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PATTERNS AND DRIVERS OF PLANT BIODIVERSITY IN URBAN AND URBANIZING LANDSCAPES

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Introduction

Global biodiversity is in decline (IPBES 2019), while urbanization is on the rise (Chen et al. 2020). While safeguarding biodiversity will not solely be decided in urban areas, their relevance for biodiversity conservation increases (Seto et al. 2012). To plan, design, and manage urban areas in ways that benefit both humans and biodiversity, it is necessary to understand drivers and patterns of urban biodiversity and underlying mechanisms driving species populations and community dynamics (McDonnell and Hahs 2013; Lepczyk et al. 2017; Kowarik and von der Lippe 2018; Piana et al. 2019).

Plant species as primary producers are key elements of ecosystems. High plant diversity supports the diversity of many other taxa (Bräuniger et al. 2010). Understanding how urban environments promote plant diversity will thus benefit other taxa as well. Moreover, plant diversity is key to the delivery of many ecosystem services (Schwarz et al. 2017). Maintaining and promoting urban plant diversity should thus be a core interest of urban stakeholders.

This chapter overviews patterns of plant biodiversity across urban and urbanizing landscapes and compares these patterns to those in non-urban areas. Specifically, we will examine four attributes of diversity – taxonomic, phylogenetic, genetic, and functional (Table 15.1) – and their responses to urban environments. We will also examine the social-ecological drivers influencing the composition, abundance, and distribution of plant biodiversity. Finally, we will make recommendations on the conservation of plant biodiversity in urban areas.

The chapter focuses principally on vascular plants, but lichen and mosses are also considered. We classify vascular plants into those occurring spontaneously (wildly) and those cultivated by humans. Both groups comprise native and non-native species. These differentiations are necessary because spontaneous and cultivated as well as native and non-native species respond differently to urban influences.

Patterns and drivers of spontaneous vascular plant diversity in and across urban areas

Taxonomic diversity

Urban areas often have a greater species richness (total number of species) than adjacent non-urban regions (e.g. Pyšek 1993; Hope et al. 2003). This richness results from a number of factors,

Table 15.1 Measures of biodiversity with definitions

<i>Measure of biodiversity</i>	<i>Definition</i>
Taxonomic diversity	Number, abundance or evenness of species, genera, or other taxonomic units
Phylogenetic diversity	Wealth of evolutionary information inherent in a species assemblage. While the term “phylogenetic diversity” has been used by Faith (1992) for measuring the sum of branch lengths in an evolutionary/phylogenetic tree, it is often used more broadly for describing phylogenetic richness (sum of accumulated phylogenetic differences among taxa), divergence (mean phylogenetic relatedness among taxa), and regularity (variance in differences among taxa) – cf. Tucker et al. (2017).
Genetic diversity	Measure of within-species diversity quantifying the diversity of alleles present within a species population
Functional diversity	Number, range, or abundance (or combinations of these) of functional traits represented within an assemblage. Different measures exist covering aspects of richness, abundance, and divergence (Villéger et al. 2008).

including urban areas being located in biological hotspots, high degree of spatiotemporal heterogeneity, introduction of non-native species, and age and size of the urban area.

Urban areas often occur in biological hotspots (Seto et al. 2012). These hotspots correspond to regions of high productivity such as deltas and estuaries, high substrate diversity, the confluence of ecotones, and moderate climates. By settling in these regions, humans capitalized on the natural resources, such as timber, game, and fisheries, productive soils for agriculture, and the confluence of rivers for transportation. Consequently, today’s urban areas are located in regions of high plant species richness (Kühn et al. 2004).

Urban areas have a high degree of spatial heterogeneity when compared to agricultural landscapes (Sukopp 1998). They consist of a range of land use/cover configurations of which each has a unique social-ecological environment (Cadenasso et al. 2007) which influences not only the abundance and distribution of species but also ecosystem functions. Sites with vegetation (Kowarik 1992) include remnants of natural landscapes (e.g. alluvial forest), patches of agrarian landscapes (e.g. hay meadows), designed urban green spaces (e.g. gardens, parks), and novel urban ecosystems (e.g. vacant lots, railways, road verges).

Non-native species contribute significantly to urban biodiversity (Pyšek 1998). Most of these have been and continue to be introduced with trade and transport (Seebens et al. 2015), either as ornamental or crop plants or unintentional introductions (Reichard and White 2001; Lambdon et al. 2008). Consequently, non-native species richness increases with urbanization (Tait et al. 2005). In addition, cities host many native generalist species as well as a number of rare and threatened species (Ives et al. 2016). Some of the latter, however, only exist in today’s urban areas due to extinction debts (Hahs et al. 2009), and on the long term, they might not be able to form viable populations (Kowarik and von der Lippe 2018). The increase in widespread non-native species and the loss of rare species can increase the similarity of urban floras across the globe (McKinney 2006; Winter et al. 2009), but the compositional similarity of urban forests among the world’s cities is scale dependent (Yang et al. 2015).

Species richness also increases with age and size of urban areas (Klotz 1990; Aronson et al. 2014). Regardless of size and age, native species richness declines, while non-native species richness increases as one moves from the rural fringe to the urban core (Lososová et al. 2012; Aronson et al. 2015).

Phylogenetic diversity

Studies focusing on species richness provide little insight into how species are related to each other. Similarly, species richness may not be the best indicator how urban environments influence biodiversity. Phylogenetic diversity is a measure of evolutionary relationships and is based on the phylogenetic similarities and differences among species (Table 15.1). In urban areas, species are more closely related to each other than species in the countryside (Knapp et al. 2008a; Ricotta et al. 2009). Across land use/cover types within urban areas, plant communities are phylogenetically clustered (i.e. less diverse than expected by chance; Čeplová et al. 2015). Possible underlying reasons are the high share of non-native species that are closely related to each other and to native species and restricted growing conditions for species mal-adapted to urban environments (Knapp et al. 2008a; Čeplová et al. 2015; Knapp et al. 2017).

Genetic diversity

Broad-scale analyses of genetic diversity across urban and urbanizing landscapes are limited, and there appears to be no general pattern emerging of genetic responses to the urban environment. Nonetheless, the urban landscape can be hostile to gene flow because the habitats remaining within the built-up matrix are highly isolated, which can promote inbreeding and genetic drift, thus decreasing genetic diversity and reproductive success within populations (Van Rossum 2008; Bartlewicz et al. 2015). Yakub and Tiffin (2017) also observed that the individuals of an urban plant population can be more closely related to individuals from other urban centers than to individuals in adjacent non-urban areas. It seems that long-distance transportation of species (which especially applies to non-native species) connects plant populations across cities, thus potentially increasing global genetic homogenization.

The urban landscape can also promote genetic diversity. Scholz (2007) describes a group of species, anecophytes, which are only found in urban landscapes, thus, potentially enhancing genetic diversity. Similarly, Johnson et al. (2018) report that genetic diversity within *Trifolium repens* increases with urbanization. The conservation of genetic diversity within urban landscapes can be achieved by enhancing genetic flow through connecting habitat (Van Rossum 2009) and improving opportunities for pollinators (Culley et al. 2007; Krishnan and Borges 2018; but see Diniz et al. 2019).

Functional diversity

Functional plant traits are anatomical, biochemical, morphological, phenological, physiological, and structural characteristics of species reflecting adaptation to environmental conditions (Kattge et al. 2011). Changes in environmental conditions can cause shifts in the trait composition of species assemblages. With urbanization increasing local temperatures, air pollutants, and nutrient deposition, and lowering soil moisture, for example (Sukopp 1998), urban and non-urban plant assemblages often differ in functional trait composition. In addition to environmental conditions, an urban area's size, history, and geographical location as well as habitat types can influence functional trait composition. Consequently, the direction and strength of trait shifts are not the same globally. Nonetheless, some general patterns are observed (Williams et al. 2015; Palma et al. 2017) including increases in

- short-lived species that reproduce by seeds and colonize disturbed sites;
- woody species, fostered by plantings of shrubs and trees in parks, gardens, or along streets, that escape cultivation and become part of spontaneous vegetation;

- tall growing species and heavier-seeded plants – related but not restricted to the presence of woody species.

By comparison, geophytes (e.g. bulbs, rhizomes, corms, tubers) as well as wind-dispersed species decrease in occurrence in urban as compared to non-urban areas. The latter might relate to land cover. For instance, Cheptou et al. (2008) observed that *Crepis sancta*, which grows in small patches often surrounded by impervious surfaces, had a higher degree of germination success for non-dispersed seeds as compared to dispersed seeds. When seeds dropped from a plant (non-dispersed), they often fall on soil and are able to germinate. In comparison, when seeds are dispersed by wind, they often fall on impervious surfaces and are unable to germinate (Cheptou et al. 2008). In contrast, Kowarik (2011) observed that forested vacant lots were dominated by wind-dispersed species. Seeds dispersed by animals and/or humans (such as those wrapped in fleshy fruits) were shown to benefit plant occurrence in urban areas (Knapp et al. 2008b) and to increase over time (Aronson et al. 2007). These contrasting examples illustrate the complexity of shifting functional traits in urban landscapes, with differences among habitats and across time (e.g. succession on vacant lots) and the drivers influencing that complexity (Aronson et al. 2016).

Urban-induced trait-shifts exist across genera (interspecific) and within species (intraspecific). The latter point towards urbanization being a driver of species evolution (Donihue and Lambert 2014). Examples of intraspecific trait shifts with increasing urban land use/cover comprise shifts from long- to short-distance dispersal (Cheptou et al. 2008), reduced production of antiherbivore defense chemicals (Johnson et al. 2018), or changes in leaf physiology (Alberti 2015).

Measures of functional diversity apart from functional composition have rarely been investigated in urban areas. Lososová et al. (2016), in a study of 32 European cities, showed that across a range of habitat types, plant communities were functionally convergent (i.e. less functional variation than expected for random communities). This low functional diversity is in contrast to high species richness found in the very same communities. It seems that urban habitats allow for a high number of species but restrict the range of functional traits that can occur. Strong environmental filtering and/or competitive exclusion among species might be reasons for this (Lososová et al. 2016).

Patterns and drivers of cultivated vascular plant diversity in designed urban green spaces

In the previous section, we examined diversity attributes for spontaneous vegetation that occurs across all four types of urban nature (Kowarik 1992). Another element of the green infrastructure in urban landscapes is the pool of cultivated species, which is primarily restricted to designed green space. Designed urban green spaces include but are not limited to household and community gardens, stormwater management sites, parks, and street plantings. They are significant land cover types in the world's cities. For instance, domestic gardens alone make up 16% of the total area of Stockholm, Sweden (Colding et al. 2006); 22% to 27% of UK cities (Loram et al. 2007); and 36% of Dunedin, New Zealand (Mathieu et al. 2007). Cultivated species are usually highly managed for aesthetics, leisure, food, or medicine. Social decisions are a much stronger influence on the selection and establishment of cultivated vegetation than on spontaneous vegetation (Swan et al. 2021).

Taxonomic diversity

Designed green spaces are biologically diverse, including both cultivated and spontaneous vegetation. Numbers of cultivated plant species can exceed numbers in natural areas (Norfolk et al. 2013;

Pearse et al. 2018). This reflects the diversity of people's preferences (Kendal et al. 2012a) and, related to that, exceptionally high proportions of non-native plant species available to select for plantings. Unfortunately, ornamental plantings are one of the most important pathways of biological invasions (Reichard and White 2001). In Europe, approximately 60% (Pyšek et al. 2009) and in Australia, 67% (Moss and Walmsley 2005) of all non-native vascular plants are escaped ornamental or horticultural species. Moreover, designed urban green spaces plantings introduce cultivars and hybrids of both native and non-native species (Galluzzi et al. 2010), which can significantly affect ecosystem structure and function (Whelan et al. 2006).

Overall, cultivated plant diversity depends on current and past availability in nurseries (Kendal et al. 2012b; Avolio et al. 2018), homeowner preferences (Cavender-Bares et al. 2020), social factors such as income (Hope et al. 2003; Leong et al. 2018), and prevailing policies (as in the case of public greenery; Kendal et al. 2012b). These relationships exemplify the strong impact of human decisions on cultivated plant diversity. In addition, management plays a significant role in the success of cultivated plants through weeding, irrigating, and applying fertilizers and biocides (Niinemets and Peñuelas 2008). These actions often lessen the effects of the urban environment (Kendal et al. 2012b) and physical attributes of the garden (Cavender-Bares et al. 2020).

Phylogenetic diversity

Less is known about the phylogenetic diversity of cultivated plant species. Studies from domestic gardens in the US indicate that homeowner preferences and economic status affect phylogenetic biodiversity. For instance, in Minnesotan gardens, phylogenetic diversity decreased with both the frequency of fertilizer application and preference for ease of maintenance but increased with preference for orderliness (Cavender-Bares et al. 2020). By comparison, Pearse et al. (2018) observed that cultivated plantings in domestic gardens across seven US cities had higher phylogenetic diversity than natural areas, reflecting the wide range of species available in the horticultural trade.

Genetic diversity

Similarly, genetic diversity across designed urban green spaces can be quite high owing to the availability of cultivars, hybrids, non-native, and native species for planting (Galluzzi et al. 2010). On the other hand, the selection of specific species, cultivars, or clones, such as for street tree plantings, can significantly decrease genetic diversity (Makeeva et al. 2018) and increase the susceptibility to insects and diseases over time (Vanden Broeck et al. 2018).

Functional diversity

Studies on the functional richness of cultivated plants in designed urban green spaces are scarce but case studies indicate that it can exceed that of natural vegetation (Norfolk et al. 2013). The functional composition of cultivated species in designed urban green spaces highly depends on human preferences (Kendal et al. 2012a). For example, aesthetic qualities are often preferred and related to plant growth form, leaf traits (e.g. foliage color, leaf width), flowering traits (e.g. flower size), and tree size (Kendal et al. 2012a; Pataki et al. 2013; Goodness et al. 2016). Similarly, species are selected for ease of maintenance, water use, and providing shade or fruits (Kendal et al. 2012a; Pataki et al. 2013). Accordingly, functional traits can be purposefully used to select those species that are adapted to local environmental conditions and that promote the provision of ecosystem services and the increase in urban functional diversity (Pataki et al. 2013; Lundholm et al. 2015; Filazzola et al. 2019).

Lichen and mosses

Taxonomic diversity

As with vascular plants, the substrate heterogeneity of urban areas promotes the diversity of lichens and mosses. For example, gardens, cemeteries, and tree-dominated habitats were shown to support high species numbers of lichens and mosses (e.g. Smith et al. 2010; Sérgio et al. 2016; Vogt-Schilb et al. 2018; Oishi 2019). Lichens can establish on different anthropogenic substrates such as brick, mortar, or tarmac (Seaward 1982; Gombert et al. 2004). Lichens and mosses can even grow on roofs because of their ability to survive extreme drought (Van Mechelen et al. 2015; Schröder and Kiehl 2020). Still, moss cover, diversity, and abundance are higher in sheltered than sun-exposed areas of roofs (Van Mechelen et al. 2015), exemplifying habitat preferences. Consequently, the composition of moss assemblages differs across urban green spaces, depending on microclimatic conditions (Zepeda-Gómez et al. 2014). Also, lichen diversity in urban woodlands increases with woodland age (Vogt-Schilb et al. 2018), indicating preferences for specific substrates and micro-climatic conditions.

Air pollutant concentrations – especially SO_2 , being toxic to lichens – are key to lichen occurrence within urban areas. In fact “lichen deserts” exist in many cities around the world. Nonetheless, lichens can recolonize areas after SO_2 concentrations decreased significantly because of clean air policies (Seaward 1982; Ranta 2001; Gombert et al. 2004; Sérgio et al. 2016). Still, other pollutants, such as traffic-related NO_2 and dust deposition, as well as extremes of temperatures and water supply can reduce species occurrence, abundance, and distribution (Seaward 1982; Sérgio et al. 2016). Consequently, lichen cover and diversity are often low in high-traffic areas (Coffey and Fahrig 2012; Llop et al. 2012). A study in Ottawa, Canada, however, reported that lichen species richness was more related to moisture and colonization sources and less to vehicle pollution (Coffey and Fahrig 2012). Similarly, in Almada, Portugal, climate, and not air pollution, was the principal driver of lichen diversity (Munzi et al. 2014).

In Germany, Knapp et al. (2008a) reported lower lichen richness in urban than non-urban protected areas but no difference in moss richness, whereas Concepción et al. (2016) found no response of moss richness to urban sprawl across Switzerland. These studies indicate that additional research is needed to quantify lichen and moss occurrence, abundance, and distributions across urban landscapes.

Other measures of diversity

Phylogenetic and genetic diversity of lichens and mosses have not been investigated in response to urban land use. Few studies on functional composition exist. For lichens, terricolous species (i.e. those growing on bare soil) tend to be less common in urban environments than saxicolous (on stone) or epiphytic species (on bark) because appropriate open soil is scarce (Seaward 1982). Oligotrophic, hygrophytic, and acidophilous lichen are sensitive to traffic-induced pollution, while eutrophic, xerophytic, basophilous, and nitrophilous lichen are more common in traffic-dominated areas (Llop et al. 2012; Sérgio et al. 2016). Overall, lichen species that reach high abundances in urban areas are often generalists (Seaward 1982), resembling a pattern that is common across many taxonomic groups (Concepción et al. 2015; Deguines et al. 2016).

For moss species, those common in urban areas are often species associated with disturbance (Landis and Leopold 2014). In comparison to non-urban habitats more dendroid (i.e. resembling the form of a tree) and thallose (without leaf-like structures) but less plagiotropic (growing more or less horizontally) moss species were found in urban sites of the Bolzano region, Italy (Spitale et al. 2020).

Mechanisms driving urban plant biodiversity

In summary, both anthropogenic and environmental drivers affect urban plant biodiversity. These can be related to (1) regional climate, biogeography, and land use; (2) human mediated biotic interchange; (3) urban form and development history; (4) socioeconomic and cultural influences; (5) local human facilitation; and (6) species interactions (Table 15.2; Aronson et al. 2016). Still, the complexity of the interactions between drivers and patterns of urban biodiversity and underlying mechanisms driving plant populations and communities dynamics remain largely unanswered (McDonnell and Hahs 2013) but are the focus of emerging research (Piana et al. 2019). One key question in urban plant biodiversity research is, of which type, size, density, connectivity, and quality (e.g. in terms of management) urban green spaces should be maintained or created to enhance long-term population viability, overall plant diversity, and the diversity of specific groups

Table 15.2 Groups of drivers of urban plant biodiversity according to Aronson et al. (2016) with non-exhaustive list of examples of drivers and mechanisms

Group	Drivers	Mechanisms
Biogeography, land use, and regional climate	Urban heat island	Urban heat is one reason behind rural-urban shifts in plant phenology, but other drivers likely interact in ways pending to be identified (Zohner 2019). It acts across local and regional scales.
	Soils	In response to urban vs. potting soil, native species mainly showed trait divergence, while non-native species mainly showed preadaptation. Strategies for living in urban areas thus comprise phenotypic plasticity and/or genetic-based differences for native but not non-native plants (Borowy and Swan 2020).
Human mediated biotic interchange	Traffic	Long-distance dispersal by vehicles is more common in non-native than native plant species, promoting plant invasions (von der Lippe and Kowarik 2007).
	(Horticultural) trade	Higher market frequency and cheap prices of seeds in horticultural trade promote invasion success (Dehnen-Schmutz et al. 2007).
Urban form and development history	Size of urban area	The larger a city, the more species it hosts (Klotz 1990), pointing towards local extinction and colonization mechanisms (cf. MacArthur and Wilson 1967) and the importance of habitat heterogeneity, which correlates to size (Knapp et al. 2008a).
Socioeconomic and cultural influences	Socioeconomic status	A series of interacting mechanisms relates affluence to plant biodiversity. Particularly in arid regions, irrigation promotes plant diversity, with affluent households able to afford irrigation (Leong et al. 2018).
Local human facilitation	Management and human selection (e.g. irrigation, weeding)	See the previous example (Leong et al. 2018) illustrating that drivers of different groups can interact in affecting urban plant diversity.
Species interactions	Plant-pollinator interactions	Insect visitation rates and Hymenoptera community diversity drive higher urban than non-urban seed set in <i>Trifolium pratense</i> and in turn are affected by patch edge density and proportion of arable land (Theodorou et al. 2020).

Table 15.3 Major approaches in the study of urban plant biodiversity

<i>Major approach</i>	<i>Examples</i>
Monitoring and observation	<ul style="list-style-type: none"> • “Urban biotope mapping” in Germany that provides basic knowledge for planning and policy (Sukopp and Weiler 1988). • Citizen/community science programs enable the collection of monitoring data across urban areas (e.g. BioBlitz – see www.nationalgeographic.org/projects/bioblitz/).
Measurements	<ul style="list-style-type: none"> • Lundholm et al. (2015) measured traits of green roof plant species and linked them to ecosystem services.
Macroecological analysis	<ul style="list-style-type: none"> • In a global analysis, Aronson et al. (2014) revealed that most plant species occurring in urban areas are native species, few are cosmopolitan, and the number of plant species per km² declined with urbanization but increased with city age.
Review and meta-analysis	<ul style="list-style-type: none"> • Williams et al. (2015) by analyzing publications across the globe identified both broadly valid plant trait patterns in response to urban environmental conditions and inconsistencies pointing towards context-dependency of trait patterns.
Experimental approaches	<ul style="list-style-type: none"> • Borowy and Swan (2020) used soil treatment with urban soil vs. potting soil in order to test for species’ preadaptation to urban conditions. • In a social-ecological experiment, Shwartz et al. (2014) investigated urban dwellers’ perception of plant diversity.

such as endangered species (Lepczyk et al. 2017; Kowarik and von der Lippe 2018)? Answering this question can inform urban biodiversity conservation and thus aid in protecting global biodiversity. A range of approaches exist for analyzing and understanding urban plant biodiversity. Some of which are summarized in Table 15.3.

Conservation and management

All four types of urban nature (Kowarik 1992) – remnants of natural landscapes, patches of agrarian landscapes, designed urban green spaces, and novel urban ecosystems – with their variety of habitats together can be home to a diversity of plant species. Consequently, all of them need to be included into measures of biodiversity conservation.

Being the core instrument of biodiversity conservation, protected areas do exist in many urban areas, with natural remnants, local natural heritage, rare species, and ecosystem functions key to human well-being (such as oxygen production) being their main target of conservation. For example, in the United States, natural remnants occupy 84% of municipal parkland (Harnik et al. 2017). Maintaining protected areas and extending their number and size should be one core strategy of urban biodiversity conservation.

Still, the amount of urban land that can be protected is restricted. Thus, in addition to legal protection, other parts of urban nature should be used in a sustainable, multifunctional way that benefits both human health and well-being and biodiversity (an approach termed “urban land sharing”; Lin and Fuller 2013). For example, designed urban parks will host higher levels of plant diversity if hedges, groups of trees, small forests, water bodies, and extensively mown meadows complement short-cut lawns. At the same time, such multifunctional green spaces will provide opportunity for a range of leisure activities as well as more ecosystem services (Lundholm 2015) such as temperature regulation and air purification.

Even novel urban ecosystems, which often host large numbers of non-native species, can be of value for biodiversity conservation. They can be found along unused railway tracks, brownfields, and other typical urban-industrial habitats. An example are emerging forests that gain rare and endangered species the older they grow, thus increasingly benefitting biodiversity (Kowarik et al. 2019).

In summary, across urban-rural landscapes, a dense network of larger and smaller green spaces of all types of urban nature will help plant species to form viable populations (Kowarik et al. 2019). To complement such networks, it is even possible to re-establish habitats of conservation interest within urban settings, such as shown by Fischer et al. (2013), who created novel urban grasslands by reintroducing native plant species into urban wasteland vegetation. The protection of plant species within urban and urbanizing regions will even support the protection of other taxa (Bräuniger et al. 2010). With urban areas growing worldwide, identifying how urban landscapes and their collective urban nature are planned, designed, and managed in order to protect global biodiversity is a research priority.

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