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Urban refugia sheltering biodiversity across world cities

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Abstract

Over the last years, world cities have emerged as multiple and complex habitats hosting numerous and varied urban refugia for biodiversity. Therefore, the published literature was systematically reviewed to investigate the increasingly acknowledged role of many urban habitats to function as refugia for species. Many plants and animals were reported to colonize a variety of urban environments: Urban forest/grassland (natural/seminatural), City park, Historical park (villa garden, botanical gardens, cemeteries, etc.), Green spaces (abandoned areas, railways, line of trees, etc.), Water body, and Built area. Refugia were found in over a hundred world cities, especially in medium- to very big-size cities. The number of papers focusing on animals (n = 66) were higher than those regarding plants and mushrooms (n = 19 and n = 1, respectively); however, the number of species recorded within refugia were the highest for plants. Plants exhibited the highest frequency (7 out of 19 papers) in Historical park, while animals in Urban forest/grassland (20 out of 66 papers). In most studies (25.9%), urban refugia were linked to Urban forest/grassland that is terrestrial natural and seminatural sites widespread within or around cities. The 22.3% of studies referred to generic Green spaces of several types interspersed within cities, both public and private. The 14.1% of refugia were found in Built area (artificial). About the 33% of studies reported the presence of species worthy of conservation (rare, endemic, endangered, or protected) for a total of 365 species. The 20% of investigated papers reported the presence of alien species for a total of 879 species. Invasive alien species recorded within refugium areas should be subjected to control measures to prevent degradation to refugia. Overall, the capability for urban areas to host a huge amount of biodiversity needs to be acknowledged by city planners so that management practices that maintain and support such diversity can be pursued. Recording and monitoring species along with their refugial habitats is fundamental to achieve this goal.

Keywords Urban conservation · Urban planning · Habitat remnants · Shelter · Green spaces

Introduction

The increasing trend of world human population is expected to continue in the future, especially in big urban areas such as metropolis and megalopolis (United Nations 2019). Besides economic growth and social benefits, this expansion implies the conversion of natural, seminatural, and agricultural areas into urban systems that can seriously deteriorate biodiversity with impacts on ecosystem services, alterations of microclimate and water flows, as well as consumption and erosion of soil (Frank et al. 2017). However, the impact caused by urban growth on the environment is going beyond the cities and may drive further future changes at multiple scales (Grimm et al. 2008). In this framework, over the last decades urban landscapes have been seen as socio–ecological systems with a new paradigm when thinking about human-environmental interactions: the co-existence of the ecological and social systems within and across cities (Haase 2021). Consequently, urban areas have become a central node for the long–term functioning of societies and ecosystems with high spatial heterogeneity and different levels of connectivity with surrounding agriculture and/or natural areas (Capotorti et al. 2020). Species can move and persist in the urban matrix despite human activities.

Actually, urban areas host a great diversity of species belonging to different kingdoms (animals, plants, fungi,

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etc.), both native and non-native coming from the regions surrounding cities (Lepczyk et al. 2017) or present as relict of past environments (Nagy and Malatinszky 2019). Within urban areas, endemic and rare species and others of conservation interest are increasingly recorded within a variety of anthropogenic habitats (Ives et al. 2016; Toffolo et al. 2021). On the other hand, built environments are optimal habitat for a plethora of alien species some of which are invasive (Shaffer 2018).

Urban areas are acknowledged to be hotspots of invasive alien species which can negatively affect ecosystem services (e.g. modifying carbon storage), homogenize biotic communities replacing some uncommon native species with common ones. Conversely, many alien species increase richness and can create habitats for other species (especially in highly degrades sites), so they can promote alternative ecosystem services in comparison to native species (Gaertner et al. 2017). At present, the presence of alien species in the city seems inevitable since in the flora of many urban areas more than one species out of three is an alien (e.g. Vojík et al. 2020; Toffolo et al. 2021).

Therefore, the question whether urban areas can host species of conservation interest and whether this biodiversity can be incorporated into urban planning remained open for a long time (Miller and Hobbs 2002; Kantsa et al. 2013).

The recent COP15 and the Post2020 Global Biodiversity Framework pointed out the need to include cities in conservation strategies (Vlaanderen and Lange 2022; Convention on Biological Diversity 2022). Particularly, "*to ensure biodiversity-inclusive urban planning, enhancing native biodiversity, ecological connectivity and integrity, and improving human health and well-being and connection to nature*" is needed (Convention on Biological Diversity 2022).

Following a conceptual change, cities are emerging across the world as multiple and complex habitats hosting unexpected and widespread refugia for biodiversity where insect pollinators or freshwater species can be found (Chester and Robson 2013; Hill 2021). In this regard, even considering the CBD's targets, urban refugia emerge as a top research priority also when they consists of small habitat remnants (Labadessa and Ancillotto 2023).

Traditionally, the terms refuge(s) or refugium (refugia) has been widely used in the context of climatic change, to describe climatically stable areas within which species survived to past warm or cold climatic stages (i.e. glacial–interglacial periods) under adverse (cold or warm) environmental conditions (Rull 2009; Gentili et al. 2015a). Recently, Monsarrat et al. (2019) have introduced the concept of Anthropocene refugia, referring to areas that provide spatial and temporal protection to species from human activities and that can remain suitable for a given taxonomic unit in the long-term. Specifically, despite the concept of Anthropocene refugia considers the key role of anthropogenic pressures from which species find realized or potential shelter, it does not ecologically define the characteristics of refuge habitats with stable and favourable environmental conditions for species' persistence, nor the matrix where unfavourable environmental conditions subsist. Therefore, Anthropocene refugia need to be further spatially and ecologically defined.

Regarding urban areas, the first likely mention of urban refugia dealt with the role of zoos in the conservation of wildlife within city as well as their role in education and research (Conway 1969).

However, over the last decades an increasing number of scientific works has differently referred to urban refugia (or refuges) (Capotorti et al. 2013; Hall et al. 2017; Hill 2021; Perez et al. 2021), that are locations within cities where biodiversity can find shelter. For instance, Caccamise et al. (1996) found that well conserved grassland patches within the airport area of Atlantic city (USA) served as refugia for avian species in comparison to habitats outside the airport. In a literature review, Löki et al. (2019) found that cemeteries and churchyards have a significant conservation role within urban areas, as even in strongly altered landscapes, since they frequently function as refugia for the populations of rare and endangered species of plants and animals.

Overall, urban refugia as particular Anthropocene refugia may function in a similar way in comparison to natural refugia, providing critical habitats and then offering new chances for species to live in a context characterized by disturbance and stress (Chester and Robson 2013).

Green areas are expected to provide the major contribution to urban biodiversity and refugia to species. However, cities host a plethora of unplanned and unexplored habitats (e.g. vacant residential properties and abandoned industrial sites) that potentially hold natural remnants embedded in an urban matrix and can support species diversity (Kwok 2018). Therefore, we aimed to perform this literature review to explore the main habitats that can offer protection to species (animal, plant, and other organisms) in urban environments. We wanted to explore main trends relating to urban refugia and discuss if and how they can be preserved and incorporated into conservation and urban planning along with the species they host.

Literature search and review

In 2022, we conducted a literature search on Scopus (temporal range: 1990–2022) with the aim to perform a systematic review on the subject of urban refugia. We used combinations of the keywords "refugia" OR "refugium" OR "refuges" OR "refuge" AND "urban" AND "plant" OR "animal" OR "fungi". The search processes returned 583 titles and after a first screening on article titles and abstracts as well as on duplicates, we retained 220 articles that dealt with the investigated subject and they were checked for a deeper investigation. After, removing review articles, descriptive articles and pieces only reporting the word “refugia” (and related words) in a generic way (not associated to species or databases of species or only present in the list of references), 85 articles were considered suitable and processed for the review (Supplementary Table 1). For instance, articles only reporting generic sentences (e.g. “green spaces within cities are biodiversity refugia”) were not considered. On the other hand, we included the papers considering one or more urban habitat(s) as refugium for species (one or more), and then as persistence area still conserving suitable conditions for species in a context of adverse conditions. The presence of the words “refugia”, “refugium” and “refuge(s)” was a discriminant for the inclusion in the database. However, we did not include papers that were not clearly carried out in urban environments and/or did not describe a well-defined association between species and refugium habitats in the urban context.

Despite the refugium concept can have different temporal scales, from sub-daily (protection from predations) to millennia (see the review of Selwood and Zimmer 2000) most of scientists traditionally apply the term refugia to localities where species last for long time; for this reason we excluded from the database the few articles mentioning short-term refugia (temporal predation refugia) or habitats simply acting as ecological traps or sinks without mentioning the terms refugia/refugium/refuge(s).

We point out that the approach of systematic review may have some limitations since it includes risks of bias due to missing results linked to the algorithm functioning of search engines, the exclusion of grey literature, etc.

From the articles we extracted the following information (see Supplementary Table 1): a) City name; b) N° of inhabitants (i.e. size of city) following the UN classification in: megalopolis (over 10 million inhabitants), metropolis (from 1 million to 9.9 million inhabitants), medium cities (from 100,000 to 999,999 inhabitants), mall cities (from 10,000 to 99,999 inhabitants), villages (< 10,000 inhabitants); c) Country; d) Continent; e) N° of samples (number of sample units in the study); f) N° of taxa recorded within refugia; g) N° of protected taxa or of conservation interest (PCI: rare, endemic, endangered, protected); h) Main habitat (water body, built area, city park, grassland, forest, historical garden, green spaces, several); i) Habitat specificity (detailed characteristics of habitats); l) Organism (Plant, Animal, Fungi); m) Organism specificity (Arthropods - excluding insects, Insects, Fishes, Amphibians, Birds, Reptiles, Mammals, Algae, Mosses, Higher plants, Fungi-lichens); n) % alien: o) N° of alien taxa: p) Year of publication: q) Publication reference; r) Digital Object Identifier (DOI).

When organizing the database, we noticed that some articles had a very coarse subdivision of urban habitats, while other articles reported the habitat types more in depth. In our analysis, we considered such aspect to detect possible trends. Therefore, we distinguished the following main habitat categories as generally mentioned in the assessed articles: Green spaces = when a not clear distinction of artificial or natural/seminatural non built-up areas within city was indicated; Historical park = when refugia were indicated in historical green spaces such as botanical gardens, sacred spaces (close to churches or temples), and cemeteries; City park = when refugia were indicated in green spaces largely accessed by the public and clearly mentioned as “city park”; Urban forest and grassland = when refugia were indicated in natural or seminatural forests, clearings, and grassland within cities; Built area = when refugia were indicated in anthropogenic habitat such as industrial sites, road sides, railways, etc.; Water bodies = when refugia were indicated in water bodies such as ditches, lakes, mires, ponds, streams, and wetlands within cities; Several = when refugia were indicated in more than one type of the previous categories and other ones (e.g. water bodies, city park, forests, sites within airports, etc.).

Other possible urban habitats (allotment and similar gardens, roofs, etc.) not found or mentioned in the selected articles, were not considered since this review was not based on habitat diversity present in urban areas but on the declared recognition of a certain habitat as refugium.

Some previous works made the distinction between refuges, existing at ecological temporal and spatial scales, and refugia, existing at evolutionary scales (Keppel et al. 2012). When referring to urban environments, we found that the two terms have been used almost indifferently across the considered literature. Therefore, we preferred to use the terms refugium/refugia that include both the ecological and evolutionary meaning. In fact, in urban environments, new evolutionary events via rapid adaptation of species or local extinction events can occur within short times (Diamond and Martin 2021; Kotze et al. 2022). For instance, Gorton et al. (2018) found rapid adaptive divergence of urban and rural populations of a ruderal species (*Ambrosia artemisiifolia* L.) while the greater heterogeneity in urban environments can influence evolution of species in cites.

Urban refugia over the world

The 27.7% of the selected papers were published between 1994 and 2010, the remaining 73.3% were published between 2011 and 2022. Most of the studies considering urban refugia included medium size to very big-size cities considering the number of inhabitants (recovered from Wikipedia) all over the world, for a total of about 80 cities and some widespread urbanized areas (Fig. 1). In particular, five papers considered megalopolis with more than 10 million of inhabitants (Hangzhou two times, Tokyo, Guangzhou, Chongqing); 39 papers included metropolis with 1 to

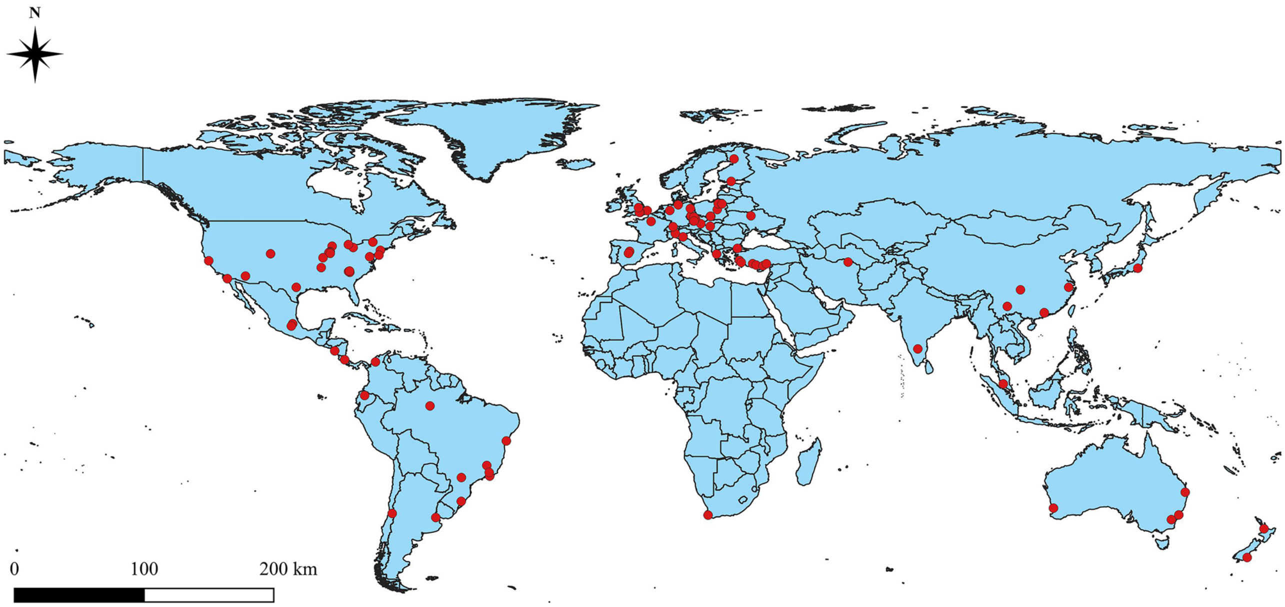

Fig. 1 World distribution map of urban refugia (red dots) mentioned in the investigated literature

9.9 million of inhabitants (e.g. Berlin, Prague, Milan, Buenos Aires, Rio de Janeiro, New York, Tokyo, Cape Town, and Sidney); 22 works included medium cities with 100 to 999 thousand inhabitants (e.g. León, Bologna, Zurich, Canberra, and Denver); ten papers described refugia within small cities from 10 to 99 thousand inhabitants (e.g. Atlantic city, České Budějovice, and Matias Barbosa). Finally, nine papers, includes more than one urban areas from about 1 to hundreds of thousands of inhabitants.

America (36 works: 24 in N-America and 12 in S-America) and Europe (32 works) were the most represented continents, while Africa accounted for only one paper (Fig. 1). USA was the country exhibiting the highest number of papers (18) followed by Brazil, Czech Republic and Germany (6 works each).

Organisms within urban refugia

With regard to life kingdoms, 65 works included animals (Animalia) belonging to several groups (28 insects, 13 mammals, 10 reptiles, 9 birds, 7 other arthropods, 5 amphibians, and 1 fishes; Fig. 2), 19 works described plants (Plantae; of which 18 referred to higher plants, 1 to algae) and one work referred to mushrooms (Fungi); finally, another work described both plants and animals (Fig. 2).

Sampling effort, number of taxa and species characteristics

The number of samplings across studies ranged between 1 and 2900 (median = 27) while the number of taxa detected within refugia ranged between 1 and 663 (median = 19). Single species' studies were 25: 22 focused on animals, 2 on plants and 1 on mushrooms. Overall, the studies on plants reported a higher number of taxa (median = 166) than those on animals (median = 10), since numerous studies on animal focused on single species (Kruskal–Wallis test: H-chi^2 = 18,24; $p < 0.001$; Fig. 3). On the other hand, the number of samplings did not show significant differences between plant and animals. About 33% of the papers reported the presence of species worthy of conservation (rare, endemic, endangered or protected) for a total of 365 species; the 51.7% of these papers referred to animals, 44.8% to plants and 3.5% to mushrooms. For instance, Padrón et al. (2020), found the endemic butterfly *Catasticta flisa* subsp. *duna* Eitschberger & T. Racheli, 1998 in the gardens and parks of Quito (Equador). With regard to plants, Kantsa et al. (2013) recorded assemblages of three endemic and/or endangered orchid taxa (*Ophrys sphegodes* subsp. *helenae* (Renz) Soó & D.M.Moore, *Ophrys cephalonica* (B.Baumann & H.Baumann) Devillers-Tersch. & Devillers and *Spiranthes spiralis* (L.) Chevall.) in the town centre of Ioannina (Greece), in public spaces along streets and in parks.

The 20% of the investigated papers reported the presence of alien species for a total of 879 species; the 66,6% of papers referred to alien plants, 33.4% to alien animals.

Habitats acting as urban refugia

In most studies (25.9%), urban refugia were linked to terrestrial natural and seminatural sites, such as forests and grasslands (Fig. 4). The 22.3% of studies referred to generic

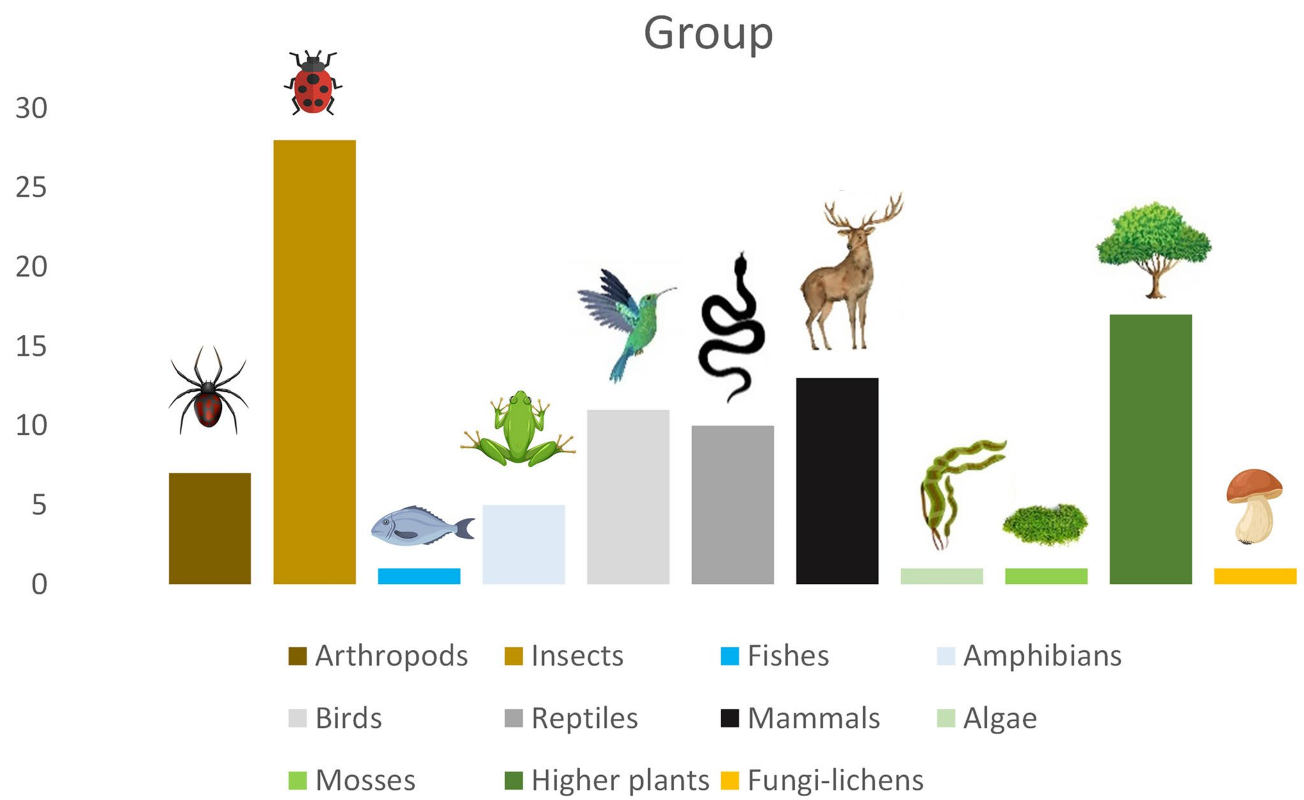

Fig. 2 Groups of organisms reported in urban refugia. The Arthropods category includes all taxonomic groups other than insects

"Green spaces" of several types interspersed within cities, both public and private. City and Historical parks (including botanical garden and sacred spaces) were specifically mentioned in 8.2% and 10.6%, respectively. The 14.1% of refugia were found in urban built artificial areas (residential, roads, industrial, etc.), while 3.6% indicated the presence of shelters for species in both semi-natural and built areas. Finally, the 15.3% of the studies were performed in both natural and artificial Water bodies (wetlands, mires, ponds, lakes, etc.).

Among unusual habitats falling in target categories of habitat, species found shelter within the following locations (Supplementary Table 1): cemeteries (Konic et al. 2021), railways (e.g. Toffolo et al. 2021), airports (Kutschbach-Brohl et al. 2010), roundabouts (Leather and Helden 2005), slag in industrial sites (Zou et al. 2019) and university campus (Taboada-Verona et al. 2019).

The habitat with the highest number of species in a single article was found in City parks (n = 663). Always concerning habitats, considering the median difference (H-chi^2 = 12.77, $p < 0.05$), Built areas exhibited the lowest value in comparison to the other main habitats (significantly in comparison to Urban forests/grasslands, Historical parks and Several).

The frequency of refugia for animals and plant species was different across the main urban habitats (Chi^2: 21.8; df = 6; $p < 0.01$). Particularly, plants exhibited the highest frequency (7 out of 20 papers) in Historical parks, while animal in Urban forests and grasslands (20 out of 66 papers). On the other hand, no trend was found when linking the groups of organisms and the main urban habitats, with the exception of higher plants that were mainly found in Green spaces and Historical parks.

Most of the main habitat types were reported to support species worthy of conservation (Fig. 5): City parks, Green spaces, Historical parks, Natural forests and grasslands, and Water bodies. On the other hand, almost the half of the alien species referred to Green spaces (47.1%).

Discussion and conclusion

Urban refugia has been acknowledged by 85 works according to our literature review. Considering the habitat-scale (i.e. wide-ranging categories) we analysed, they can be defined as *habitats or sites within cities supporting the survival of one or more species in the general context of unfavourable environmental conditions of disturbance and stress present in urbanized matrixes*. In other worlds, urban refugia consist of anthropogenic (mainly), seminatural, and natural (sometimes) spaces with no to moderate disturbance and sufficient resources for species to survive within the urban matrix. Considering the investigated literature, in some cases the description of habitats functioning as refugia was very

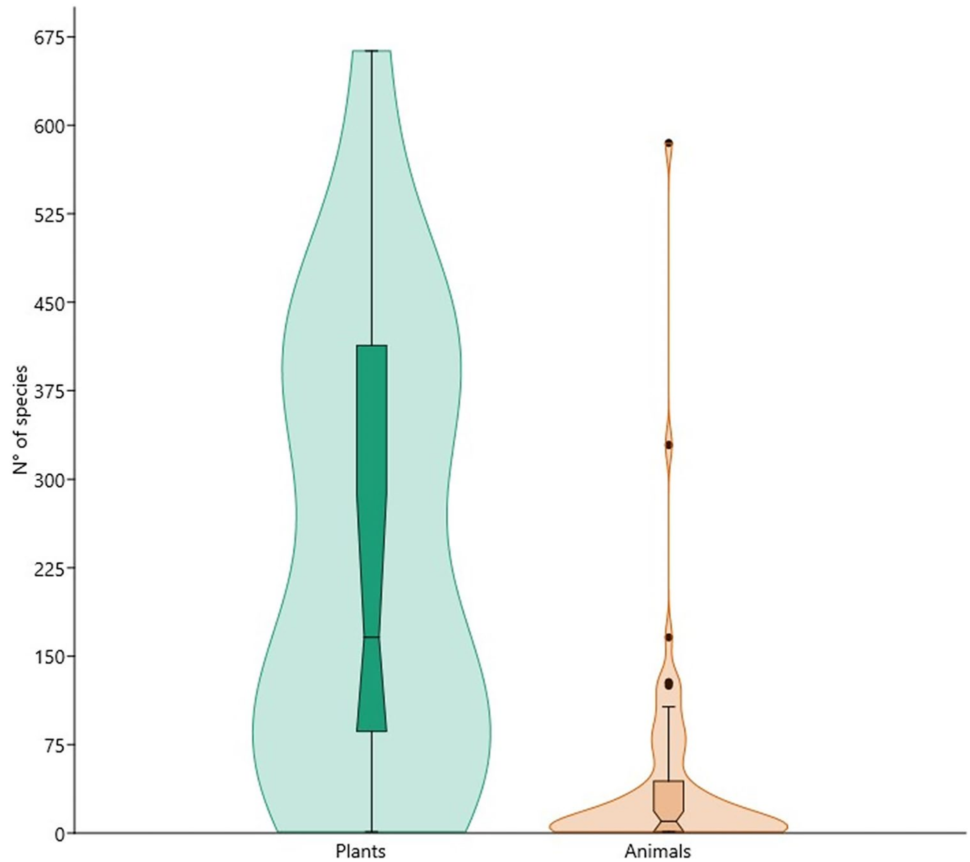

Fig. 3 Violin plot of number of plants and animals recorded in the papers mentioning urban refugia. A violin plot shows distributions of numeric data using density curves (i.e. the width of each curve corresponds with the frequency of data in each region). The boxes have the same meaning of box-plot (maximum and minimum values, median, and quartiles)

coarse (e.g. green spaces), in most cases was quite detailed (e.g. semi-arid grassland patches around ancient walls).

On the other hand, the urban biodiversity literature points out that the question whether urban habitats act as refugia or rather as ecological traps or sinks is not answered, yet (Lepczyk et al. 2017). Likely, across urban areas an extinction debt exists with some species facing extinction or strong decline. In fact, this aspect is masked by the fact that most studies treating urban refugia only record short-time presence-absence / occurrence and not the abundance of species over time (Hahs et al. 2009) since it should be pointed out that urban biodiversity studies are relatively recent. These aspects can be a limit when exploring trends about literature on urban refugia.

An important aspect to consider in this definition concerns alien species that are very common in cities (e.g. over 35% in Vojík et al. 2020) and, in some cases, are among listed taxa within refugia. In turns, some alien woody plants within city parks or green spaces can function as habitat refugia for other species, especially animals. Indeed, the majority of populations of alien woody species can support conservation objectives in densely built-up urban areas since they form new ecosystems contributing to ecosystem services (Kowarik et al. 2013) such as favouring plant succession and niche availability for other species and finally biodiversity (Kowarik 2008; Kowarik et al. 2019). In any case, despite the alien species are listed in 20% of the investigated papers, such a topic is no or scarcely addressed in association with urban refugia. Probably, this is due to peculiar conditions of cities that include harsh and stressful environments favourable to alien species which are then considered as obvious in the urban areas. In addition, the evolution of invasive species in urban context is an acknowledged but still unexplored phenomenon that could disclose novel biodiversity patterns and ecosystem mechanisms with respect to native species (Borden and Flory 2021).

This review enhances the knowledge about the biodiversity in urban spaces within cities of different size, from megalopolis and metropolis (most studies) to small cities. The literature search indicated the increase in articles regarding urban refugia over time. Particularly, it is highlighted how recent research on urban biodiversity has changed perspective on the biological value of species inhabiting cities and on the importance of habitats widespread within built environments and the built matrix itself. Many places within cities have the ability or the potential to provide refugia for numerous native species. Therefore, these species can find shelter in urban landscapes holding a plethora of unique, unusual, and complex habitats in locations which are absent

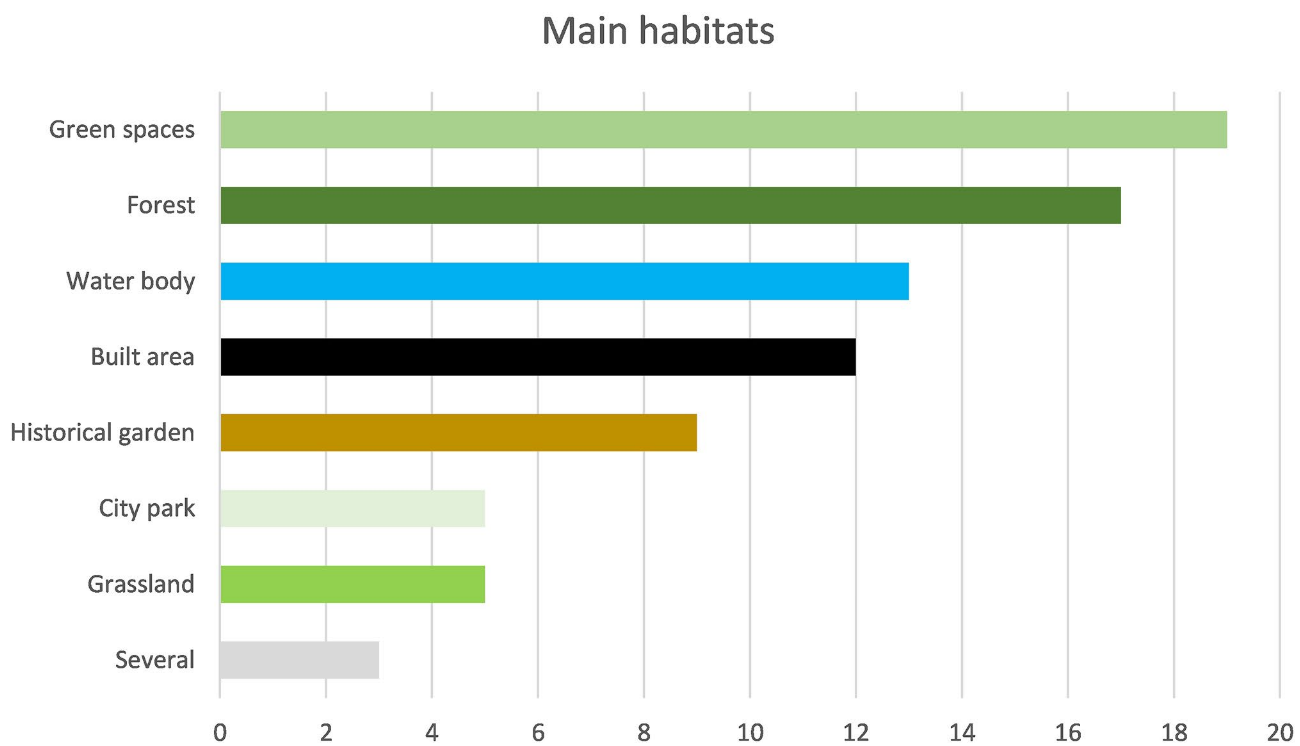

Fig. 4 Main habitats where the urban refugia have been recorded

or rare in semi-natural and rural landscapes surrounding cities. In addition, it has been stressed that urban regions are favourable to some species (e.g. bees) sensitive to chemicals released in intensive monocultures which are common in rural areas (Casiker et al. 2021).

It has been emphasised that the exceptional environmental conditions existing in cities have species-specific impacts; these can range from negative to neutral or positive, depending on each species life-history and adaptation ability (Sol et al. 2014; Spotswood et al. 2021). Depending on the geographic context where cities are situated, different environmental conditions between cities and their surrounding landscapes create unique gradients in biotic and abiotic factors (Spotswood et al. 2021). Mainly, this unicity derives from the highly artificial context within which such habitats are included, the urban matrix, and from their isolation with respect to analogous habitats outside the cities.

From our review, it appears that natural and seminatural habitats within cities offer the highest number of refugia to species in comparison to more artificial habitats. Numerous of these species are of conservation interest (Stewart et al. 2017). Indeed, as already stressed by other authors (e.g. Pregitzer et al. 2020), near-natural areas of urban forests can provide more benefits than designed landscapes in conserving native species and suppressing or controlling invasive ones. There is also evidence that forest patches widespread in cities harbour valuable rare, endemic, protected, and endangered species. Subsequently, they may hold a significant potential for the preservation of biodiversity from the gene to the ecosystem level (see Alvey 2006). Besides their habitat function and the role in protecting biodiversity, urban forests provide multiple ecosystem services like health benefits to citizens, the regulation of water resources, and help in mitigating climate change (Berglihn and Gómez-Baggethun 2021). Although less mentioned than forests as refugia, grasslands have a beneficial role for biodiversity and ecosystem functioning within cities, as observed by Onandia et al. (2019).

Like forested areas, city parks have been frequently mentioned as biodiversity refugia across the investigated literature. However, city parks have a different role in comparison to natural and seminatural landscapes. Indeed, even if they can host a similar number of species than natural areas, there are differences in the species composition, in the traits selected and in the community structure (Banaszak-Cibicka et al. 2018). For instance, Chen and Cheng (2022) reported that the network of city parks promotes interactions between metacommunities of different animals like birds, reptiles, frogs, and butterflies. In any case, many land-use practices (e.g. mowing) and environmental factors (e.g. proximity to water bodies) have an effect on biodiversity in city parks in terms of species composition, vegetation structure, and ecosystem services (Talal and Santelmann 2019).

Fig. 5 Types of urban refugia where different groups of species (here associated as an example to different habitats) can find shelter including several protected species

Water bodies includes multiple near-natural habitats suitable to serve as urban refugia especially for amphibian and aquatic or hygrophilous plants. Water bodies can have the function of stepping stone refuges, which assist species movement across aquatic landscapes, providing connectivity between natural or seminatural wetlands and running waters (Chester and Robson 2013). In urban areas, aquatic habitats, and the species they host (e.g. invertebrates, amphibia, and plants), are severely affected by the water quality and the hydrological process of urban wetlands. For this reason, they need frequent management activities and are subject to restoration actions (Hale et al. 2019).

Numerous species have been reported to find refugia in built areas offering physical structures analogous to their natural habitat. Man-made structures, like ancient walls, roads, or industrial sites (waste deposits), can often supply new chances for species to utilise urban spaces (Fenu et al. 2016). In this direction, archaeological sites can play an important role in sustaining natural habitats and biodiversity they hold (Ceschin et al. 2014). All these areas cannot be comparable to natural environments but may still have suitable habitat characteristics for some species. In any case, it is well known that biodiversity in built areas is significantly lower than in other urban green areas or semi-natural areas (Kondratyeva et al. 2020; Toffolo et al. 2021).

On the other hand, historical parks, and green spaces (botanical gardens, sacred spaces, cemeteries, etc.) have a peculiar refugium function for higher plants (e.g., Jaganmohan et al. 2018). They can be halfway between man-made (built) and other green areas previously mentioned. Urban green spaces refer to a variety of habitat types ranging from remnant patches of native vegetation to roundabouts and private gardens have been frequently cited to function as urban refugia. The ecological function of green spaces is widely recognized both for urban planning and management of natural remnants in cities as well as for the conservation of biodiversity and restoration activities (Lepczyk et al. 2017).

Overall, all kinds of refugia emphasizes their potential for the conservation of species in urbanized areas including species worthy of conservation that in our synthesis were found in 33% of studies. Indeed, as stressed by Aronson et al. (2014), despite the low density in green spaces and species, cities can host rare, endemic, protected and endangered native species, thus providing prospects for biodiversity conservation efforts and education activities for citizens. In this direction, Ives et al. (2016) highlighted that cities are becoming hotspot for threatened species and that the species assemblages of individual cities are distinct from those of other ones. In any case, considering very recent studies on urban evolution in cities (Diamond and Martin 2021), also common or alien species can take on a different value or role in urban *versus* other environments. In this regard, species' populations living in cities can have different mutation rates, shifts in methylation patterns, phenotype and trait selection, and fitness in comparison to rural populations (Diamond et al. 2018; Sepp et al. 2020; Diamond and Martin 2021, and cited references within). In other words, populations of plants and animals living in urban refugia may undergo speciation as frequently observed in climatic refugia (Gentili et al. 2015b). Indeed, all evolutionary forces such as selection, adaptation, mutation etc., may act in urban landscapes and especially in refugia thanks to a combination of isolation, habitat specificity in patches of good quality (in comparison to the surroundings) and genetic drift.

Despite the presence of a peculiar biodiversity, all kind of urban spaces are continuously under pressure due to urban compaction and expansion, construction plans or incorrect environmental restoration (Boulton et al. 2020). Consequently, due to the fast changes to which cities are subjected, urban refugia and the species that they hold can be undoubtedly prone to constant human pressure and extinction.

However, the expected decline of biodiversity with rapid urban growth may be stopped if anthropogenic, semi-natural, and natural urban refugia are considered in urban and landscape plannings (Alvey 2006; Fingland et al. 2022; Hall et al. 2017; Salinitro et al. 2018), making citizens involved and aware of the role of refugia in saving biodiversity. Urban refugia should be acknowledged, monitored, and managed by practitioners (city planners and conservationists, ecologists, foresters, etc.) to improve their role in supporting the species they host and promote further biodiversity. Management activities should promote the increase of biodiversity in all aspects of urban green spaces, from trees along streets to city parks and near-natural forests. Parallelly, avoiding conflicts and mitigate disservices among the management practices to be promoted will be fundamental. Mainly efforts should be directed towards conservation and restoration of native vegetation across all kinds of urban landscapes. For instance, some possible action should envisage the following activities:

- listing of refugia and biodiversity they hold in each city;
- continuous monitoring of biodiversity in the refugia also involving citizen (Callaghanet al. 2020);
- creation of green infrastructures (Hostetler et al. 2021);
- improving of ecological corridors both within cities and with peri-urban and rural areas in terms of quality and connectivity (Huang et al. 2021);
- planning and implementing a correct management of forest and grassland vegetation (selective clear-cuttings, mowing, control of invasive alien species, etc.), to maintain the habitat functionality over the seasons (Chollet et al. 2018; Pregitzer et al. 2019).

For the future, researches assessing the record of new urban refugia, their connection (structural and or functional) with other habitats outside cities, and speciation potential of isolated populations they host would be welcome.

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Declarations

Competing interests The authors declare no competing interests.

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References

Alvey AA (2006) Promoting and preserving biodiversity in the urban forest. Urban for Urban Green 5:195–201. https://doi.org/10.1016/j.ufug.2006.09.003

Aronson MFJ, La Sorte FA, Nilon CH, Katti M, Goddard MA, Lepczyk CA, Warren PS, Williams NSG, Cilliers S, Clarkson B, Dobbs C, Dolan R, Hedblom M, Klotz S, Kooijmans JL, Kühn I, MacGregor-Fors I, McDonnell M, Mörtberg U, Pyšek P, Siebert S, Sushinsky J, Werner P, Winter M (2014) A global analysis of the impacts of urbanization on bird and plant diversity reveals key anthropogenic drivers. Proc R Soc b: Biol Sci 281:20133330. https://doi.org/10.1098/rspb.2013.3330

Banaszak-Cibicka W, Twerd L, Fliszkiewicz M, Giejdasz K, Langowska A (2018) City parks vs. natural areas - is it possible to preserve a natural level of bee richness and abundance in a city park? Urban Ecosyst 21:599–613. https://doi.org/10.1007/s11252-018-0756-8

Berglihn EC, Gómez-Baggethun E (2021) Ecosystem services from urban forests: The case of Oslomarka, Norway. Ecosyst Serv 51:101358. https://doi.org/10.1016/j.ecoser.2021.101358

Borden JB, Flory SL (2021) Urban evolution of invasive species. Front Ecol Environ 19(3):184–191. https://doi.org/10.1002/fee.2295

Boulton C, Dedekorkut-Howes A, Holden M, Byrne J (2020) Under pressure: Factors shaping urban greenspace provision in a mid-sized city. Cities 106:102816. https://doi.org/10.1016/j.cities.2020.102816

Caccamise DF, Reed LF, Bennett KA, Dosh JJ (1996) The avian community of a suburban grassland refugium: population studies at an airport in Northeastern United States. Acta Ornithol 31:3–13

Callaghan CT, Ozeroff I, Hitchcock C, Chandler M (2020) Capitalizing on opportunistic citizen science data to monitor urban biodiversity: A multi-taxa framework. Biol Conserv 251:108753. https://doi.org/10.1016/j.biocon.2020.108753

Capotorti G, Del Vico E, Lattanzi E, Tilia A, Celesti-Grapow L (2013) Exploring biodiversity in a metropolitan area in the Mediterranean region: The urban and suburban flora of Rome (Italy). Plant Biosyst 147:174–185. https://doi.org/10.1080/11263504.2013.771715

Capotorti G, Bonaquisti S, Abis L et al (2020) More Nature in the city. Plant Biosyst 154:1003–1006. https://doi.org/10.1080/11263504.2020.1837285

Casiker CV, Jagadishakumara B, Sunil GM, Chaithra K, Devy MS (2021) Bee diversity in the rural–urban interface of bengaluru and scope for pollinator-integrated urban agriculture. In: Hoffmann E, Buerkert A, von Cramon-Taubadel S, Umesh KB, Pethandlahalli Shivaraj P, Vazhacharickal, PJ (eds) The Rural-Urban Interface. The Urban Book Series. Springer, Cham. https://doi.org/10.1007/978-3-030-79972-4_18

Ceschin S, Bartoli F, Salerno G, Zuccarello V, Caneva G (2014) Natural habitats of typical plants growing on ruins of Roman archaeological sites (Rome, Italy). Plant Biosyst 150:866–875. https://doi.org/10.1080/11263504.2014.990536

Chen RQ, Cheng ST (2022) Detecting nestedness in city parks for urban biodiversity conservation. Urban Ecosyst 25:1839–1850. https://doi.org/10.1007/s11252-022-01272-1

Chester ET, Robson BJ (2013) Anthropogenic refuges for freshwater biodiversity: their ecological characteristics and management. Biol Conserv 166:64–75. https://doi.org/10.1016/j.biocon.2013.06.016

Chollet S, Brabant C, Tessier S, Jung V (2018) From urban lawns to urban meadows: Reduction of mowing frequency increases plant taxonomic, functional and phylogenetic diversity. Landsc Urb Plan 80:121–124. https://doi.org/10.1016/j.landurbplan.2018.08.009

Convention on Biological Diversity (2022) Kunming-Montreal Global biodiversity framework. https://www.cbd.int/article/cop15-final-text-kunming-montreal-gbf-221222

Conway WJ (1969) Zoos their changing role. As urban refuges of wildlife, zoos have opportunities for education, conservation, and research. Science 163:48–52. https://doi.org/10.1126/science.163.3862.4

Diamond SE, Chick LD, Perez A, Strickler SA, Zhao C (2018) Evolution of plasticity in the city: Urban acorn ants can better tolerate more rapid increases in environmental temperature. Conserv Physiol 6:coy030. https://doi.org/10.1093/conphys/coy030

Diamond SE, Martin RA (2021) Evolution in Cities. Annu Rev Ecol Evol Syst 52:519–540. https://doi.org/10.1146/annurev-ecolsys-012021-021402

Fenu G, Bacchetta G, Bernardo L, Calvia G, Citterio S, Foggi B, Fois M, Gangale C, Galasso G, Gargano D, Gennai M, Gentili R, Larroux G, Perrino EV, Peruzzi L, Roma-Marzio F, Uzunov D, Vagge I, Viciani D, Wagensommer R- P, Orsenigo S, (2016) Global and Regional IUCN Red List Assessments: 2. Ital Bot 2:93–115. https://doi.org/10.3897/italianbotanist.2.10975

Fingland K, Ward SJ, Bates AJ, Bremner-Harrison S (2022) A systematic review into the suitability of urban refugia for the Eurasian red squirrel *Sciurus vulgaris* Mamm Rev 52:26–38. https://doi.org/10.1111/mam.12264

Frank B, Delano D, Caniglia S (2017) Urban systems: a socio–ecological system perspective. Sociol Int J 1:1–8. https://doi.org/10.15406/sij.2017.01.00001

Gaertner M, Wilson JRU, Cadotte MW, MacIvor JS, Zenni RD, Richardson DM (2017) Non-native species in urban environments: patterns, processes, impacts and challenges. Biol Invasions 19:3461–3469. https://doi.org/10.1007/s10530-017-1598-7

Gentili R, Bacchetta G, Fenu G, Cogoni D, Abeli T, Rossi G, Salvatore MC, Baroni C, Citterio S (2015a) From cold to warm-stage refugia for boreo-alpine plants in southern European and Mediterranean mountains: the last chance to survive or an opportunity for speciation? Biodivers 16:247–261. https://doi.org/10.1080/14888386.2015.1116407

Gentili R, Baroni C, Caccianiga M, Armiraglio S, Ghiani A, Citterio S (2015b) Potential warm-stage microrefugia for alpine plants: Feedback between geomorphological and biological processes. Ecol Complex 21:87–99. https://doi.org/10.1016/j.ecocom.2014.11.006

Gorton AJ, Moeller DA, Tiffin P (2018) Little plant, big city: a test of adaptation to urban environments in common ragweed *Ambrosia artemisiifolia* Proc R Soc b: Biol Sci 285:20180968. https://doi.org/10.1098/rspb.2018.0968

Grimm NB, Faeth SH, Golubiewski NE, Redman CL, Wu J, Bai X, Briggs JM (2008) Global change and the ecology of cities. Science 319:756–760. https://doi.org/10.1126/science.1150195

Haase D (2021) Continuous integration in urban social-ecological systems science needs to allow for spacing co-existence. Ambio 50:1644–1649. https://doi.org/10.1007/s13280-020-01449-y

Hahs AK, McDonnell MJ, McCarthy MA, Vesk PA, Corlett RT, Norton BA, Clemants SE, Duncan RP, Thompson K, Schwartz MW, Williams NSG (2009) A global synthesis of plant extinction rates in urban areas. Ecol Lett 12:1165–1173. https://doi.org/10.1111/j.1461-0248.2009.01372.x

Hale R, Swearer SE, Sievers M, Coleman R (2019) Balancing biodiversity outcomes and pollution management in urban stormwater treatment wetlands. J Environ Manage 233:302–307. https://doi.org/10.1016/j.jenvman.2018.12.064

Hall DM, Camilo GR, Tonietto RK, Ollerton J, Ahrné K, Arduser M, Ascher JS, Baldock KC, Fowler R, Frankie G, Goulson D, Gunnarsson B, Hanley ME, Jackson JI, Langellotto G, Lowenstein D, Minor ES, Philpott SM, Potts SG, Sirohi MH, Spevak EM, Stone GN, Threlfall CG (2017) The city as a refuge for insect pollinators. Conserv Biol 31:24–29. https://doi.org/10.1111/cobi.12840

Hill A (2021) Cities as Refugia for Ecosystems Adrift. How the built environment can serve as future habitat for species under threat. Retrieved from https://thisismold.com/urban-ecologies/cities-as-refugia-for-ecosystems-adrift. Accessed on 31 October 2022.

Hostetler M, Allen W, Meurk C (2021) Conserving urban biodiversity? Creating green infrastructure is only the first step. Landsc Urb Plan 100:369–371. https://doi.org/10.1016/j.landurbplan.2011.01.011

Huang X, Wang H, Shan L, Xiao F (2021) Constructing and optimizing urban ecological network in the context of rapid urbanization for improving landscape connectivity. Ecol Indic 132:108319. https://doi.org/10.1016/j.ecolind.2021.108319

Ives CD, Lentini PE, Threlfall CG, Ikin K, Shanahan DF, Garrard GE, Bekessy SA, Fuller RA, Mumaw L, Rayner L, Rowe R, Valentine LE, Kendal D (2016) The importance of cities for threatened species. Glob Ecol Biogeogr 25:117–126. https://doi.org/10.1111/geb.12404

Jaganmohan M, Vailshery LS, Mundoli S, Nagendra H (2018) Biodiversity in sacred urban spaces of Bengaluru, India. Urban for Urban Green 32:64–70. https://doi.org/10.1016/j.ufug.2018.03.021

Kantsa A, Tscheulin T, Junker RR, Petanidou T, Kokkini S (2013) Urban biodiversity hotspots wait to get discovered: The example of the city of Ioannina, NW Greece. Landsc Urb Plan 120:129–137. https://doi.org/10.1016/j.landurbplan.2013.08.013

Keppel G, Van Niel KP, Wardell-Johnson GW, Yates CJ, Byrne M, Mucina L, Schut AGT, Hopper SD, Franklin SE (2012) Refugia: identifying and understanding safe havens for biodiversity under climate change. Glob Ecol Biogeogr 21:393–404. https://doi.org/10.1111/j.1466-8238.2011.00686.x

Kondratyeva A, Knapp S, Durka W, Kühn I, Vallet J, Machon N, Martin G, Motard E, Grandcolas P, Pavoine S (2020) Urbanization effects on biodiversity revealed by a two-scale analysis of species functional uniqueness vs redundancy. Front Ecol Evol 8:73. https://doi.org/10.3389/fevo.2020.00073

Konic J, Essl F, Lenzner B (2021) To Care or Not to Care? Which factors influence the distribution of early-flowering geophytes at the Vienna Central Cemetery Austria. Sustainability 13:4657. https://doi.org/10.3390/su13094657

Kotze DJ, Lowe EC, MacIvor JS, Ossola A, Norton BA, Hochuli DF, Mata L, Moretti M, Gagné SA, Handa IT, Jones TM, Threlfall CG, Hahs AK (2022) Urban forest invertebrates: how they shape and respond to the urban environment. Urban Ecosyst 25:1589–1609. https://doi.org/10.1007/s11252-022-01240-9

Kowarik I (2008) On the Role of Alien Species in Urban Flora and Vegetation. In: Marzluff, JM et al., Urban Ecology, Springer, Boston, MA. https://doi.org/10.1007/978-0-387-73412-5_20

Kowarik I, Hiller A, Planchuelo G, Seitz B, von der Lippe M, Buchholz S (2019) Emerging Urban Forests: Opportunities for Promoting the Wild Side of the Urban Green Infrastructure. Sustainability 11:6318. https://doi.org/10.3390/su11226318

Kowarik I, von der Lippe M, Cierjacks A (2013) Prevalence of alien versus native species of woody plants in Berlin differs between habitats and at different scales. Preslia 85:113–132

Kutschbach-Brohl L, Washburn BE, Bernhardt GE, Chipman RB, Francoeur LC (2010) Arthropods of a semi-natural grassland in an urban environment: the John F. Kennedy International Airport, New York. USDA National Wildlife Research Center - Staff Publications, 1897. Retrieved from: https://digitalcommons.unl.edu/icwdm_usdanwrc/1897, Accessed on 31 October 2022

Kwok R (2018) Accidental urban oases. PNAS 115:4800–4804. https://doi.org/10.1073/pnas.1806197115

Labadessa R, Ancillotto L (2023) Small but irreplaceable: The conservation value of landscape remnants for urban plant diversity. J Environ Manage 339:117907. https://doi.org/10.1016/j.jenvman.2023.117907

Leather SR, Helden AJ (2005) Magic Roundabouts? Teaching conservation in schools and universities. J Biol Educ 39:102–107. https://doi.org/10.1080/00219266.2005.9655975

Lepczyk CA, Aronson MFJ, Evans KL, Goddard MA, Lerman SB, Macivor JS (2017) Questions for Understanding the Ecology of Urban Green Spaces for Biodiversity Conservation. Bioscience 67:799–807. https://doi.org/10.1093/biosci/bix079

Löki V, Deák B, Lukács AB, Molnár AV (2019) Biodiversity potential of burial places – a review on the flora and fauna of cemeteries and churchyards. Glob Ecol Conserv 18:e00614. https://doi.org/10.1016/j.gecco.2019.e00614

Miller JR, Hobbs RJ (2002) Conservation where people live and work. Conserv Biol 16:330–337. https://doi.org/10.1046/j.1523-1739.2002.00420.x

Monsarrat S, Jarvie S, Svenning J-C (2019) Anthropocene refugia: integrating history and predictive modelling to assess the space available for biodiversity in a human-dominated world. Philos Trans R Soc Lond B Biol Sci 374:20190219. https://doi.org/10.1098/rstb.2019.0219

Nagy KM, Malatinszky Á (2019) Unique botanical values in a metropolitan area and the landscape history reasons of their occurrence on the Széchenyi Hill, Budapest. Nat Conserv 32:35–50. https://doi.org/10.3897/natureconservation.32.30807

Onandia G, Schittko C, Ryo M, Bernard-Verdier M, Heger T, Joshi J, Kowarik I, Gessler A (2019) Ecosystem functioning in urban grasslands: The role of biodiversity, plant invasions and urbanization. Plos One 14:e0225438. https://doi.org/10.1371/journal.pone.0225438

Padrón PS, Vélez A, Miorelli N, Willmott KR (2020) Urban areas as refuges for endemic fauna: description of the immature stages of *Catasticta flisa duna* Eitschberger T. Racheli, 1998 Lepidoptera: Pieridae and its ecological interactions. Neotrop Biodivers 6:109–116. https://doi.org/10.1080/23766808.2020.1769993

Perez KE, Najev BSL, Christoffersen B, Nekola JC (2021) Biotic homogenization or riparian refugia? Urban and wild land snail assemblages along a subtropical precipitation gradient. J Urban Ecol 7:juab002. https://doi.org/10.1093/jue/juab002.

Pregitzer CC, Ashton, MS, Charlop-Powers SA, D'Amato AW, Frey BR, Gunther B, Hallett RA, Pregitzer KS, Woodall CW, Bradford MA (2019) Defining and assessing urban forests to inform management and policy. Environ Res Let 14:085002. https://doi.org/10.1088/1748-9326/ab2552

Pregitzer CC, Charlop-Powers S, Bradford MA (2020) Natural area forests in us cities: opportunities and challenges. J For 119:141–151. https://doi.org/10.1093/jofore/fvaa055

Rull V (2009) Microrefugia J Biogeogr 36:481–484. https://doi.org/10.1111/j.1365-2699.2008.02023.x

Talal ML, Santelmann MV (2019) Plant Community Composition and Biodiversity Patterns in Urban Parks of Portland. Oregon Front Ecol Evol 7:201. https://doi.org/10.3389/fevo.2019.00201

Salinitro M, Alessandrini A, Zappi A, Melucci D, Tassoni A (2018) Floristic diversity in different urban ecological niches of a southern European city. Sci Rep 8:15110. https://doi.org/10.1038/s41598-018-33346-6

Selwood KE, Zimmer HC (2020) Refuges for biodiversity conservation: A review of the evidence. Biol Conserv 245:108502. https://doi.org/10.1016/j.biocon.2020.108502

Sepp T, McGraw KJ, Giraudeau M (2020) Urban sexual selection. In: Szulkin M, Munshi-South J, Charmantier A (eds) Urban Evolutionary Biology. Oxford University Press, New York, pp 234–252

Shaffer HB (2018) Urban Biodiversity Arks Nat Sustain 1:725–727. https://doi.org/10.1038/s41893-018-0193-y

Sol D, González-Lagos C, Moreira D, Maspons J, Lapiedra O (2014) Urbanisation tolerance and the loss of avian diversity. Ecol Lett 17:942–950. https://doi.org/10.1111/ele.12297

Spotswood EN, Beller EE, Grossinger R, Grenier JL, Heller NE, Aronson MFJ (2021) The Biological Deserts Fallacy: Cities in Their Landscapes Contribute More than We Think to Regional Biodiversity. Bioscience 71:148–160. https://doi.org/10.1093/biosci/biaa155

Stewart RA, Clark TJ, Shelton J, Stringfellow M, Scott C, White SA, McCafferty DJ (2017) Urban grasslands support threatened water voles. J Urb Ecol 3:jux007. https://doi.org/10.1093/jue/jux007

Taboada-Verona C, Sermeño-Correa C, Sierra-Serrano O, Noriega JA (2019) Checklist of the superfamily Scarabaeoidea Insecta, Coleoptera in an urban area of the Caribbean Colombia. Check List 15:579–594. https://doi.org/10.15560/15.4.579

Toffolo C, Gentili R, Banfi E, Caronni C, Montagnani C, Citterio S, Galasso G (2021) Urban plant assemblages by land use type in Milan: floristic, ecological and functional diversities and refugium role of railway areas. Urban For Urban Green 62:127175. https://doi.org/10.1016/j.ufug.2021.127175

United Nations (2019) World Urbanization Prospects. The 2018 Revision**.** UN, Department of Economic and Social Affairs, Population Division, New York

Vlaanderen S, Lange N (2022) COP15: Biodiversity and Urban Planning. DLA Piper, Retrieved from https://www.dlapiper.com/en/insights/publications/2022/12/cop15-biodiversity-and-urban-planning. Accessed on 30 May 2023

Vojík M, Sádlo J, Petřík P, Pyšek P, Man M, Pergl J (2020) Two faces of parks: sources of invasion and habitat for threatened native plants. Preslia 92:353–373. https://doi.org/10.23855/preslia.2020.353

Zou HX, Anastasio AE, Pfister CA (2019) Early succession on slag compared to urban soil: A slower recovery. Plos One 14:e0224214. https://doi.org/10.1371/journal.pone.0224214