Chapter 5 Drivers of Vegetation Species Diversity and Composition in Urban Ecosystems

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5.1 Introduction: The Role of Plants in Terrestrial Ecosystems

In terrestrial systems, plants are the base of the food web, and their population growth is generally limited by resource availability rather than by higher trophic levels (Hairston et al. [1960](#page-12-0)). Plants are also important components of the biogeochemical cycles that drive the movement of energy and resources. As primary producers, plants make energy available to higher trophic levels by converting sunlight, via photosynthesis, into biomass. Plants also create highly textured and structured habitat that provides food and cover for wildlife. Patterns of vegetation are shaped by variation in climate, soils, and disturbances, and provide the environmental template that drives patterns of species interactions throughout food webs. Where in this picture do urban areas fit?

5.2 Vegetation in Terrestrial Urban Systems

Ecologists increasingly recognize the pervasive impacts of human activities on the diversity, structure, and function of vegetative communities, as well as their ecosystem services (e.g. Turner [2010](#page-15-0)). With the majority of the world's growing human population living in cities (Chap. 1, Grimm et al. [2008\)](#page-12-1), rapid urbanization has led to the realization that built environments must provide a diverse suite of ecological functions for both people and wildlife. Today, research foci have shifted from

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whether substantial biodiversity exists in cities to instead what the specific mechanisms are that determine the abundance and functional role of biodiversity within cities (e.g., Blaustein [2013\)](#page-11-0).

Urbanization is a combination of many processes, not all of which vary similarly across the landscape, and thus it is not clear to what extent the ecological theory developed in less human-impacted systems applies to urban systems. Decomposing urbanization gradients into the component parts may help to identify specific drivers of vegetation patterns. A mechanistic understanding of urban vegetation patterns is necessary for effectively managing urban areas, and for predicting the consequences of changes in urban vegetation for other trophic levels and for ecosystem functioning. In this chapter, we briefly review research on urban vegetation structure and function and recommend future research directions.

5.2.1 Relationship of Vegetation to the Abiotic Environment: Plant–Soil Interactions

Plant–soil interactions are tightly coupled, and urbanization can influence these relationships. The diversity, productivity, and composition of plant species can be significantly altered by soil microbial communities and related ecosystem functions, such as carbon and nitrogen cycling (Zak et al. [2003](#page-15-1); van der Heijden et al. [2008\)](#page-15-2). One consistent effect of urbanization is an increase in the heterogeneity of urban soils, due to direct (e.g., urban infill at construction sites or lawn nutrient amendments), as well as indirect human impacts (e.g., changes in microclimatic, water availability, amount of stormwater runoff, heavy metals, and other pollutants) (Pavao-Zuckerman [2008](#page-14-0)). Understanding the relationship between heterogeneous urban soils and plant communities requires an understanding of the relative importance of contemporary and local plant–soil interactions, compared to the importance of longer-term and broader-scale phenomena. These broader-scale phenomena include legacies of past land-use or the overall level of urban development in the region surrounding vegetative patches.

The results of empirical studies of plant–soil interactions in urban systems have been mixed. For example, a study of the relative importance of land-use and vegetation structure for litter decomposition in urban soils found that land-use (landfill or urban park) was more important than current vegetation composition for determining rates of decomposition, although the diversity of the vegetation had a significant effect on the abundance of soil biota (Vauramo and Setälä [2011](#page-15-3)). However, Elgersma et al. ([2011](#page-12-2)) showed that 2 years after manipulating vegetation in forest patches containing invasive plants, the historical abundance of invasive vegetation had a stronger effect than contemporary vegetative community on microbial community structure and function. Heneghan et al. ([2006\)](#page-13-0) found similar legacy effects on soils, caused by the invasive shrub *Rhamnus cathartica.* Groffman et al. [\(2006](#page-12-3)) determined that forest productivity and nitrogen cycling rates were more strongly related to soil type than to the relative amounts of urban land cover surrounding

forest patches, but that forest species composition was more strongly associated with the amount of surrounding urban land cover. Future research should explicate the complex interactions between urban vegetation and the abiotic environment. This type of research will improve our ability to design and manage urban green spaces that provide for humans and wildlife alike.

5.2.2 Relationship to Other Trophic Levels

Plant communities in urban environments form a "template" for other functional groups of species. These communities are assembled through a combination of natural processes and direct human manipulation (e.g., gardening). Thus, while humans generally do not directly manipulate other groups of species in the urban environment, they do have an indirect influence on their diversity and abundance through alterations to the vegetation.

For example, the potential for small-scale urban agriculture to provide food security in low-income neighborhoods has led to interest, from both researchers and practitioners, in urban pollinator communities. Pollinators are necessary for successful production of many agricultural crops, and the extent to which urban environments support a pollinator community is strongly affected by vegetation structure and diversity. Hennig and Ghazoul [\(2011,](#page-13-1) [2012](#page-13-2)), in studies conducted in Zürich, found increased floral diversity and abundance increased rates of pollinator visitation to focal patches throughout the city. However, the effect of local plant diversity was strongly mediated by landscape attributes such as the amount of habitat fragmentation and the proportion of green space surrounding the patch. Thus, increasing the availability of local floral resources will not always lead to increased wildlife and ecosystem services (e.g., pollination; Matteson and Langellotto [2011](#page-14-1)), and management activities aimed at increasing the availability of floral resources for wildlife may need to consider the regional context of local habitat patches (Goddard et al. [2010](#page-12-4), see Chaps. 12, 14).

Urban vegetation also provides valuable food resources for wildlife. The regional distribution of vegetation patches in urban environments mediates the importance of local habitat for arthropods (Sattler et al. [2010;](#page-14-2) Vergnes et al. [2012\)](#page-15-4), birds (Marzluff and Ewing [2001](#page-14-3); White et al. [2005;](#page-15-5) Litteral and Wu [2012](#page-13-3)) and mammals (FitzGibbon et al. [2007](#page-12-5); Gomes et al. [2011](#page-12-6); Hale et al. [2012](#page-12-7)), all of which use plants for food and cover. Species respond to patch connectivity and size differently depending on their functional characteristics (e.g Sattler et al. [2010](#page-14-2); Litteral and Wu [2012\)](#page-13-3). There is not a simple formula for predicting the effectiveness of manipulation of urban vegetation for supporting desired wildlife, because the spatial scales at which plant diversity and abundance most strongly influence other trophic levels varies by taxa.

5.2.3 Relationship to Humans

Urban vegetation is important in human systems (Chaps. 3, 6), and human activities are another important driver of urban vegetation dynamics. People value the nature they experience "in their own backyards"; their every-day experiences close to home may change the way they perceive the environment, and can positively affect their relationship to nature (Miller [2006;](#page-14-4) Fuller et al. [2007\)](#page-12-8). Accordingly, people select plant communities for particular locations and purposes based on the traits they possess and their ability to fulfill desired objectives. For example, street trees are selected based on their ability to tolerate local site conditions or based on aesthetic preferences. Sometimes, human preferences for a particular type of landscape can lead to problematic ecological results, such as the devastating loss of millions of American elm ( *Ulmus americana*) trees to the introduced Dutch Elm Disease. American elm was one of the most popular and widely-planted species of street tree in the early twentieth century, and their broad-scale decimation led to increased awareness of the potential for heavy impacts of nonnative pest species on urban monocultures and a push to increase the diversity of urban tree plantings (Raupp et al. [2006](#page-14-5)). By increasing the diversity of street trees, urban arborists can increase community resilience to disturbance and promote wildlife diversity. Urban foresters also balance a need for diversity with human aesthetic preferences and species' ecological tolerances. For example, they select for species that require minimal maintenance, tolerate a variety of urban stressors (e.g., high-soil compaction, low oxygen available to roots, drought, and salt sensitivity), and grow to a size appropriate for their location in the landscape (Bassuk et al. [2009](#page-11-1)).

5.3 Vegetation Structure in the Urban Environment

Colonization of urban areas by both native species and escaped ornamental plants shapes urban plant diversity in unique ways. The diversity and characteristics of plant species that can colonize a site strongly influence how species are sorted, successional trajectories, and community response to disturbances. Unlike other taxonomic groups, overall plant species richness generally increases in urban areas, compared to species pools in surrounding rural landscapes (McDonnell and Hahs [2008\)](#page-14-6). This increase in species richness is attributed primarily to the importation and distribution of ornamental plant species, many of which are not of native origin (Hope et al. [2003;](#page-13-4) Walker et al. [2009](#page-15-6); Marco et al. [2010\)](#page-14-7). Many of these ornamental species escape cultivation and become semi-naturalized or invasive (Kowarik [2003;](#page-13-5) Colautti et al. [2006\)](#page-12-9). The purposeful introduction of nonnative plant species combined with unintended extirpation of plant species intolerant of environmental conditions in urban areas shifts the composition of urban regional species pools relative to less urbanized areas by increasing in the relative abundance of invasive, nonnative species (Williams et al. [2009](#page-15-7)).

Table 5.1 Summary of empirical results from five studies that have measured shifts in plant functional traits along urban-rural gradients. Data are shown for all traits examined by at least two of the studies. Under "Urban Abundance," the number of + reflects the number of studies documenting a change in trait abundance/proportion. The relevant citations are listed for each trait

Trait	Urban abundance			Citations
	Increase	Decrease	No change	
Dispersal				
vector				
Wind		$^{++}$	$^{++}$	Knapp et al. 2008, 2012; Thompson et al. 2008: Burton et al. 2009
Animal	$+++$		$^{++}$	Knapp et al. 2008, 2012; Thompson et al. 2008; Burton et al. 2009
Human	$^{++}$			Knapp et al. 2008, 2012; Burton et al. 2009
Water	$+++$	$++$		Knapp et al. 2008, 2012; Thompson et al. 2008; Burton et al. 2009
Seed weight		$^{++}$	$+$	Thompson et al. 2008; Vallet et al. 2010; Knapp et al. 2012
Pollination				
vector				
Insect	$+$		$++$	Burton et al. 2009; Vallet et al. 2010; Knapp et al. 2012
Wind		$^{+++}$	$^{+}$	Knapp et al. 2008, 2012; Thompson et al. 2008; Burton et al. 2009
Self	$^{++}$		$^{+}$	Knapp et al. 2008, 2012; Thompson et al. 2008; Burton et al. 2009
Life duration				
Annual	$^{+++}$			Knapp et al. 2008, 2012; Vallet et al. 2010
Biennial	$^{++}$		$^{+}$	Knapp et al. 2008, 2012; Vallet et al. 2010
Perennial	$+$	$^{++}$		Knapp et al. 2008, 2012; Vallet et al. 2010
Leaf longevity				
Evergreen		$^{+}$	$+$	Burton et al. 2009; Knapp et al. 2012
Deciduous		$^{+}$	$^{+}$	Burton et al. 2009; Knapp et al. 2012
Specific leaf area	$^{+++}$			Knapp et al. 2008; Thompson et al. 2008; Vallet et al. 2010
Plant height	$+$		$^{+}$	Thompson et al. 2008; Vallet et al. 2010
Vegetative reproduction			$^{++}$	Knapp et al. 2008; Thompson et al. 2008

Plant species that are successful in urban environments tend to share a similar suite of traits, tolerances, and life-histories (Table [5.1](#page-4-0)). For example, species that are wind-pollinated, have propagules that are wind-dispersed, are evergreen, have a low specific leaf area, and are perennial occur less frequently in urban environments than in surrounding, less developed areas. However, further work is needed to empirically determine relationships between functional traits and plant responses to the environmental changes caused by urbanization. Increasingly, phylogenetic and functional trait approaches are used to describe not just the number of species in a region, but their relationships and functional roles. Incorporating these descriptions into assessments of urban biodiversity has led to the documentation of a common pattern of phylogenetic and functional homogenization of urban plant communities across the globe (McKinney [2006](#page-14-8); Ricotta et al. [2009](#page-14-9); Shochat et al. [2010;](#page-15-9) Knapp et al. [2012\)](#page-13-6). Functional diversity, in particular, has been highlighted as an important metric for generalizing patterns of biodiversity and comparing between study sites (McGill et al. [2006](#page-14-10)). This is because functional traits, even those that are loosely linked to physiological functioning in plants, still can be valuable for describing how plant communities are sorted along environmental gradients of stress or disturbance (Grime [1977](#page-12-10); Weiher et al. [1999;](#page-15-10) Lavorel and Garnier [2002\)](#page-13-7). For example, specific leaf area is often used as a proxy for the more difficult to measure traits such as relative growth rate, palatability, or plant reaction norms (Weiher et al. [1999](#page-15-10)).

5.3.1 Plant Invasions in Urban Environments

The proportion of nonnative plant species is consistently greater in urban environments, compared to rural areas (Winter et al. [2009](#page-15-11)). One explanation for the high rate of urban invasions is the theory of increased propagule pressure, defined as a combination of the number of individuals released into a location and the number of times they are introduced (Lockwood et al. [2005](#page-13-8)). The propagule pressure model suggests that humans increase the probability of a species being invasive by repeatedly introducing it (Colautti et al. [2006](#page-12-9)).

In addition to the propagule pressure model, two additional concepts are useful for predicting and explaining likelihood of invasion: species invasiveness and habitat invasibility. Habitat invasibility refers to the abiotic or biotic community conditions that make successful invasion more likely to occur at a location. A change in disturbance regime or low diversity of the resident community, which leaves niche space available, are two conditions that often increase invasibility (Funk et al. [2008\)](#page-12-11). The abiotic environment in urban areas may be more easily invaded, due to increased nutrient availability, human-aided transport of materials and propagules across the landscape, and the fragmentation of habitat. Habitat edges, which increase in proportion to habitat interiors as fragmentation increases, are zones of contact between contrasting patches, often share characteristics of both bordering patches, and can alter the rate of flux of species and materials, compared to habitat interiors (Cadenasso et al. 2003; Minor et al. [2009](#page-14-11)). For example, plants with winddispersed seeds tend to be less common in urban areas than in surrounding rural landscapes, because fragmentation of habitat makes it more difficult for seeds to arrive in favorable patches for germination (Cheptou et al. [2008](#page-12-12); Knapp et al. [2012\)](#page-13-6). Small, fragmented habitat patches may experience higher levels of disturbance as well, although changes in disturbance regimes are no longer considered the primary factor for predicting habitat invasibility (Moles et al. [2012\)](#page-14-12).

On the other hand, species invasiveness refers to the likelihood that a particular species, with a particular suite of traits, is expected to become invasive. Traits that might predict invasiveness include polyploidy (having multiple copies of chromosomes; te Beest et al. [2011](#page-15-12)), low seed mass and short juvenile periods (Rejmanek and Richardson [1996\)](#page-14-13), and self-compatibility (not needing pollen from another individual to reproduce sexually; Hao et al. [2010](#page-13-9)). In addition, human selection for desirable ornamental characteristics, such as attractive berries, may inadvertently increase urban species' potential invasiveness (Kitajima et al. [2006\)](#page-13-10).

Traits that correlate with species invasiveness often are combined with models of habitat invasibility to predict areas of the landscape that may be particularly vulnerable to invasion. For example, species with life history traits less similar to species in the extant community may be more likely to invade a particular habitat patch (Funk et al. [2008;](#page-12-11) MacDougall et al. [2009](#page-13-11)). Overall, a more synthetic approach, incorporating multiple interacting processes, is necessary to explain, predict, and manage complex patterns of invasions into urban systems. Regardless of the specific causes, the consequential shifts in plant community can lead to shifts in community function (Hillebrand [2008](#page-13-12); Raupp et al. [2010;](#page-14-14) Rodewald [2011](#page-14-15); Eviner et al. [2012\)](#page-12-13). Ultimately, reducing the diversity of functional traits present in a community may lead to reduced community resilience (i.e., the ability of a community to return to its original, pre-disturbance state) in the face of changing environmental conditions, by narrowing the range of environmental conditions under which the community is pre-adapted to succeed (i.e., the "insurance hypothesis," Yachi and Loreau [1999;](#page-15-13) MacDougall et al. [2013](#page-13-13)). For example, more diverse communities have experimentally been shown to recover more quickly after a disturbance, such as drought, than less diverse communities, regardless of the initial biomass of the communities (Van Ruijven and Berendse [2010](#page-15-14)). Also, communities in which nondominant species were experimentally removed were less drought resistant and also less resilient than communities in which both dominant and nondominant species were allowed to coexist (Mariotte et al. [2013](#page-14-16))

5.3.2 Human Preferences for Urban Plant Assemblages

Whereas typical environmental variables tend to be similar in patches that are closer together in space (e.g., patterns of rock formations influence where water is available), urban land use is arranged by human design, and often decoupled from the underlying environmental features (Chap. 3). Studies conducted in Phoenix, Arizona residential yards, for example, showed strong patterns of plant community composition associated with human neighborhood-scale preferences for xeric or mesic landscapes (Walker et al. [2009\)](#page-15-6). Many other studies have found "neighborhood effects" for vegetation structure and composition (Zmyslony and Gagnon [1998;](#page-15-15) Martin et al. [2004;](#page-14-17) Warren et al. [2008\)](#page-15-16). Nassauer et al. [\(2009](#page-14-18)) tested whether homeowners were more likely to prefer yards that conformed to broad cultural norms (e.g., a well-cut lawn) or yards that matched immediately neighboring lawns, and determined that the local neighborhood effect was much stronger than broad cultural preferences. Similarly, Peterson et al. [\(2012](#page-14-19)) determined through surveys that while most homeowners preferred a yard that contained 50% native plants, they

assumed that their neighbors preferred turf grass dominated yard designs, and their landscaping choices were most influenced by incorrect assumptions about neighbors' preferences. Hope et al. [\(2003](#page-13-4)) found that plant species diversity was correlated with socioeconomic variables, as they varied across a city. Wealthier neighborhoods tended to have greater species diversity than lower income neighborhoods, a pattern that they termed the "luxury effect." Complicating the relationship between socioeconomic status and diversity, however, is the legacy of past land-uses and the age of neighborhoods, which can interact with present conditions to influence relationships between neighborhood variables of interest (Luck et al. [2009](#page-13-14); Lowry et al. [2011\)](#page-13-15). In a study of neighborhoods in Baltimore, Maryland, tree canopy coverage increased with age of houses in neighborhoods (Grove et al. [2006](#page-12-14)). Martin et al. [\(2004](#page-14-17)) discovered the opposite pattern in Phoenix, Arizona, as vegetation diversity decreased with increasing time since neighborhood development. These contrasting findings may reflect differences in the way in which cities are built, and demonstrate that careful consideration of the spatial and temporal patterns of urban development may be just as important for understanding the structure of urban vegetation as environmental predictors such as soil quality, water availability, and habitat connectivity.

Within neighborhoods, variation in individual homeowner choices and management strategies can influence local plant diversity. Private gardens or backyards have been estimated to cover from 16 to 36% of total urban areas (Goddard et al. [2010\)](#page-12-4); thus, the role of variation in individual preferences for particular types of landscapes may play a significant role in determining city-wide patterns of species composition and diversity. The frequency with which homeowners undertake particular landscaping activities has been shown to have a significant relationship to characteristics of vegetative composition and diversity (Loram et al. [2011\)](#page-13-16). A recent study of people's preferences for particular plant traits and the composition of their garden flora showed that these preferences can drive significant variation in garden flora composition (Kendal et al. [2012](#page-13-17)). Thus, human preferences (e.g., for plants with evergreen leaves and large, colorful fruits) may be a strong selective force in urban environments, alongside changes in environmental variables and landscape connectivity (Williams et al. [2009\)](#page-15-7).

5.3.3 Heterogeneity in Urban Plant Communities in Space and Time

The majority of studies of spatial patterns of urban biodiversity have used an urban-rural gradient approach (McDonnell and Hahs [2008](#page-14-6)). The "urbanization" gradient is made up of a combination of many different environmental gradients, not all of which are changing at the same rate or in the same direction. Thus, using particular "urbanization" measures, such as percentage of impervious surfaces or population density, may obscure other environmental variables that are changing in contradictory manners. Even so, general patterns have emerged in the literature, including an increase in native plant species extirpation with urbanization (Williams et al. [2005\)](#page-15-17).

The intermediate disturbance hypothesis has been one of the primary models used to interpret patterns of urban plant diversity (Connell [1978](#page-12-15)). This model predicts that the highest levels of species coexistence in a system will occur at intermediate disturbance frequency, magnitude, or time since a disturbance. The theory has been applied to explore the coexistence of native and nonnative species along urban-rural gradients, or within the urban environment, between patches that vary in disturbance level (e.g., Porter et al. [2001;](#page-14-20) Mandryk and Wein [2006](#page-13-18); Catford et al. [2012\)](#page-12-16). The expectation is that species diversity will be maximized at intermediate locations, where both native and invasive species occur in the same communities, in relatively even proportions. These gradients of disturbance, however, may interact with patterns of urban land use and neighborhood characteristics, and obscure expected relationships (Porter et al. [2001\)](#page-14-20).

Another commonly used framework for understanding patterns of urban plant diversity is borrowed from island biogeography theory. Island biogeography is a quantitative predictive model of a dynamic equilibrium of local species richness set solely by island size and distance from the source pool of immigrants (MacArthur and Wilson [1963](#page-13-19)). Island biogeography's core theories have been applied to help understand how habitat fragmentation and alteration in urban areas may change patch-level and regional-level species diversity. For example, Honnay et al. [\(1999](#page-13-20)) found that smaller and more isolated forest patches in a suburban matrix harbored fewer plant species. A study of vacant lot plant diversity showed that older vacant lots had greater plant diversity, and that diversity levels seemed to approach equilibrium after 30 months (Crowe [1979\)](#page-12-17).

Metacommunity theory is a relatively recently developed framework that is beginning to be applied to patterns of urban biodiversity. A metacommunity is conceived as multiple local species assemblages structured by local environmental constraints and biological interactions and connected by dispersal between patches (Leibold et al. [2004](#page-13-21); Cottenie and De Meester [2004;](#page-12-18) Urban [2004;](#page-15-18) Chase [2005;](#page-12-19) Stevens [2006](#page-15-19)). Species interact and are assembled along local environmental gradients, but are connected via dispersal to a broader, common regional species pool. Metacommunity theory incorporates elements of other earlier frameworks, especially that of island biogeography. In urban ecosystems, human activities not only fundamentally alter environmental gradients and the strength and direction of interspecific interactions, but also the broader-scale movement and displacement of species, due to human management choices and land use patterns.

Fragmented landscapes reduce connectivity between ecological communities. A reduction in dispersal is generally thought to reduce regional-scale population persistence, and may also lead to a loss of genetic diversity as populations become isolated. In urban ecosystems, connectivity may be constrained by dispersal of organisms through corridors like parks, riparian zones, and median strips. The result of a loss of connectivity can be a reduction in local species diversity, or an increase locally in the relative abundance of species exhibiting greater dispersal ability, and which are less affected by reductions in habitat connectivity. However,

human actions may effectively enhance dispersal for particular species, and counteract expected losses in individual abundances or population diversity. This may occur directly via planting efforts, as in the context of landscaping, restoration, and gardening, or indirectly via the spread of nonnative species (e.g., as a contaminant in seed or soil mixes).

Variation in homeowner preferences for plant species composition is likely to contribute more to regional plant diversity than simply the number of species people harbor at a particular location. A survey of urban garden biodiversity patterns in Sheffield, UK demonstrated that although the local diversity of urban gardens did not vary significantly from the local diversity of areas termed "semi-natural" and "urban derelict" land, the regional diversity of all the urban gardens surveyed in the study was more than twice as high as that found in any other type of plot surveyed, including pasture and woodlands on either acidic or alkaline soils (Thompson et al. [2003\)](#page-15-20). Spatial heterogeneity in environmental conditions in urban environments, coupled with variation in human actions at multiple organization levels (e.g., residential, neighborhood, jurisdictional) underscores the need to consider compositional turnover, in addition to levels of local diversity, to understand patterns of plant biodiversity at the scale of an entire city, and the relative contribution to overall diversity that specific portions of the urban landscape provide. For example, to plan effective citywide conservation strategies it is important to understand whether privately owned land contributes more to overall regional diversity than publicly owned land, such as city-managed parks or streetscape plantings.

Plant community composition changes through time in urban ecosystems, but the rate and distribution of this change is mediated by human activity. Ecologists often rely on successional climax theory to conceive how species composition at a location changes through time. In general, fast-growing ruderal species with the ability to disperse more widely are expected to colonize newly opened habitat. These are replaced slowly by more slow-growing species that may be more efficient at gathering and using resources. In urban ecosystems, this traditional perspective may not apply broadly to explain the composition of differently-aged communities. The urban landscape is extensively disaggregated, with a high degree of heterogeneity in human influence on ecological organization. This spatial heterogeneity does not remain static, but changes over time.

Shifts in patch-level land use can reset the colonization process in three ways. First, in some cases all plants are removed and no attempt is made to establish a community (e.g., following demolition of a building structure, if land is left vacant as in the case of urban vacant lots or brownfields, Fig. [5.1](#page-10-0), left). The colonization process proceeds with species composition developing as a consequence of local habitat filters and the availability of colonists from the regional species pool. In such cases, one often observes dominance of a few species relative to nonurbanized environments, as well as high proportions of nonnative species.

Second, management or use of land with an already established plant community may simply stop. In this case the colonization process is not reset, and the initial species composition of the community initiates the trajectory of post-abandonment species assembly (Fig. [5.1,](#page-10-0) center, as in secondary-succession). Lack of human management may result in the decline of species that require care to persist in the

Fig. 5.1 Three scenarios illustrating the shifts in community composition in urban ecosystems. Each symbol represents a unique species or functional group. Sets of three boxes represent a metacommunity of three patches of similar initial type. The degree of shading reflects the magnitude in compositional similarity among habitat patches within each metacommunity. The *Bare Soil* category describes areas where vegetation was removed and sites are allowed to colonize naturally from the regional species pool. *Abandoned* areas are locations where humans once designed community composition via selective planting but then left unattended. This category could potentially consist of remnant habitat patches that have become surrounded by the urban matrix and no longer are connected to the original species pool, since supplanted by urban species. *Designed* areas, like Abandoned, initially comprise combinations of human selected species, but proceed along different assembly trajectories based on human behavior/ decision-making. Under the reasonable assumption that diversity of urban ruderal species ( *open symbols*) is lower than plant species chosen by humans ( *closed symbols*), and that the composition of each grouping are distinct, community assembly should proceed with different compositional outcomes that depend on the initial conditions and the role humans play in facilitating coexistence. When land is completely open to colonization (Bare Soil, *left*) it is colonized predominately by urban ruderals, with constrained shifts in composition in space and time. Alternatively, where humans formally maintained coexistence by selecting species (Abandoned, *center*), ruderal species replaced human-selected species prone to local extinction without human intervention. This leads to convergence in community composition. Designed communities ( *right*) may shift in one of three ways. Assemblages maintained by humans may not change at all through time. Community composition of human selected species may change over time as preferences shift for some species over others. Designed communities may cease to be maintained, and the disinvestment by humans leads to replacement with urban ruderals

urban landscapes, with replacement by the more ubiquitous urban plant species. While initial composition might vary, over time plant communities may converge in species or functional composition (e.g., Fukami et al. [2005\)](#page-12-20), or remain divergent or randomly assembled with respect to the regional species pool (e.g., Schleicher et al. [2011](#page-14-21)).

In the third case, community composition is selected based on particular landscape design goals (e.g., maintained gardens, landscaped parks, or restorations Fig. [5.1](#page-10-0), right). Of the three described, this scenario of human-influenced succession can create the greatest temporal and spatial variation in composition. Initial composition reflects a purposeful process that is constrained by human perception and valuation of space. Maintenance of composition through time does not parallel the traditional successional sequence. The level of maintenance (e.g., weeding or replacement of species as they senesce and superseding natural colonization-extinction patterns) and change through time may instead reflect the ability for individuals or organizations to make an economic investment in landscape composition (luxury effect as described in Hope et al. [\(2003](#page-13-4))).

Conclusion

As of yet, few studies have monitored long-term dynamics of urban communities or used a chronosequence approach (replacing space for time) to explore how urban communities change through time, while controlling for variation in initial starting composition, land use, disturbance regimes, and environmental variables. Overall, complex patterns of spatial and temporal heterogeneity in urban plant community composition are a product of multiple drivers, including human perception of what plant species are desirable, the direct and indirect effects of human presence on local environmental conditions and shifting land use practices. Future studies of urban vegetative communities should focus on explicitly addressing these different drivers, and exploring how they vary in intensity and direction across the urban landscape.

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