller cities, we found five studies that described the effects of pollution, with four of them relating to the consequences of soil pollutants. Overall, we found that the comparisons between smaller cities and megacities do not demonstrate different proportions of negative, neutral, and positive results in general responses of plants to urbanization (Fig. 4). It is essential to consider that even small cities can significantly negatively impact their local biodiversity.

The publications of the last eleven years demonstrate that most studies evaluating the effects of urbanization on biodiversity are still concentrated in the Northern hemisphere, which means our knowledge about the patterns exhibited in plants is biased (Werner, 2011).

Cities are located in different biomes of the world that are likely to have floras differentially pre-adapted to persistence in urban environments. Williams et al. (2009) predicted stronger filtering effects in environments where the natural biome differs more dramatically from that found in cities (e.g., those in tropical forest environments vs. those in temperate grassland environments). Alternatively, they predict that fragmentation effects may be particularly evident in tropical environments where a high fraction of native species heavily depends on biotic interactions for pollination and dispersal, leaving them more vulnerable to isolation. Indeed studies in tropical/subtropical biomes showed communities with fewer species that are dispersed by animals compared with species that have other modes of dispersion, such as dispersion by humans and abiotic dispersion in urban areas (Guerra et al., 2017; Nero, 2019). These findings are consistent with those reported by Oliveira et al. (2019), who stated that the endangered brazilwood tree



**Fig. 4.** Number of negative, neutral, and positive responses separated by their occurrences in megacities (more than 1 million habitants - according to the United Nations' World Economic Situation and Prospects) and small cities.

(*Paubrasilia echinata*) demonstrated a reduction in reproductive success in the urban ecosystem in Recife, Brazil, indicating a depletion in the pollination process. Oliveira et al. (2019) also observed changes in the visiting behavior of an effective pollinator that behaved like an occasional pollinator in urban habitats. In contrast, Lobo et al. (2016) found a remarkable diversity and abundance of bee species in the inflorescences of *Tabebuia aurea* in the city of Brasília, Brazil. These authors attributed this result to the conservation of large parks and green zones in Brasília as part of the territorial planning of this recently founded (1960) city. Further studies in cities located in tropical and subtropical biomes are still needed to understand which Urban Drivers may be most important in the urban community assembly in these locations. Also, it is essential to consider the process of forming cities as a factor that will differentiate the consequences of urbanization on local biodiversity.

## 5. Conclusion

Research on how plants have responded to urbanization has increased in recent years, but many gaps remain to be filled. How each Urban Driver acts separately continues to be challenging to disentangle. This article contributes to the documentation of recent findings on the changes driven by urbanization at two ecological levels: plant species and communities. We found generally negative responses at both levels and a few cases of acclimatization and promising results demonstrating the potential adaptation of species to anthropogenic disturbances. The main weakness in this literature review was the lack of studies on biomes other than temperate, which results in limited knowledge of the patterns exhibited in plant species and communities. Another interesting finding was that even small cities could suffer from megacities' same consequences on their biodiversity. This reinforces the importance of conducting studies on a broad geographic scale and sampling from different cities to predict different forces among Urban Drivers in a variety of urban contexts. More studies are needed to elucidate whether there are different outcomes from the urban flora in other biomes.

It is increasingly necessary to identify which factors put biodiversity at risk, applying the methodologies needed in each area of knowledge to explore how this process can be more fully mitigated. Urban environments are of intrinsic ecological interest, and cities are open laboratories where evolutionary changes occur in real-time. More studies that integrate different aspects of plant communities and species, such as reproductive, physiological, and genetic traits, and monitoring climatic conditions and pollution within cities are vital to establishing priorities for conservation. The establishment of more model species for these large-scale studies is a robust alternative to understand better the processes and patterns of plant responses to urbanization. More broadly, it is essential to outline strategies for continuous monitoring and documenting the progress of species in perpetuating themselves in this new type of environment.

## Data Availability

Data will be made available on request.

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## Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

## Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.gecco.2022.e02243](https://doi.org/10.1016/j.gecco.2022.e02243).

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