

# The process of natural succession in urban areas

Wayne C. Zipperer

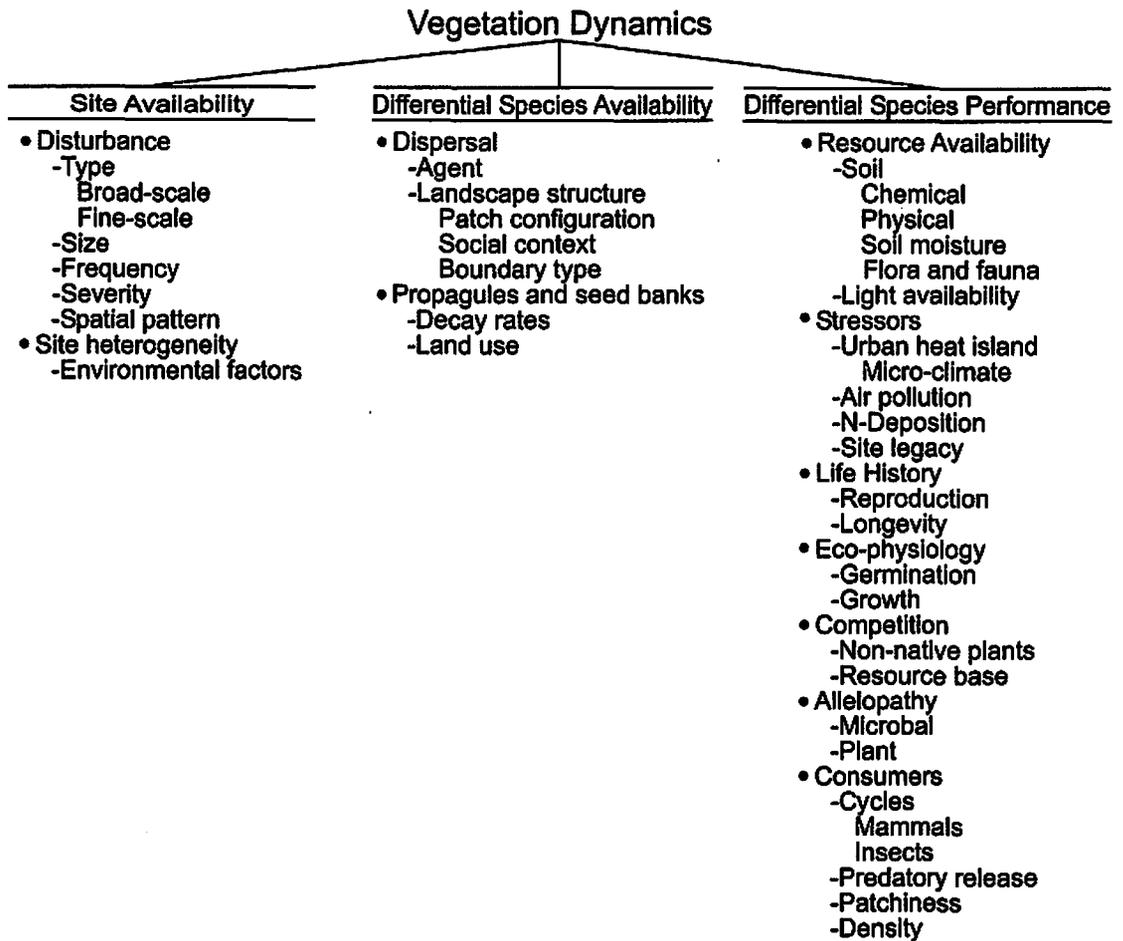
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## Introduction

Succession has been a fundamental concept in ecology. Its classical definition is the orderly change in vegetation at a site that is predictable and directional towards a climax state or end point (Clements 1916). A general assumption of succession is that early seres are governed by allogenic processes, environmental processes external to the site, and early seres facilitate later successional stages. As the community matures, autogenic processes, biotic interactions, become important in facilitating later-successional assemblages and the movement of the community towards an end point (Connell and Slatyer 1977). Field studies often showed trajectories were not always predictable, end points were not always achieved, and allogenic processes played an important role in community dynamics throughout successional development. To shift the focus of successional studies away from descriptive to mechanisms or interactions that contribute to successional change, Connell and Slatyer (1977) proposed three distinct mechanisms—facilitation, tolerance, and inhibition—at the community level. This shift enabled experimental approaches to studying succession, but it failed to capture the complexity of vegetation dynamics (Pickett *et al.* 1987a).

Clements (1916) lists five basic causes of succession: (1) a disturbance opening a site; (2) migration of propagules to the site; (3) establishment of species; (4) biotic interactions; and (5) modification of the site by organisms. Pickett *et al.* (1987a, 1987b) synthesized this list into a single-organized framework that captures vegetation dynamics at multiple scales. At the highest level of hierarchical organization, three general and universal conditions exist: (1) site availability; (2) differential species availability; and (3) differential species performance (Figure 16.1) (Pickett *et al.* 1987b). At the next lower or intermediate level, an individual mechanism or causation is defined for each condition as, for example, the availability of species depends on dispersal and propagule pools. This level in turn can be examined further for a particular process.

Most successional studies have been conducted in non-urban landscapes. Although these studies can provide a framework to study succession in an urban landscape, they do not capture the uniqueness of the urban matrix (see Rebele 1994). In this chapter, I will use the hierarchy of causes of vegetation dynamics—site availability, differential species availability, and differential species performance—to examine factors and mechanisms influencing succession in urban landscapes and overview some examples of successional studies in cities.



*Figure 16.1* Vegetation dynamics is illustrated as a hierarchy ranging from the most general phenomenon of community change to detailed interactions within a mechanism or causation. Adapted from Pickett *et al.* (1987b) and Pickett and Cadenasso (2005).

### Site availability

Site availability includes not only sites created by disturbances (broad scale) (Pickett and White 1985), but also the death of an individual and existing site conditions (fine scale) (Brand and Parker 1995). A disturbance is defined as “any discrete event in time that disrupts [landscape], ecosystem, community, or population structure and changes resources, substrate availability, or physical environment” (Pickett and White 1985). Natural disturbances that affect urban landscapes include wind and ice storms, fire, and flooding as well as herbivory (e.g. insect outbreaks), pathogens, and stress-induced mortality. A disturbance can be classified by its seasonality, distribution, frequency, magnitude, and severity (Pickett and White 1985) and, collectively, all of the disturbances affecting a landscape are called the disturbance regime.

The primary site disturbance in the urban landscape is land clearing for development. Site clearing can range from an area less than 0.25 hectare for a single structure, thus possibly leaving the adjacent vegetation relatively intact, to clearing the entire area for an entire subdivision (e.g. >50 ha). Site clearing can include not only removing existing vegetation cover but also removing soil and possibly altering drainage patterns (Effland and Pouyat 1997). Such extensive clearing can

create a new substrate as A and B horizons of the soil profile are removed. Successional processes on these sites would be defined as primary succession rather than secondary succession since this new substrate has not previously supported vegetation, does not contain a seed bank, and possibly has not accumulated organic matter. In general, primary succession is associated with glaciated and volcanic sites rather than urban sites. In the urban landscape, primary succession is associated with stone and brick walls, demolition sites, spoil heaps from industrial waste, and abandoned roads and sidewalks (Rebele 1992, 1994). Contrary to vegetation dynamics in adjacent rural areas where secondary succession dominates, both primary and secondary successional processes are important ecological processes in urban landscapes.

The disturbance regime changes as a landscape is urbanized. Some disturbances such as fires and flooding are suppressed because of their devastating effects on property and the potential for loss of life. For instance, fire suppression reduces the frequency and alters the intensity of fire events. A subsequent outcome is a shift away from fire-dependent species to more mesic species and new plant communities. In the Chicago Metropolitan area, fire suppression has changed the oak savannah from a community dominated by *Quercus* spp. and grasses to one containing *Acer saccharum* and exotic species (Kline 1997).

Similarly, humans introduce new disturbances. Sharpe *et al.* (1986) observed an increase in frequency of fire because of arson, trampling, dumping of yard and garden waste, and vandalism in urban woodlands in the Milwaukee metropolitan area. A study of reforested vacant lots in Syracuse, New York revealed that 80 percent of sites sampled were disturbed intensively and extensively by human activities such as vandalism, fire, trampling, and dumping (Zipperer 2002). Matlack (1993) called this human effect a sociological-edge effect because most human activities occurred within 82 m of the edge.

Even though these novel disturbances create new sites for colonization, they affect the germination and growth of species. For instance, trampling is a novel, small-scale, frequent disturbance which many native species have not evolved mechanisms to cope with. Without natural barriers such as high stones and down-woody debris to create micro-safe sites, trees did not regenerate in remnant forest in Helsinki, Finland because of trampling (Lehvävirta *et al.* 2004).

Management activities can also be considered a type of disturbance. The type, frequency, and intensity of management will significantly influence vegetation dynamics (Zipperer *et al.* 1997). For instance, if a vacant lot is regularly managed by mowing, its structure and composition would differ from a vacant lot that is left unmanaged (*sensu* Godefroid and Koedam 2007). Overall, site management activities, such as mowing, clearing, and weeding, inhibit or alter successional processes.

Brand and Parker (1995) recognized that seasonality, environmental heterogeneity within the site, and environmental factors of the site can influence germination and growth. Environmental factors particularly important to urban landscapes include urban heat island, atmospheric pollution (e.g. nitrogen deposition and ozone), altered soil properties (physical and chemical), soil moisture, and light availability (Rebele 1994; Pickett *et al.* 2001) (see species performance section for more detail).

Another aspect of site condition is its landscape structure and social context. Landscape structure refers to site location in an urban landscape with respect to adjacent land uses as well as site configuration (e.g. shape, size, and orientation). Both attributes have been shown to influence site composition (see Godefroid and Koedam 2003). Social context refers to the social attributes of the site and adjacent sites. A study of plant diversity in Phoenix, Arizona, a city in the Sonoran desert of the United States, showed that in addition to elevation, former land use, home owner income and housing age were significant site attributes influencing vegetation dynamics (Hope *et al.* 2006).

## Differential species availability

Differential species availability depends on the species' ability either to survive the disturbance, vegetative or in the seed bank, or disperse to the site (Pickett and Cadenasso 2005). In an urban landscape, species pool includes native and non-native species (Kühn *et al.* 2004). Rather than overview the quite extensive plant dispersal and seed bank literature (e.g. Leck *et al.* 1989; Poschlod *et al.* 2005), I will focus on three human-mediated dispersal (HMD) mechanisms—(1) vehicle, (2) horticultural stock, and (3) footwear—that augment natural dispersal in urban landscapes (Wichmann *et al.* 2009).

### Vehicles

The importance of vehicles as dispersal vectors has been recognized for some time (e.g. Ridley 1930), but it has been only recently that they have been intensively studied. In Sheffield, England, Hodkinson and Thompson (1997) collected mud in the fall and summer from wheel-wells of parked vehicles. They observed that small seeds were commonly found in the mud and their densities varied seasonally. The most frequent occurring species included *Plantago major* (29.2 percent), *Poa annua* (16.5 percent), *Poa trivialis* (10.5 percent), *Urtica dioica* (6.4 percent), and *Matricaria discoidea* (5.6 percent). To quantify deposition and the movement of seeds into and out of a city, von der Lippe and Kowarik (2007, 2008) initiated a series of studies using seed traps in traffic tunnels leading into and out of Berlin. The studies showed that egress traffic was transporting, to a greater extent, more non-native species into the peri-urban than ingress traffic was transporting native species into the city. Consequently, sites within the urban core would be colonized locally by non-native species, whereas peri-urban sites could be colonized by native and non-native species occurring locally as well as those non-native species being transported by cars.

### Horticultural stock

There are two aspects of horticultural stock that influence species availability—(1) the actual species being planted, and (2) contamination of the horticultural stock with non-native seeds or plants. Although a number of invasive, non-native species were introduced because of agricultural or forestry practices during the nineteenth and early twentieth centuries, horticultural or ornamental materials are becoming the primary sources for invasive species in the urban landscape (Reichard and White 2001). These introductions often expand the native range of the species and facilitate expansion of the species as new sites become locally available (Kowarik 2003). Without these introductions and secondary expansions, many of the invasive species would not have expanded their natural range as quickly as observed (Pyšek and Hulme 2005).

The contamination of plotted soil can be thought of as a subset of a much broader category of topsoil, which may contain seeds that have been removed from one site and transported to another (Hodkinson and Thompson 1997). By planting contaminated plots or augmenting existing soil with imported topsoil, new species can be added to a site where they otherwise may not have occurred.

### Footwear

Although footwear can be a dispersal agent for any habitat visited by humans, I have included it here because of the density of footwear in urban areas and the movement of people from

private to public lands and from urban to rural areas. Footwear serves as a secondary dispersal mechanism. Seeds, which are picked up by footwear, have the potential to be carried farther than if dispersed by natural means only. Wichmann *et al.* (2009) observed for two species of *Brassica* that the maximum distance of dispersal by wind was 250 m, whereas dispersal distances by footwear exceeded 5 km.

### *Urban landscape*

In the previous section, social context and landscape position were identified as important site factors. Similarly, the urban landscape, itself, affects species availability. For instance, the size of the city will determine the number of available native and non-native species. Larger cities will have more non-native species, whereas smaller communities and villages have a higher proportion of native species (Pyšek 1998). Similarly, Williams *et al.* (2009) report that the urban landscape serves as a filtering mechanism through habitat transformation, fragmentation, urban environmental conditions, and human preferences. These filters work synergistically to influence floristic composition. Habitat transformation and fragmentation remove or alter existing habitat patches, thus eliminating species or drastically reducing their density. The urban environment, as previously discussed and will be discussed in greater detail in the section, creates a unique environment to which many species have not adapted, thus they are not able to survive or compete. Human preference is a socio-economic filter that captures human preferences for specific phenotypic characteristics, thus many new species (i.e. non-native species) are introduced into the urban landscape that otherwise would not have occurred (Williams *et al.* 2009).

### **Differential species performance**

Once a species has colonized a site, its performance depends on its interactions with abiotic and biotic conditions (Pickett and Cadenasso 2005) (Figure 16.1). Unfortunately, auteological studies of native and non-native species in urban landscapes are lacking. Rather than focusing on how an individual species may perform within the urban matrix, I will overview those factors—soils, physical stressors, and consumers—that have unique attributes in the urban landscape and significantly affect species performance.

### *Soils*

Soil factors influencing species performance include higher soil temperature due to the urban heat island effect; lower soil moisture due to soil hydrophobicity; higher concentrations of heavy metals due to emissions; and greater nitrogen and calcium deposition also due to emissions (White and McDonnell 1988; McDonnell *et al.* 1997; Lovett *et al.* 2000). In addition, the biotic environment also has been altered. When compared to rural woodlands, urban woodlands had lower densities of soil micro-invertebrates and fungi (Pouyat *et al.* 1994) but a higher density of earthworms (Steinberg *et al.* 1997) (see also Chapter 15 this volume). Nitrogen studies of rural and urban woodland soils have indicated that soils in urban woodlands have a substantial amount of extractable soil nitrate and nitrify rapidly (Pouyat *et al.* 1996; Carreiro *et al.* 1999). Vallet *et al.* (2008) observed also that soil pH and nitrogen content were important indicators of species occurrence in remnant forest patches along urban-to-rural gradients in Angers and Rennes, France.

When overlaying the disturbance regime of a site, anthropogenic inputs and materials, environmental factors, and atmospheric deposition, a mosaic of soil patches occur across the

urban landscape that range from highly disturbed in industrial wastelands to relatively undisturbed conditions in remnant forest patches. A comparison of soil attributes across this matrix reveals significant differences for bulk density, pH, and concentrations of potassium, phosphorus, sodium and aluminum (Pouyat *et al.* 2007). Bulk density was the discerning variable between forest and other land uses, whereas soil pH differentiated residential land use from other non-forested land uses.

### *Physical stressors*

The primary physical stressors in the urban landscape are the urban-heat island, elevated carbon dioxide (CO<sub>2</sub>), and atmospheric pollution. It is important to note that these stressors do not act independently of each other but rather synergistically. Likewise, their effects can vary across urban landscape because of the spatial heterogeneity within that landscape.

The urban heat island is an important anthropogenic climate modification because of its effect on biological processes. It is the temperature differential between the rural and urban landscape (often the urban core) at dusk. This differential can be as great as 12°C depending on the size of the city and its morphology (Oke 1973 and Chapter 11 this volume). In general, larger cities have a greater temperature differential from adjacent rural landscape than smaller cities and towns. When one considers the potential additive effect of the projected increases in mean global temperatures by 1.7 to 4.9°C from global climate change with the urban-heat island effect, the additional heat loading on species will significantly affect ecosystem structure and function (Carreiro and Tripler 2005).

In addition to temperature, urban landscapes have elevated CO<sub>2</sub> concentrations because of fossil fuel consumption, a phenomenon called urban CO<sub>2</sub> dome (Idso *et al.* 2002). In Phoenix, Arizona, Idso *et al.* (2002) observed that the urban core and surrounding suburban landscape had a 67 percent and a 33 percent increase, respectively, in CO<sub>2</sub> concentration over the value (370 ppmV) observed for the rural landscape. From a species performance perspective, the increase in CO<sub>2</sub> coupled with the increase in temperature from the urban heat island effect has a significant effect on species productivity. Ziska *et al.* (2004) observed an increase in plant height, biomass and seedling number for *Chenopodium album*, a native forb species in the United States, in urban sites when compared to rural sites. Similar enhanced-growth patterns have been observed for non-native forb species, and this urban effect may be one of the possible factors leading to their invasiveness (Ziska 2003).

This increase in productivity is further augmented by nitrogen deposition, wet and dry in the urban landscape. Lovett *et al.* (2000) observed that N inputs for urban-remnant forests in New York City were 17 times greater than found in rural remnant forests. Analysis of throughfall over the course of the growing season for remnant forest in Louisville, Kentucky showed that N deposition was 33 percent greater than rural remnant forest (Carreiro and Tripler 2005). Nitrophilous species have been identified as a primary functional group occupying early successional sites (Godefroid 2001).

Urban areas also have high concentrations of many gaseous, particulate, and photochemical pollutants including NO<sub>x</sub>, HNO<sub>3</sub>, SO<sub>x</sub>, H<sub>2</sub>SO<sub>4</sub>, O<sub>3</sub> and volatile organic compounds (Lovett *et al.* 2000; Gregg *et al.* 2003). O<sub>3</sub> may be detrimental to plant growth (Krupa *et al.* 1998); however, the effect of O<sub>3</sub> on growth may be offset by warmer temperatures from the urban heat island effect and higher concentrations of nitrogen and CO<sub>2</sub> (Ziska 2003). The synergetic effect of these physical stressors on a species performance needs to be a focus of future research if we are to gain a better understanding of vegetation dynamics for different site conditions.

## Herbivory

Published studies examining the effect of wildlife populations on regeneration on urban sites are limited. Parker and Nilon (2008) have observed squirrel densities in urban areas exceeding 33 individuals per hectare. At these high densities, intensive seed predation by squirrels can eliminate opportunities for regeneration. In fact, high squirrel densities have been attributed to the poor regeneration of oaks in urban woodlands in New York City (Sisinni and Emmerich 1995).

Likewise, the number of species and density of insectivores may be reduced in urban landscapes because of habitat fragmentation and loss. For instance, Christie and Hochuli (2005) observed a decline in insectivorous birds and an increase in insect herbivory in small remnant forest patches when compared to edge sites and large forest remnant patches. Similarly, a species, whose vigor is already reduced because of the urban environment, may be more susceptible to insect attacks. In Gainesville, Florida, southern pine beetle (*Dendroctonus frontalis*), a native insect, attacked loblolly pines weakened by an extended drought ([www.interfacesouth.org/products/pdf/case\\_studies1.pdf](http://www.interfacesouth.org/products/pdf/case_studies1.pdf)). The outbreak moved from the city into the surrounding areas. The mechanisms driving herbivory (e.g. predator release) in the urban landscape are complex and the diversity of responses by plant species to the synergistic effect of the urban environment and herbivory needs to be studied in more detail (Christie and Hochuli 2005).

## Plant traits

In general, the urban environment tends to select for specific plant traits. For waste lands or vacant lots, these traits include a tolerance for nitrogenous conditions; soils that are dry, rocky, alkaline, and fertile; shade intolerance, and small seeds (Pyšek *et al.* 1995, 2004; Godefroid and Koedam 2007; Thompson and McCarthy 2008). Although these traits may provide insights into what species may be present, they do not provide insights into how a species will respond to the urban environment. More long-term monitoring of plant communities across a range of habitats need to be conducted for urban landscapes to successfully identify mechanisms and species responses that influence vegetation dynamics.

## Succession in the urban landscape

A limited number of successional studies have focused on the urban landscape and these studies have principally examined the vacant/wasteland lots within European cities (see Rebele 1992; Pyšek *et al.* 2004; Rebele 2008). In general, successional pathways on vacant lots followed those observed for abandoned fallow lands in rural landscapes. Prach and Pyšek (2001) observed after 12 years native woody species dominating ruderal-urban sites in the Czech Republic. On nutrient poor sites, *Populus tremula* dominated, whereas on moderately rich nutrients sites *Sambucus nigra* and *Salix caprea* dominated. Similarly, site conditions rather than seasonality were observed to be important conditions for different successional pathways (Rebele 2008). In Berlin-Dahlem, Germany, Rebele (1992) tested three substrates—commercial topsoil, ruderal (landfill) soil, and sand—to assess vegetation dynamics over a five year period. On the topsoil, annuals gave way to biennials and perennials. On the ruderal soil, *Solidago canadensis* dominated the site after the first year. On sandy soils, *Betula pendula* and *Populus nigra* colonized the plot after five years. By comparison, sites that were continuously disturbed tended to remain being dominated by ruderal species (Pyšek *et al.* 2004).

Successional studies in rural landscapes, however, may not always be applicable to vegetation dynamics in urban landscapes. For instance, a comparative study of native grasslands in southeastern

Australia and South Africa showed that vegetation dynamics in remnant patches of grasslands along roads and railways in rural landscapes differed from remnant grasslands in urban landscapes (Cilliers *et al.* 2008). In rural landscapes, non-native species occurrence was principally an edge effect, whereas in the urban landscape occurrence resulted from both edge effect and gap-phase dynamics in the interior portion of the grasslands. Predicting vegetation dynamics based on the rural grassland remnants would not have identified the patterns of occurrence in the interior of grassland in urban landscapes.

For remnant forest patches, vegetation dynamics have been documented by comparing current vegetation with historical records rather than following permanent plots through time (e.g. Rudnický and McDonnell 1989; Godefroid 2001). Rudnický and McDonnell (1989) reported for a virgin forest stand in the Bronx Botanical Garden, New York, that composition shifted from slow growing *Quercus* spp. to fast growing *Betula* and *Prunus* spp. and structure shifted from larger diameter to smaller diameter trees. These shifts were attributed to increases in seed predation, loss of regeneration from trampling by visitors, and changes in the structure of the forest floor.

## Conclusion

Vegetation dynamics in urban landscapes differ from those in rural landscapes. Both primary and secondary successional processes are important processes in urban landscapes as opposed to adjacent rural landscapes. Likewise, the availability of species shift from rural to urban. In urban landscapes non-native species play a significant role in vegetation dynamics especially in vacant/wasteland sites and there is a decline in native species richness (Kühn *et al.* 2004; McKinney 2006). Finally, the urban environment and land transformation create unique environmental conditions that species must adapt to in order to survive and mature.

The loss of native species and the increase in non-native species as a landscape becomes more urbanized have led to the concept of biotic homogenization—the same “urban-adaptable” species becoming increasingly widespread and locally abundant in urban areas (McKinney 2006). Likewise, a comparison of species similarity across plant communities in urban and rural landscapes showed that urban communities were more similar in composition than the rural communities (McKinney 2006). Even though species composition is becoming more homogenous, the combination of native and non-native species creates novel communities that have not been documented before (Hobbs *et al.* 2006). These emergent communities create new niches and the opportunity for evolutionary development. How these combinations influence vegetation dynamics as well as ecosystem structure and function have yet to be determined.

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*Edited by Ian Douglas, David Goode,  
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