5

Nonnative Invasive Plants: Maintaining Biotic and Socioeconomic Integrity along the Urban–Rural–Natural Area Gradient

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Abstract

In this chapter, we evaluate nonnative invasive plant species of the urban–rural–natural area gradient in order to reduce negative impacts of invasive plants on native species and ecosystems. This evaluation includes addressing (i) the concept of urban areas as the primary source of invasive plant species and characteristics of urban nonnative plants, including their documented impacts on associated native plants and biodiversity along the urban–rural–natural area gradient, (ii) the most vulnerable land uses and potential barriers to invasion along the urban–rural–natural area gradient, and (iii) possible mitigation of invasions and urbanization using restoration or rehabilitation. Finally, we introduce three possible solutions: (i) use of spatially explicit land use planning and management that places invasion barriers between the urban core and the rural–natural area interfaces, (ii) increasing native and exotic species interactions within the urban core and rural–natural area interface, thereby increasing the number of pathogen and enemy interactions or the loss of novel weapons, and (iii) changing the horticultural trade and people's behavior, such that propagule pressure is kept below threshold levels required by growing invasive plant populations.

The rate of urbanization in the United States is increasing (Alig et al., 2004); more than 8% of U.S. land may be classified as urban by the year 2050 (Nowak and Walton, 2005). Urbanization rates are on the rise globally as well (United Nations Population Division, 2006; Grimm et al., 2008). Among other ecological impacts, the expansion of urban areas is potentially increasing the rate of plant invasions and the extent of their corresponding effects on native plant species (Kareiva et al., 2007; McDonald et al., 2008; Williams et al., 2009). The goal of this chapter is to evaluate the reduction and containment of nonnative invasive plant species along the urban–rural–natural area continuum to prevent or alleviate their negative impacts on native species. Such negative impacts include local and global homogenization of plant species (McKinney, 2006), native species and community compositional changes, the displacement of native plant populations (Moffatt et al., 2004), and cascading effects on associated fauna (Callaway and Maron, 2006; Kagata and Ohgushi, 2006). We have organized this chapter into three sections: (i) urban areas as biodiversity hot spots and the primary source of nonnative invasive plant species, (ii) the urban–rural–natural area gradient in which both sites vulnerable to invasion and potential barriers to invasion

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may exist, and (iii) restoration, rehabilitation, or mitigation of patches with nonnative invasive plant species along the gradient and when it may be best to take each approach—or to do nothing.

Characterized by disturbed and open habitats and human-mediated introductions of horticultural plants, urban areas are epicenters of nonnative invasive plant species recruitment (Alston and Richardson, 2006; Smith et al., 2006). Indeed, nonnative plants have enhanced the ability of urban areas to provide ecosystem services for their human inhabitants. In many cases these nonnative introductions have resulted in biodiversity values higher for urban and suburban areas than for the native plant communities these land uses have replaced. However, there is some evidence that these urban-introduced nonnative plants are spreading within and beyond the urban–rural interface into rural and natural areas (Guo et al., 2006; Duguay et al., 2007; McDonald et al., 2008) and have become the target for natural area restoration efforts. Urban landscapes are a mosaic of remnant, managed, or abandoned patches (e.g., vacant lots) and the urban–rural–natural area continuum is a gradient of these patch types. These patch types vary in their vulnerability to invasion by nonnative plants, with the least vulnerable patches serving as potential barriers to invasion (Theoharides and Dukes, 2007). A lack of herbivores or predators promotes some plant invasions (Mitchell et al., 2006), but other biotic interactions, such as a dependency on mutualisms (Marler et al., 1999), may put some nonnative plants at a disadvantage and consequently act as a barrier to invasion. Efforts to restore or rehabilitate nonnative invasive plant species–infested sites may take place all along the urban–rural–natural area gradient. However, some patches along the gradient or within the urban mosaic are composed of novel assemblages of species that include nonnative invasive plant species. These nonnative invasive plant species may provide similar functions as the previous community before invasion (Zipperer, 2002; Hejda and Pyšek, 2006) or novel functions on which a new species assemblage is now dependent (Lugo, 2009). Attempting to restore historic conditions may be unreasonable in many cases, and accepting some novel ecosystems in urban areas and the urban–rural interface may enable these areas to maintain biotic and socioeconomic integrity.

We end the chapter by evaluating three possible management solutions to help reduce urbanization-mediated invasive plant impacts: (i) employing spatially explicit land use planning and management that places invasion barriers between the urban areas and natural systems; (ii) increasing native and nonnative species interactions within urban areas and the urban–rural interface, thereby increasing the number of herbivore and pathogen interactions with nonnative invasive plant species; and (iii) influencing the horticultural trade and people's behavior such that propagule pressure is kept below threshold levels required by spreading invasive plant populations.

Urban Areas as Plant Biodiversity Hot Spots or Epicenters of Nonnative Invasive Plant Species Introductions

Evidence of Urbanization Impacts on Native Plants: Homogenization and Plant Species Extinctions

Wilcove et al. (1998) estimated that 57% of the threatened or endangered plants in the United States are imperiled by alien plants. Gurevitch and Padilla (2004) reanalyzed the Wilcove et al. (1998) paper and concluded that only 4% of the imperiled plants were affected by invasive plants alone (excluding, e.g., habitat loss, alien herbivory). Levine et al. (2003) found 30 studies in which the impacts of invasive plants on native plants were examined, but also noted that 90% of these studies were solely observational comparisons between invaded and noninvaded locations, in which separating the effects of the invasive plant from other confounding effects, such as habitat loss, fragmentation, disturbance, and site history (e.g., urbanization), was not possible. Thus, while some plant invasions may cause the demise of some native plant species, it is very difficult to separate the invasion from other factors, including those associated with urbanization. We do not attempt to separate the factors affecting plant invasions from urbanization in this chapter, but instead provide support for the assumption that where there is urbanization, there are also likely to be plant invasions.

Theoretically, homogenization occurs as regionally distinct native communities are replaced by locally expanding, cosmopolitan, nonnative communities, essentially creating a "New Pangaea"—in other words, there are no barriers to expansion (McKinney and Lockwood, 1999; Collins et al., 2002; Olden and Rooney, 2006). There is mounting evidence of plant species homogenization and urbanization being one of the causes. Urbanization and its associated anthropogenic activities (e.g., housing development and road building) and consequences (e.g., habitat loss and fragmentation) have a tendency to overcome biogeographical barriers to dispersal (La Sorte et al., 2007), increasing the chances of homogenization. For instance, Schwartz et al. (2006) showed that California counties with the highest percentage increase in urbanization had very similar nonnative plant species compositions, but very different rare native plant species compositions. They also showed that California counties with higher human population densities had more extirpations of rare plants, as well as more nonnative invasive plants. Olden et al. (2006) found that plants in North America (including Mexico) had the highest level (22%) of homogenization, in contrast with fishes (14%), reptiles and amphibians (12%), mammals (9%), and birds (8%). The homogenization of plants was strongest in the northeastern states of the United States (Olden et al., 2006).

Homogenization does not necessarily equate to low diversity (in which species dominance is part of the equation), which suggests there are instances where homogenization can occur with few plant species extinctions and an increase in plant species richness. Rosenzweig (2001) and Vermeij (2005) argued that homogenization might occur in the short term, but that divergence and speciation will counteract homogenization unless all physical geographic barriers are removed and all species isolation is prevented. Furthermore, the loss of species within intratrophic levels is rare, and competition between native and nonnative plants is not likely to result in extinctions (Davis, 2003).

Homogenization has not occurred in all urban areas. For example, Kühn and Klotz (2006) showed that the more urbanized cells in Germany were more similar in native species composition than nonnative species (post-1500 CE species only) composition compared to the more rural cells. Remnants of native habitats within the urban areas were given as the possible explanation for maintaining similar native species populations. Different nonnative plant species invade different urban areas (Kühn and Klotz, 2006), decreasing the likelihood of global homogenization. Similarly, Celesti-Grapow and Blasi (1998) compared the species composition of five Italian cities and found that the species composition of the Mediterranean cities (e.g., Rome) reflected the vegetation of the surrounding landscapes, was rich in native species, and did not share the same nonnative species composition as the other Italian cities. They attributed this finding to the Mediterranean climate, in which the urban heat island effect is minimized. They also suggested that existing archaeological sites and ruins of the Mediterranean cities served as native species refugia within the urban core and also increased connectivity with other patches dominated by native species (Celesti-Grapow and Blasi, 1998; Celesti-Grapow et al., 2006).

Thus, while the general result of urbanization and homogenization is an increase in the nonnative invasive plant/native plant species ratio (NNIPS/NS) (McKinney, 2006), this ratio depends on the stage of invasion of a sampled site and the number, size, shape, composition, and degree of connectivity of any existing patches of native species (Kumar et al., 2006). Sites in the early stages of establishment and invasion will tend to differentiate themselves with relatively rare nonnative plants (NNIPS/NS < 1), while sites at later stages of invasion are more likely to have NNIPS/NS > 1 (McKinney, 2004). Plants in early stages of invasion are more likely to be neophytes (introduced post-1500 CE) as opposed to archaeophytes (introduced pre-1500 CE) (Kühn and Klotz, 2006). Plants from greater distances (e.g., outside a country's borders vs. within a country) are also more likely to be in the early stages of invasion or new nonnative invasive plant species (McKinney, 2005).

While homogenization may not equate to increased rates of extinction, we are currently experiencing the sixth major extinction event in history. An estimated 5050 plants species have gone extinct since 1700 (Jablonski, 1986; Given, 1990). Each of the past five mass extinctions eliminated more than 50% of the existing species. Current trends suggest that this most recent mass extinction is also showing more than 50% of species in most taxa in decline (McKinney and Lockwood, 1999). Lavergne et al. (2005) concluded that between 1886 and 2001, rare plant species in the Mediterranean region were more likely to go extinct if they were located in zones where human population density, cultivation, or livestock density had increased the most. In the Swiss lowlands, rare plant species are more likely to go extinct than common plant species, and rare plant species in wetlands and disturbed sites were more likely to go extinct than rare plant species in forests (Stehlik et al., 2007).

In a recent review of plant species extinctions and urban areas, Hahs et al. (2009) suggested that urban areas could be organized into three types: Type 1, in which most transformation from native vegetation occurred before 1600 CE; Type 2, in which transformation of native vegetation occurred after 1600 CE with intensive agricultural transformation before or in association with city establishment; and Type 3, in which transformation occurred late and urban expansion occurred in relatively intact native plant communities and large areas of native plant communities were still present. Type 1 and 2 urban areas experience the highest levels of plant species extinctions, but Type 3 urban areas may be carrying an extinction debt that will be evident with time (Hahs et al., 2009). Celesti-Grapow and Blasi's (1998) study on Italian Mediterranean cities and Kühn and Klotz's (2006) study on urban areas in Germany may be examples of Type 3 urban areas, whereas the urban areas studied by Schwartz et al. (2006) and Olden et al. (2006), located in North America, may be examples of Type 2 urban areas.

Urbanization may be an important cause of plant extinctions, but extinction risk in plants could be associated more with young and fast-evolving plant lineages than with anthropogenic effects, such as urbanization (Davies et al., 2011). In areas with increasing plant speciation, there are more plant extinctions. This observation may suggest that managing for plant extinctions by controlling urbanization may not be as effective as it would be for other taxa, such as vertebrates, at least not in the species-rich Cape of South Africa, where the research of Davies et al. (2011) research took place. Schwartz and Simberloff (2001) found that North American plant groupings with more species had disproportionally more rare species than did plant groupings with few species. However, Pilgrim et al. (2004) reported that rare species in the United Kingdom were more often associated with species-poor habitats than with any particular plant taxonomic grouping. Nonetheless, it is possible that the strong association between urban areas and plant extinctions could be due to, in part, higher plant speciation rates in urban areas (Davies et al., 2011).

There may also be patterns of species extinction based on plant characteristics. For instance, Williams et al. (2005) found that species with wind- and ant-dispersed seed in western Victoria, Australia, were more likely to go extinct in urban areas than in rural and natural areas because of the degree of landscape fragmentation associated with urban areas. Williams et al. (2005) also concluded that common and rare plant species were about equally likely to go extinct in urban areas, whereas rare species were more susceptible to extinction in suburban (peri-urban) and rural areas. If this pattern holds true, managing only for rare plant species while ignoring equally threatened common plants in urban areas could result in the loss of additional functionally important dominant plant species.

Species richness and extinction of species may not be as important to an ecosystem as species composition, relative species dominance, and the functional make-up of the ecosystem. For example, *Cortaderia jubata* (Lemoine) Stapf (perennial nonnative tussock grass) invasions in coastal plant communities of California and Oregon have resulted in such a reduction in relative abundance of native shrub species that what was once a shrubland has now become primarily a perennial grassland.[1] Moreover, a significant loss of arthropods dependent on the native shrubs has also occurred (Lambrinos, 2000). In contrast, Hejda and Pyšek (2006) found that *Impatiens glandulifera* Royle (Himalayan impatiens), which is a nitrophilous plant invading riparian habitats in the Czech Republic, takes over the role of other dominant native nitrophiles, such as *Urtica dioica* L. (stinging nettle) and *Chenopodium album* L. (lambs quarters), but does not displace these species completely. Invasion by Himalayan impatiens did not cause observable changes in functioning of the plant community. More importantly, certain relatively inhospitable urban patches may be colonized only by nonnative invasive plant species that are adapted to less than optimal growing conditions (e.g., infertile and compacted soils). These particular nonnative invasive plant species may in turn serve important green-space ecosystem services by providing shade, sequestering carbon and pollutants, and serving as a food source for pollinators, herbivores, and pathogens.

Urban Areas and Urban–Rural Interface Definitions

Urban regions may be defined (though definitions vary by country) as areas with a human population density of 100 to 500 people km^{-2} (Niemelä, 1999; U.S. Bureau of the Census, 2011b), and areas that have a built-up core dominated by industrial, transportation, commercial, communication, and utility components, as well as residential areas (Weng, 2007). For our purposes, it is most useful to think of urban, rural, and natural areas not as separate entities, but rather as a gradient or interface of human influence, with the urban areas manifesting the most human influence (Radeloff et al., 2005; Theobald and Romme, 2007; Weng, 2007). This gradient often includes the urban and suburban core, surrounded by

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[1] Nomenclature follows the Integrated Taxonomic Information System (http://www.itis.gov, accessed June 2011).

exburbia and exurban (sometimes referred to as peri-urban) remnants or pockets of urban development, which in turn are embedded in the rural areas, surrounded by the natural areas or a hinterland matrix. Rural areas are primarily agricultural land. As a comparison, urban areas may be defined as having 10 to 25 people ha^{-1}, while rural areas have 0.025 to 0.3 people ha^{-1}. The suburban and exurban areas, thus, have between 0.3 and 10 people ha^{-1} (Theobald, 2004; Fig. 5–1). Others have combined the suburban, exurban, and rural components into the wildland–urban interface and consider this interface where houses and natural areas coincide (Stewart et al., 2007). They further divide the wildland–urban interface into the intermix, in which at least 50% of the area is naturally vegetated, and the interface, in which less than 50% of the area is naturally vegetated but still within 2.4 km of a contiguous and large natural area. With increasing urbanization and urban sprawl in the United States (i.e., the deconcentration of housing out of urban areas), the extent of the wildland–urban interface intermix (82%) is increasing compared to the wildland–urban interface interface (18%; Hammer et al., 2009). Every component of this complex and dynamic gradient is an ecosystem with shared structure (e.g., trophic levels and species interactions) and processes (e.g., nutrients, water, and light) (Rebele, 1994; Bolund and Hunhammar, 1999) and with similar concerns about sustainability of economic growth and biotic integrity (Wu, 2008). More importantly, as the word "gradient" implies, the urban–wildland interface will reflect a gradation of shared site and species characteristics of urban, rural, and natural areas. The focus of this chapter is on how to decrease the impact of urban encroachment on rural and natural areas along the gradient.

Urban Area Uniqueness

Despite potential similarities and shared components, urban areas are quite different from rural and natural areas. The higher degree of human influence in urban areas creates a variety of different habitats, some of which may not occur elsewhere. Indeed, landscape complexity within urban areas tends to increase with time as the population of the urban area grows and the number of smaller and different patches increases (Ellis et al., 2006). These patches or habitats may support a high level of both α and β species diversity (Niemelä, 1999; Pickett et al., 2008) compared with surrounding rural and natural areas. These patches include (i) industrial and commercial areas, (ii) residential areas, (iii) abandoned lots that may be without vegetation or may be converting back to vegetation, (iv) roads and other corridors that may or may not be tree-lined, (v) gardens, (vi) parks, (vii) emergent forests (afforested) (Zipperer, 2010), and (viii) remnant forests. More importantly, the high richness and diversity associated with urban areas are not due just to increases in nonnative species; in some cases less common or even rare native species are found within an urban area (Wania et al., 2006; Pickett et al., 2008). As discussed previously, however, urban areas tend to have a higher proportion of new nonnative plants or neophytes compared to rural and natural areas (Wania et al., 2006). There may also be a luxury effect, in which wealthier neighborhoods within urban areas have greater species richness, especially in terms of perennial nonnative species (Hope et al., 2003). Consequently, the habitats in urban areas are often distinct patches separated from each other by a matrix of the built-up core. The pattern of habitat patches and dynamics of these patches are determined by both ecological and socioeconomic factors. Ecologically, these patches may function as islands, suggesting that the theories of island biogeography (Long et al., 2009), metapopulation (Hanski and Ovaskainen, 2003), and patch dynamics (Zipperer et al., 2000) typically used in nonurban ecosystems may also apply to urban systems. On the other hand, urban planning is influenced by historic infrastructure and the availability of current wealth to alter such infrastructure (Polasky et al., 2011). Individuals' behavior in terms of choice in landscaping, living locations, and desired quality of life may also play a significant role in the pattern formation of habitat patches in the urban core, as well as the wildland–urban interface interface (Alvey, 2006).

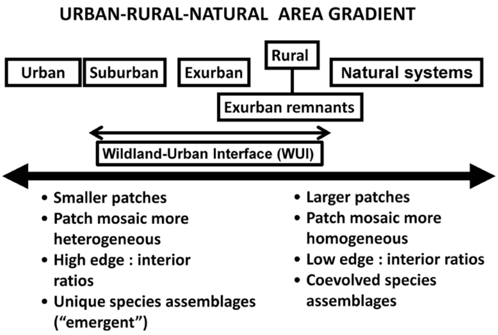

Fig. 5–1. The six main components of the urban–rural–natural area gradient and their associated characteristics. Modified from Carreiro et al. (2009).

The physical environment of urban areas also contributes to their uniqueness. Cities, with a larger percentage of paved surfaces, often create heat islands, with night temperatures differing from surrounding rural areas by as much as 10°C. Precipitation may be higher in urban areas (and downwind of cities) than in surrounding areas because of meteorological effects and higher levels of particulates in the atmosphere (Oke, 1995; Botkin and Beveridge, 1997; Pickett et al., 2001), but this pattern is not consistent (Lovett et al., 2000; Ziska et al., 2004). Large amounts of impervious surfaces also lead to increased stormwater runoff, which may contain high levels of nutrients or toxins (Leishman and Thomson, 2005; Gill et al., 2007) as well as nonnative invasive plant species seeds. Deposition of inorganic nitrogen throughfall has been found to be higher in urban areas than in suburban and rural areas (Lovett et al., 2000). Urban areas often have higher levels of air pollutants and soil heavy metals compared to rural and natural areas (Pouyat and McDonnell, 1991; Pickett et al., 2001; Nowak, 2010). The high heat loading associated with urban areas may play a role in shallower leaf litter depths associated in urban forest remnants compared with rural and natural area forests (Kostel-Hughes et al., 1998a). Higher earthworm densities (especially nonnative earthworms in glaciated soils) in urban areas compared to nearby rural areas may also play a role in leaf litter depths in urban areas (Steinberg et al., 1997; Pouyat et al., 1997; McDonnell et al., 1997). Shallow litter depths have been correlated with increased likelihood of establishment of nonnative invasive plant species (Bartuszevige et al., 2007; Marshall and Buckley, 2008). The fragmented landscape of urban areas as well as atmospheric deposition of nitrogen and pollutants may explain the lower macrofungal species diversity associated with urban forest trees compared to trees of rural and natural areas. For instance, the long-term stability of ectomycorrizal fungi on oak (*Quercus* spp.) roots may be dependent on the fungal species' ability to colonize other forest patches (Carreiro, 2005). Higher carbon dioxide concentrations, higher soil temperatures, increased irrigation, and higher inorganic N deposition in urban areas compared to rural areas may lead to higher plant productivity in urban areas than in rural areas (Ziska et al., 2004).

Integrating complex social structures and processes with ecological principles is required to truly understand urban ecosystems (Pickett et al., 1997) and devise ways of ameliorating any negative influences on surrounding areas, including the spread of nonnative invasive plant species into rural and natural areas. Pickett et al. (2001) suggested that the best approach to integrating the social and ecological systems within urban areas is to focus on social differentiation and hierarchies, or define who gets what resources, when, how and why. Theoretically, this information can be incorporated into a patch dynamics framework much like the ecological characteristics of an urban area. Studies accomplishing this integration are few, however. Martin et al. (2004) showed a significant correlation between socioeconomic status (i.e., higher incomes and better education) and higher vegetation richness and cover. Hope et al. (2003) showed a significant correlation between socioeconomic status (income) and increased plant diversity. Grove et al. (2006b) concluded that lifestyle behavior and housing age were more reliable variables than income or education. Lifestyle behavior was determined using a factor analysis of several variables including social rank (income and education), household age and size, mobility (length of residency), ethnicity, housing density, and housing type (owner or renter). They suggested that this knowledge could lead to more practical management approaches involving marketing strategies for greener neighborhoods; strategies would build on particular social groups' desire for social status and group identity. These linkages between social factors and plant species are not too surprising because humans often directly control plant richness and abundance in terms of what they choose to plant, whereas they may not have as much control over other functional groups (i.e., herbivores, predators, and parasites; Grimm et al., 2008).

Ten to twenty years may elapse between human socioeconomic factors (e.g., social stratification) and changes in urban plant abundance or composition (Martin et al., 2004; Pickett et al., 2008; Luck et al., 2009). This lag time effect may be due to different rates of social change (e.g., landscaping trends, housing density) and ecological change (e.g., growth and survival of those plant species). It may also be caused by the fact that it takes time for particular horticultural plants to gain popularity, but as they gain popularity and become common fixtures on many properties (both commercial and residential), propagule availability increases and spread is more likely. For species that take time to become commercially popular, the lag time effect may provide the opportunity to mitigate potential effects of invasive plants. More research is needed to determine densities of plants needed to reach spread thresholds.

The environmental conditions and the presence of human-preferred horticultural plants that are both associated with urban areas could lead to differential selection of native plants and nonnative invasive plant species within urban areas (Williams et al., 2009), resulting in novel species compositions and interactions. One result could be the formation of emergent ecosystems with novel species and social assemblages that have no analogs in rural or natural environments (Hobbs et al., 2006). If such emergent properties result in a lack of coevolution with native species within the urban area, interactions with native species of rural and natural areas may be less likely or less predictable, limiting our ability to influence the potential impact urban plant species may have in surrounding areas to which they may spread. Moreover, it is important to distinguish novel functioning urban ecosystems from novel "ecological traps," in which the occurrence of some plants depends on a constant flux from outside systems; that is they are not self-sustaining, reproducing populations. Rare native species in urban areas that are dependent on a flux of propagules from outside the urban area may be more susceptible to such ecological traps, especially if the urban area has high or increasing rates of disturbance (Kowarik, 2011) (Box 5–1).

Box 5–1. Urban Areas of Developing Countries

The relationships associated with urban areas described previously pertain mainly to urban areas of developed countries and not developing countries. The per capita resources in developing countries are many times lower than in developed countries, and growth is still concentrated around the urban core rather than surrounding suburban neighborhoods (Pauchard et al., 2006). An increasingly disproportionate number of low- to middle-income people live in urban areas in developing countries, and this disparity in urban vs. nonurban populations continues to widen (Cohen, 2004). Thus, urban areas of developing countries may be more homogeneous than urban areas of developed countries because of less income differentiation, but they still experience the loss of native habitat as the urban built-up core expands. However, some cities in developing countries, such as Brazil and Thailand, do have isolated forest fragments that allow some native species to persist (Turner and Corlett, 1996). By 2030 most of the residents of developing countries in Asia and Africa, like Latin America now, will be located in urban areas (Cohen, 2006; Montgomery, 2008). The poor are urbanizing at a faster rate than the rest of the population in developing countries (Ravallion et al., 2007). Consequently, urban areas in developing countries may be less likely to have as many remnants of native ecosystems over time, and are also likely to import relatively fewer new horticultural, potentially invasive plants than more affluent urban areas. The end result could be urban areas with relatively low plant species biodiversity that may serve as sinks for already existing invasive plants, but that may not yet serve as a source of invasive plants.

Plant Species Composition in Urban Areas

While urban areas are unique, in part, because they contain both native and nonnative plants, not all nonnative plants become invasive. Instead, many follow the "tens rule," which states that 1 in 10 imported nonnative species will become introduced (escape from planted location into the natural areas), 1 in 10 introduced nonnative species will become established (form self-sustaining populations), and 1 in 10 of established species will become invasive or pests (manifesting a potential negative economic impact on society). While angiosperm, Pinaceae species, and pasture species appear to follow the tens rule, edible crop species do not because they fail to become established even though they are frequently introduced into natural environments (Williamson and Fitter, 1996).

Several studies document nonnative plant occurrence in urban areas. For example, Burton et al. (2005) documented that the nonnative invasive shrub *Ligustrum sinense* Lour (Chinese privet) and the invasive tree *Albizia julibrissin* Durazz (silk tree) were more abundant closer to an urban area (Columbus, GA) along the urban–rural gradient within riparian communities. They also showed that plant species diversity increased with increasing distance from the urban area (Burton et al., 2005). Also, Loewenstein and Loewenstein (2005) evaluated the understories of 15 riparian watersheds in western Georgia. The two watersheds that were primarily urban contained between 24 and 29% nonnative plant species, while the four watersheds that were primarily mixed forest contained between 4.3 and 12% nonnative plant species. However, the nonnative plant species occurred in the urban watersheds at a relatively low frequency and abundance, which in fact, did not differ significantly from the frequency and abundance of nonnative plants in the forested areas. In contrast, the watersheds in the urban–rural interface, which were experiencing high levels of development, had nonnative plants more frequently and abundantly than any other watershed. Nonnative plant species importance values were as large as 45% compared to nonnative plant species importance values of 28% or less for nonnative plants found in the urban watersheds. Not all the nonnative plant species in the Loewenstein and Loewenstein (2005) study are necessarily invasive, but the overall abundance of the nonnative plants found in the developing rural (exurban) areas was due primarily to three noted invasive nonnative plants, namely *Ligustrum sinense* Lour (Chinese privet), *Lonicera japonica* Thunb. (Japanese honeysuckle), and *Microstegium vimineum* (Trin.) A. Camus (Japanese stiltgrass).

As another example, we compared four large cities (Atlanta, GA; Chicago, IL; Los Angeles, CA; and New York, NY) for nonnative invasive plant species composition and found that the woody plant species growing in each city were 3.0, 21.3, 25.5, and 32.9% invasive, respectively (Fig. 5–2). Clemants and Moore (2003) compared a similar set of cities (Boston, MA; New York; Philadelphia, PA; Washington, DC; Detroit, MI; Chicago; Minneapolis, MN; and St. Louis, MO), and found 45.7, 34.8, 36.4, 34.3, 30.6, 32.9, 19.3, and 23.0% nonnative plant species, respectively. In their study, Minneapolis had the most dissimilar flora, suggesting that homogenization was lower in the city with the smallest percentage of nonnative species. Clemants and Moore's (2003) percentages for New York and Chicago are likely higher than what we found because they include herbaceous species and all nonnative plants, not just invasive nonnative plants. Only woody invasive species ≥2.5 cm in diameter at breast height (dbh) are included in our comparison, which comprises canopy trees, smaller subcanopy trees, and larger shrubs. Woody species were considered invasive if they were included on compiled national invasive weed lists (Huebner et al., 2007; U.S. Department of the Interior, Bureau of Land Management, 2008; The University of Georgia, Center for Invasive Species and Ecosystem Health, 2010; USDA Forest Service, Fire Effects Information System, 2011), or on compiled individual state lists (University of Georgia, Georgia Exotic Pest Plant Council, 2006; California Invasive Species Advisory Committee, 2010; New York State Department of Environmental Conservation, 2011; University of Georgia, Center for Invasive Species and Ecosystem Health, 2011), or were listed as potentially invasive because they were invasive in an adjacent state. If we include all nonnative woody species, we find 7.4, 48.1, 83.9, and 45.0% for Atlanta, Chicago, Los Angeles, and New York, respectively, which are higher than the values found by Clemants and Moore (2003). This result indicates that woody species in urban areas, especially cities located in nonforested matrices, appear to have disproportionally more nonnative species than do nonwoody species. Atlanta's smaller values, compared with the other three cities, could be due to the predominantly forested matrix surrounding the city and the presence of many forest remnants. Moreover, Atlanta has the smallest metropolitan population size of the four cities (2010 data), approximately 5.3 million people

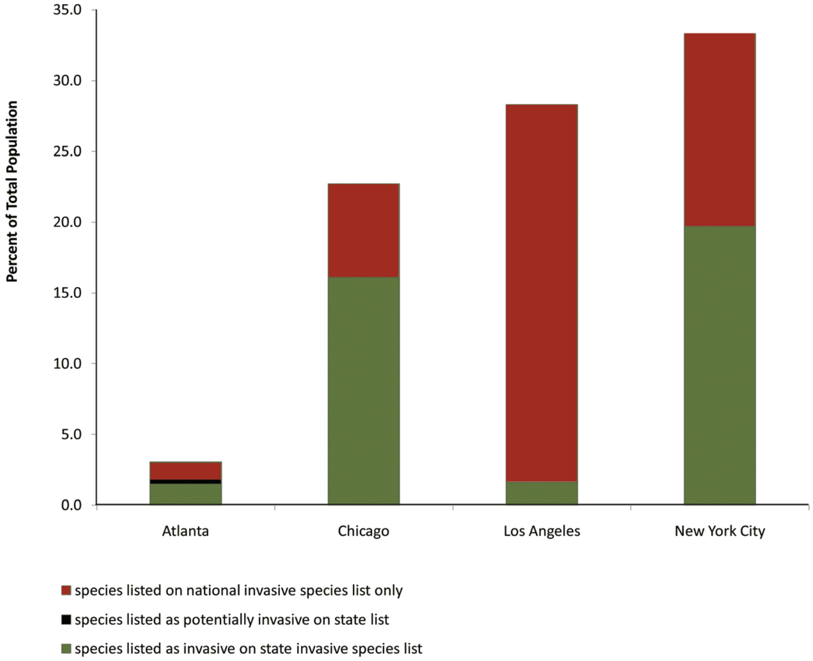

Fig. 5–2. Percentage of total woody plant species that is included on (i) a compiled national invasive species list and not on either of the two following lists: (ii) a compiled state invasive plant species list, and (iii) species listed as invasive in adjacent states.

compared to 18.9 million in New York City, 9.5 million in Chicago, and 12.8 million in Los Angeles (U.S. Bureau of the Census, 2011a). In all cities but Los Angeles, the invasive plants listed by each state tended to be more common than those invasive plants listed on national lists but not on individual state lists, suggesting that the national lists tend to be weighted more toward western species. The fact that each urban area had a few invasive species in adjacent states, but not yet in the urban area, indicates that adjacent states have similar invasive species problems. However, we must keep in mind that these lists contain the commonly recognized invaders and not newly established invaders (Box 5–2).

In another study in Baltimore, only 5.2% of the overall tree species in the metropolitan area were invasive, showing some similarity to Atlanta. When a neighborhood in southwest Baltimore was evaluated at the local scale, however, approximately 53% of the tree and shrub species were nonnative invasive plant species (D. Nowak,

Box 5–2. Case Study 1.

In our analysis, *Ailanthus altissima* (Miller) Swingle (tree of heaven; Fig. 5–Box 2a) was the most abundant invasive species (in terms of number of stems) in Atlanta, Chicago, and New York, while *Acacia melanoxylon* R. Br. (black acacia) was the most common invasive tree in Los Angeles. In terms of overall invasive tree leaf biomass and leaf area (abundance), *Acacia* spp. (mimosa species), *Lagerstroemia indica* L. (common crape myrtle), and *Pinus strobus* L. (Eastern white pine) were most dominant in Atlanta, while *Acer platanoides* L. (Norway maple; Fig. 5–Box 2b) stood out as the most dominant in Chicago, and Norway maple and *Morus alba* L. (white mulberry) were the most dominant in New York. Eastern white pine is at its southern-most native range near Atlanta, GA, and it is possible that some of the stems originated from natural populations. However, Eastern white pine is also commonly cultivated and planted and is an aggressive seeder (Dirr, 1998). Tree of heaven may not be a dominant species in terms of leaf area because most of its stems in each city were small (below 30.5 cm dbh in Chicago and New York and below 15.2 cm dbh in Atlanta). Also, Norway maple in Chicago may be regenerating more slowly or have fewer opportunities for regeneration, in terms of habitat availability, than Norway maple in New York City; most of the stems are over 30.5 cm dbh in Chicago, while most Norway maple stems in New York City are less than 30.5 cm dbh in size.

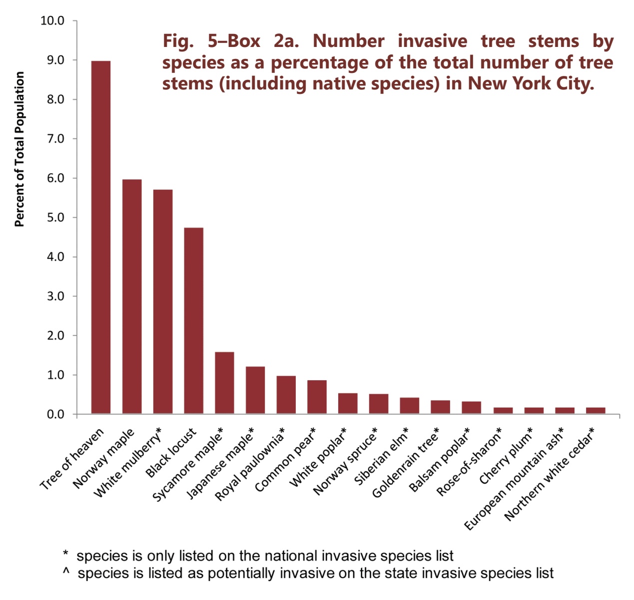

Fig. 5–Box 2a. Number invasive tree stems by species as a percentage of the total number of tree stems (including native species) in New York City.

* species is only listed on the national invasive species list
^ species is listed as potentially invasive on the state invasive species list

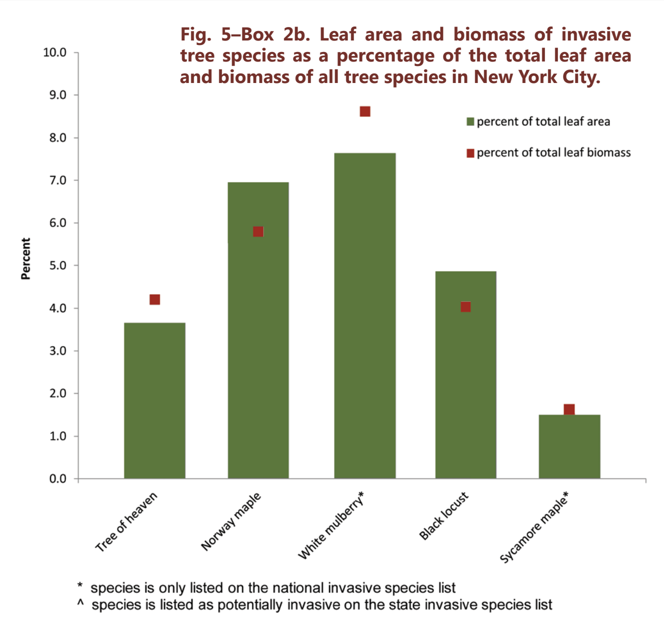

Fig. 5–Box 2b. Leaf area and biomass of invasive tree species as a percentage of the total leaf area and biomass of all tree species in New York City.

* species is only listed on the national invasive species list
^ species is listed as potentially invasive on the state invasive species list

R. Pouyat, and I. Yesilonis, 2006, unpublished data). Thus, there appears to be a mosaic of highly invaded vacant lots and emergent woodlands and less-invaded remnant urban forests mixed in with the built-up areas. Similarly, Walker et al. (2009) found that while species richness was higher in Phoenix, AZ than in the surrounding desert, species richness at a local plot scale was lower in the urban core compared to the surrounding desert. The flora of Berlin, Germany comprises 34.6% invasive plants (neophytes). Of these neophytes, 92.2% are *Ailanthus altissima* (Mill.) Swingle (tree of heaven) (Kowarik, 2008), suggesting that even among nonnative invasive plant species, some species are more likely to adapt and prosper in the urban environment. Nowak et al. (2002) also found that tree of heaven dominated Brooklyn, NY, but potentially high mortality (20% of this species' stems were dead) indicates that tree of heaven may have low long-term survival there. This species is, nevertheless, likely to sustain its Brooklyn populations for some time because most of its individuals were saplings. In contrast, Norway maple, which is also common in Brooklyn, appears to be sustained by replanting efforts or natural regeneration (Nowak et al., 2002). Cities surrounded by more forests than other land uses may have more area classified as urban or suburban forests than cities surrounded by other land uses such as agriculture (Nowak, 2010). The highly invaded and disturbed fragments (e.g., vacant lots) and emergent forests of urban areas may be serving as the primary source populations for invasions into urban remnant forest patches as well as into the urban–rural interface.

Evidence indicates that invasive plants can spread within urban forests without any additional plantings. For example, between 1988 and 2010, Norway maple presence has increased in abundance in Van Cortlandt Park, Bronx, NY (Fig. 5–3). Likewise, nonnative plant species increased in Pelham Bay Park, NY, by 39.7% between 1947 and 1998 (DeCandido, 2004). In fact, there are distinct species assemblages associated with natural forest interiors that urban forests' compositions fail to mimic, even in their interiors (Moffatt et al., 2004). Thus, persistence of remnant forests in urban areas as native species refugia could be deceptive. While native species are present in such forests, some are in decline or have been eliminated (Moffatt et al., 2004; Clemants and Moore, 2005). It is reasonable to predict that eventually most urban forest remnants that are subject to continual and additional fluxes of nonnative invasive plant species propagules will be dominated by nonnative invasive plant species with a loss in native biodiversity, although overall species richness may remain the same. Such forests may then serve as sources of nonnative invasive plant species propagules rather than sinks. Indeed, urban forest remnants may be dominated by native

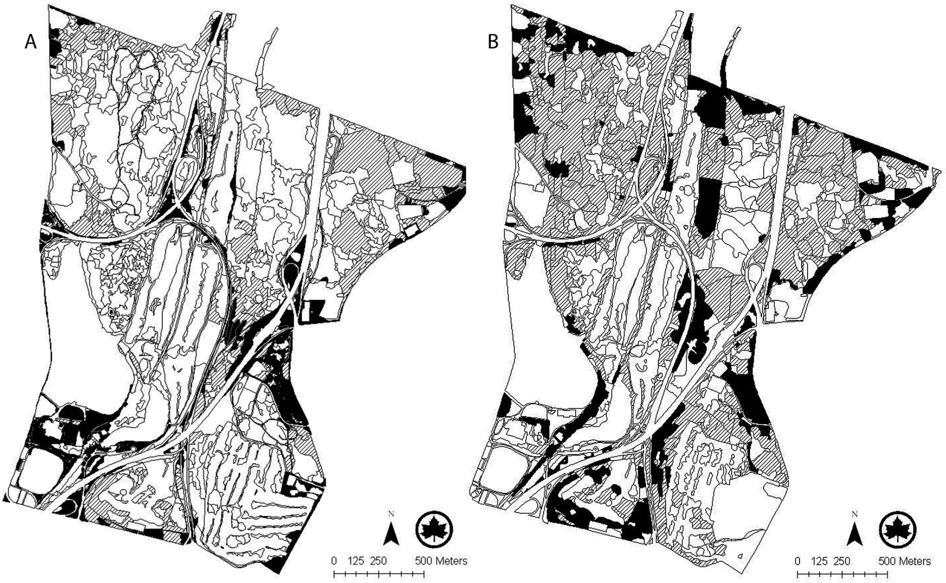

Fig. 5–3. Evidence of increasing abundance of Norway maple in Van Cortlandt Park, New York, NY between the years 1988 (a) and 2010 (b). White areas have no Norway maple, hatched areas have Norway maple present but not dominant, and solid gray areas have Norway maple as the dominant tree. Dominance was determined by visual estimates of the most abundant tree species present under a closed canopy. Maps were produced by Tim Wenskus and Clara Pregitzer of the City of New York, Parks and Recreation, Natural Resources Group and were used with permission.

canopy trees with few if any nonnative invasive trees or vines, but still have invasive plant species as components of the understory or seed bank. For instance, Kostel-Hughes et al. (1998b) found that the underlying soil seed bank of a New York City urban forest remnant contained nonnative invasive tree and vine seeds at low densities. Such forests may eventually convert to nonnative invasive plant species–dominated communities if a disturbance results in the removal of some of the canopy trees.

Thus, in terms of urban area nonnative invasive plant species composition, it is clear that urban areas may vary both in terms of the percentage of nonnative invasive plant species and native species and in possible projections of future compositions or turnover of species. However, the potential for a loss of native species exists for all urban areas as new nonnative invasive plant species are introduced. Nonnative invasive plant species may be more likely to increase in dominance and adapt more quickly to the urban environmental conditions than may remnant native species. Moreover, the pattern of invasion of forest remnants (i.e., going from sink to source of nonnative invasive plant species propagules) that we witness for a particular urban area may serve as an example of what to expect for the forest patches along the urban–rural gradient.

Traits of Plants Found in Urban Areas

According to Williams et al. (2009), urban floras are a mixture of native species originally present in the area, native species that were absent from the area originally, and nonnative species. Urban floras are further defined by four environmental filters: (i) habitat transformation (i.e., conversion), (ii) habitat fragmentation, (iii) urban environmental conditions, and (iv) human preference. Both habitat transformation and fragmentation (i.e., habitat loss) are not unique to urban systems and are human-caused filters found in most ecosystems. These filters may also be considered top-down anthropogenic drivers (Walker et al., 2009). In contrast, urban environmental conditions and human preference are unique to urban systems and may help us define any unique traits associated with urban floras. Moreover, human plant preferences and environmental conditions associated with urban areas may be considered bottom-up drivers of change (Walker et al., 2009).

If habitat loss is the primary result of habitat transformation in urban areas, then the urban flora is predicted to be relatively simple in terms of diversity and functional traits. However, novel habitats may result from a transformation in which diversity and functionality broaden. Habitat fragmentation generally selects for species with high dispersal capacity, high seed production, seed banking capabilities, and independence from mutualisms, such as specific pollinators and specialized mycorrhizae. The result may be a simplification to a flora dominated by pioneer and early-successional native species. However, invasive plant species share a number of these characteristics and, at least in the short term, could increase species diversity by colonizing urban areas (Williams et al., 2009). Other plant-trait patterns are also worth noting. For example, native, perennial plants with gravity (barochores) or wind dispersal (anemochores) mechanisms are more common to natural and rural forest remnants than to urban areas, and nonnative, woody plant species with animal-dispersed (endozoochores) seeds are more common to urban areas (Moffatt and McLachlan, 2004). Also, seeds of pioneer species and many invasive species in the urban areas are well adapted to seed dispersal via vehicles along roadsides. Indeed, seeds of both native and nonnative plants are more likely to travel outbound (from urban to rural) than inbound (from rural to urban; von der Lippe and Kowarik, 2008). Dispersal along roadside corridors is likely to lead to extra-range dispersal or dispersal into new habitats (Wilson et al., 2009). The fragmented patches found in urban areas may provide stepping stones for dispersal by birds and mammals as they forage in or maintain territories. The relatively large amount of edge (with more available light) associated with smaller patches may increase fleshy fruit production of many invasive plants as well as increase fruit removal by birds and mammals. The abundance of perches (trees or manmade structures such as telephone wires) found in urban areas along corridors also results in enhanced fleshy-fruited seed deposition by roosting birds (Gosper et al., 2005). The distance between perches and fruit-source patches is important in terms of dispersal by most vectors including wind, birds, and mammals. Wind dispersed species tend to have dispersal distances of approximately 200 to 300 m; bird-dispersed species typically have dispersal distances of around 1 km (Robinson and Handel, 1993; With, 2002). Birds have been shown to disperse seeds as far as 1200 m (Gosper et al., 2005) or even further (e.g., 6 km, Haas, 1995). Understanding the spatial characteristics of the urban landscape and the potential dispersal guilds that can be attributed to the species within the urban community may enable better predictions about species spread.

In response to habitat transformation and fragmentation, nonnative invasive plant species associated with urban environments may be best defined as opportunists that occupy:

1. Novel niches (given the unique environmental characteristics of urban areas) not previously occupied by a native species.
2. Niches that are empty because of a disturbance.
3. Existing niches, where they may coexist with native species or displace native species by outcompeting them (Moles et al., 2008).

As opportunists, invasive plants may be described as passengers of change rather than drivers of change, such as habitat loss and environmental conditions (MacDougall and Turkington, 2005). Invasive species may affect resource availability and subsequently suppress native species abundance, but only in response to the changes caused by a disturbance (Didham et al., 2005). Even with niche stasis, opportunistic urban flora may still share genetic and functional species traits in response to habitat loss and fragmentation.

Rapid shifts in either fundamental or realized niches could be occurring in response to urban environmental conditions and human preference filters. Evidence shows that environmental changes directly related to plant invasions (drivers of change rather than passengers) have occurred. Examples include measured changes in ecological processes after invasions, such as increases in soil N availability, altered N fixation rates, or litter with higher rates of decomposition (Ehrenfeld, 2003; Gómez-Aparicio and Canham, 2008b), evolution of species traits due to changes in species genetic make-up, and evidence of rapid adaptation to new conditions (Pearman et al., 2008). Changes in disturbance regimes, such as fire frequency, are also attributed to some nonnative invasive plant species, such as *Bromus tectorum* L. (cheat grass; Mack and D'Antonio, 1998). If niche shifts are the norm, the traits we are associating with nonnative invasive plant species may be best defined as post-invasion characteristics that have formed in response to the urban environment. The bottom-up effects of the urban environmental conditions and human preferences filters may enable such direct changes in ecosystem processes. Changes in ecosystem processes may then halt succession such that assembly rules for successional species are altered, new persistent plant communities are formed, and nonnative plants may become the dominant species (Holdaway and Sparrow, 2006; Ricotta et al., 2008).

However, the ability to change ecosystem processes directly may not be a requirement for stalled succession trajectories or the formation of alternate stable states. Stalled succession could also be a product of habitat transformation or fragmentation, that is, the top-down filters of change. For example, cheat grass may invade passively and persist without any changes in ecosystem function in terms of decomposition rates, N mineralization rates, plant cover, or soil nutrients, but still negatively impact soil biota species richness (Belnap et al., 2005). Richness of the soil biota appears to be less important than the presence of key species with the ability to maintain the ecosystem functions that can still support the previous native plant community once the dominant nonnative is removed (Belnap et al., 2005). Thus, depending on a variety of complex factors, including original and current species composition (Ehrenfeld, 2003), restoration of urban patches with seemingly stalled succession may still be possible. Nonetheless, persistently degraded invaded sites that seemingly have stalled succession are more likely to occur in sites that are abiotically limited (e.g., low soil fertility), intensively disturbed, and fragmented with limited colonization by native species (Cramer et al., 2008); these conditions may describe many patches of an urban area except urban forest remnants.

The urban physical environment may serve to filter species that are able to persist in species assemblages that can tolerate more stressful environments or rapidly take advantage of resource-rich conditions that exist in some urban habitats. In some cases, such species assemblages have a higher degree of taxonomic similarity (Ricotta et al., 2008). There is support for both a negative and positive relationship between native and nonnative invasive species relatedness and the degree of invasiveness of the nonnative species. Some findings support Darwin's assertions that more closely related species are less likely to be invasive because they share resource needs and vulnerabilities to herbivores and pathogens (Darwin, 1859; Strauss et al., 2006). On the other hand, Duncan and Williams (2002) in New Zealand and Daehler (2001) in Hawaii found that nonnative species were more likely to be invasive in environments in which there are closely related native species also present; they both concluded that the nonnative plants may be more successful because they are pre-adapted to the environmental conditions. Lambdon and Hulme (2006) found no consistent pattern between plant species relatedness and invasiveness, which may indicate that functional traits rather than taxonomic relatedness are more important when we evaluate the ability to invade a community successfully. According to Fargione et al. (2003), existing native species are most likely to inhibit their own displacement by an invading species if the existing and invading species share the same functional guild (i.e., legumes, forbs, C_3 grasses, and C_4 grasses). Urban areas have high biodiversity in part because existing native species assemblages are likely dominated by early-successional species that share functional attributes with many invading nonnative species. High plant species diversity within urban areas is also attributable to urban patch types varying in terms of light availability, allowing for colonization by both shade-intolerant and shade-tolerant nonnative invasive plant species. The shade-tolerant nonnative invasive plant species may, in turn, share niche requirements of the native K-selected (or late successional) plant species. Nonetheless, while forests are not immune to invasions (Martin et al., 2009), rapid invasion by shade-tolerant nonnative invasive plant species is still more likely in forest patches with high edge/interior ratios (Martin and Marks, 2006). The effects of relatedness between native and nonnative plants is likely to vary among Hahs et al.'s (2009) three types of urban areas. Type 3 urban areas, in which there are several remnant native communities, share the fewest functional attributes with any nonnative invasive plant species. The native species here inhibit their displacement by nonnative invasive plant species by occupying niches that nonnative invasive plant species are less likely to invade. The archaeophytes of older urban areas (i.e., Type 1) can be difficult to distinguish from indigenous flora due to a lack of historical information and are thus considered naturalized. Nonetheless, archaeophytes were cultivated for nutritional, medicinal, fiber, dyes, and possibly, though less likely, purely ornamental reasons. Neophytes may have been cultivated for the same reasons, but, more recently, most appear to be purely ornamental (Wittig, 2004). Nonetheless, archaeophytes, early-successional native species, and neophytes still share similar functional roles, leading to coexistence rather than exclusion. Although complete loss of archaeophytes in these older urban environments is unlikely, neophytes appear to be reducing their overall abundance at least in typical Type 1 cities found in central Europe (Wittig, 2004).

Given that the stressful habitats with low soil fertility and the unusually productive habitats with high soil nutrients (e.g., due to storm-water runoff or N deposition) may not encompass the entire urban area, but instead are found in isolated patches, the patches with such environmental conditions could be colonized by species that are selected specifically for those conditions, thus increasing overall biodiversity. Indeed, the unique climatic conditions associated with urban areas may create new urban niches, resulting in selection for plant species, such as tree of heaven, adapted to climate warming and stressful environments as well as rapid utilization of such abundant resources, such as light and nutrients (Kowarik, 1995; Willis et al., 2010). Such species may more easily increase their range as the climate warms, making urban areas potential refugia for species adapted to comparatively warmer environments. Species richness may not change, but instead genetic sorting within each species may be a response to the unique urban environmental and fragmented conditions. For example, populations of *Brassica rapa* L. (field mustard) have been shown to become more phenologically similar in response to climate change, such that populations are less reproductively isolated (Franks and Weis, 2009). Phenological changes associated with climate warming most often result in earlier flowering and seeding, which could potentially place any species migrating from urban areas into nearby rural areas and natural areas at a reproductive advantage. (Box 5–3)

Nonetheless, environmental variables may be less important than putative propagule sources (Moffatt et al., 2004; Alston and Richardson, 2006). Richness of nonnative invasive plant species found in vulnerable rural and natural sites is positively associated with shorter distances to the urban propagule source (Alston and Richardson, 2006). Human preference impacts urban species composition both through increasing propagule pressure and the selection of particular species. For example, the number of nonnative trees and shrubs has increased in some cities over time compared to other plant habits (i.e., herbs and graminoids; Celesti-Grapow and Blasi, 1998). In Florida, horticultural species that are aquatic herbs and vines or have larger native ranges (Africa or Asia) are more likely to become naturalized (Pemberton and Liu, 2009). Popular species in urban areas are more likely to have greater numbers of individuals, which in turn increases their probability of becoming an invasive plant (Lockwood et al., 2005, 2009; Colautti et al., 2006; Duggan et al., 2006). Propagule pressure includes not only number of individuals at a given time but also introduction frequency and time since first introduction. Species that have been introduced multiple times for a relatively long time period are more likely to become

Box 5–3. Case Study 2.

Plasticity to a wide range of environmental conditions, including response to various levels of soil moisture, light, and nutrient availability has been attributed to nonnative invasive plant species (Funk, 2008). Japanese stiltgrass' ability to compensate in variable environments has been well documented (Claridge and Franklin, 2002), but there do appear to be limits to this plasticity. For example, plants growing in relatively drier environments produce smaller seeds, and such seeds appear to be less viable (Huebner, 2011). Consequently, it may be possible to utilize known weaknesses of nonnative invasive plant species to prevent further spread from urban areas.

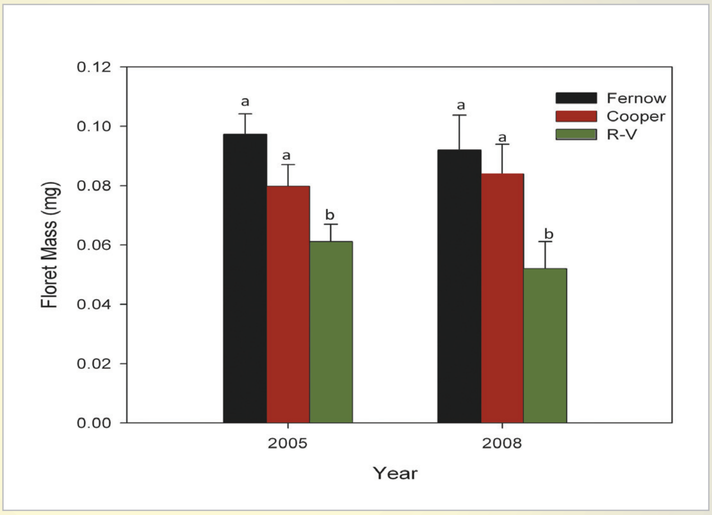

Fig. 5–Box 3. Seed weight across a moisture gradient. The Fernow and Cooper sites are located in the relatively wetter Allegheny Plateau, and the R-V sites are located within the drier Ridge and Valley region West Virginia, with the Cooper sites being somewhat intermediate in location (closer to the R-V sites). From Huebner (2011).

invasive than species with few introductions over a shorter time (Křivánek et al., 2006; Lockwood et al., 2009). It is also possible for propagule pressure to be so high that less than optimal environments or environments normally resistant to invasion are overwhelmed by the volume of propagules (Von Holle and Simberloff, 2005). In fact, the lag time effect is attributed to several nonnative plants, perhaps because these species may require 20 or more years to accumulate sufficient numbers of propagules before they are recognized as invasives (Crooks, 2005; Simberloff, 2009). There may also be a socioeconomic connection to propagule pressure. Dehnen-Schmutz et al. (2007) found that horticultural plants that had high market frequency (more commonly available in stores) and cheap seed prices were more likely to become invasive after 20 yr than less frequently available species with more costly seeds.

However, a reduction in overall plant density or cover compared to that of the surrounding natural areas is a known dramatic outcome of urbanization (Walker et al., 2009), suggesting that while urban areas may be the primary source of different plant species invading surrounding rural areas and natural areas, overall propagule pressure from urban areas may not be sufficient to explain the spread of invasive nonnative plants into these rural and natural areas. Instead, characteristics associated with the urban–rural–natural area interface may be equally or more important as the traits of potential plant invaders from urban areas.

Urban–Rural–Natural Area Gradient

Rural and Natural Areas Most Vulnerable to Invasion

Rural areas tend to have greater connectivity among habitat types that are made up of relatively large patches with small edge/interior ratios, high canopy closure values, and high soil moisture values when compared to urban areas (Moffatt and McLachlan, 2004). There is an environmental gradient extending from urban, rural, and natural areas with decreasing temperatures (Oke, 1995), lower light transmittance (Moffatt and McLachlan, 2004), and lower heavy metal concentrations in the soil (Pouyat and McDonnell, 1991).

The most vulnerable nonnative invasive plant species propagule sinks within rural and natural areas from urban areas may be characterized as three land use types: (i) abandoned old fields or agricultural lands, (ii) new housing developments, and (iii) transportation corridors. Abandoned agricultural lands, which are increasing in number (Cramer et al., 2008), have been shown to have a legacy effect that makes them more susceptible to invasion, possibly because historically cultivated lands often have higher soil cation concentration and soil pH values than noncultivated lands (Kuhman et al., 2011). Abandoned agricultural lands may also be more susceptible to invasion because the pathways of native species succession have been altered due to the absence of biological legacies (Franklin, 2007). Moreover, much of this agricultural land is being converted to residential or housing developments, which is usually followed by commercial and industrial land uses or more of those exurban patches throughout the interface (Westphal, 2001). Traditional types of agriculture, such as terracing, appear to facilitate native vegetation recovery and are less likely to be invaded by nonnative invasive plant species, possibly because such forms of agriculture reduce soil erosion and the removal of natural vegetation (Pretto et al., 2010). Active agricultural fields have proven to serve as barriers to spread of at least one invasive shrub, *Lonicera maackii* (Rupr.) Herder (Amur honeysuckle) in southwestern Ohio landscapes (Hutchinson and Vankat, 1998). Maestas et al. (2003) also found that active pasture or ranch land had lower nonnative plant cover and richness than exurban developments and a nature reserve in the same Colorado landscape. Active agricultural fields have also served as barriers to the movement of understory bird species in the fragmented landscape of an island off the coast of Chile (Sieving et al., 1996), which may in turn limit the dispersal of many nonnative plant species. Hess (1994) has also found that both urban and agricultural land areas may block the spread of disease, such as rinderpest in wildlife populations.

Richness of nonnative invasive plant species is positively related to distance to the nearest house and cover is positively related to the density of houses in a given area (Sullivan et al., 2005; Gavier-Pizarro et al., 2010a,b). While housing developments serve as likely sources of nonnative invasive plant species once occupied and maintained by the residents, new developments are linked to high levels of disturbance, including the removal of trees and the installation of infrastructure (sewer and water lines, roads). Likewise, roadsides serve as disturbance corridors that provide environmental conditions favorable for establishment of nonnative invasive plant species and also provide pathways for dispersal vectors of nonnative invasive plant species propagules (Theoharides and Dukes, 2007; von der Lippe and Kowarik, 2008).

Compared to these three land use areas characteristic of exurban landscapes, relatively undisturbed forests are considered among the least likely habitats to be invaded by nonnative invasive plant species, mainly due to low-light conditions and possibly due to relatively high native species biodiversity, which may make them more resistant to invasions. Biodiversity as a potential barrier to invasion has been shown to occur at a local scale in grasslands (Tilman, 1994; Naeem et al., 2000; Kennedy et al., 2002). However, forest types with higher species richness and diversity have also been shown to be more susceptible to invasion at both local (Gilbert and Lechowicz, 2005; Huebner and Tobin, 2006) and regional scales (Stohlgren et al., 1999) than are less diverse forest types. Vilà et al. (2007) looked at a very broad range of habitats across northeastern Spain and found that invasive plants were more likely to invade habitats with intermediate native plant richness instead of the two extremes of very high or very low richness. The discrepancies about whether diverse communities are more or less vulnerable to invasion by nonnative invasive plant species may be best explained by focusing on functional (shared morphological and physiological traits) diversity rather than species diversity (Pokorny et al., 2005). We have already discussed the fact that many nonnative invasive plant species share traits with native early-successional and shade-intolerant species. Because mature forests are primarily composed of K-selected species, shared functions with nonnative invasive plant species may be less likely to occur. In addition, both nonnative invasive plant species and high forest native understory plant diversity are also correlated with sites rich in soil nutrients and with relatively high pH, potentially explaining the correlation between forest sites high in native species diversity and likelihood of nonnative invasive plant species establishment. Environmental conditions that favor native species richness also often favor nonnative invasive plant species richness (Gilbert and Lechowicz, 2005).

Disturbance or management of forests of any type makes them more susceptible to invasion by nonnative invasive plant species (Hobbs and Huenneke, 1992). Moreover, the landscape configuration of abandoned habitats and emergent woodlands or grassland habitats within the fragmented urban–rural interface may increase the probability of certain disturbance events, such as wildfire spread in the wildland–urban interface interface (Radeloff et al., 2005). Fire may be more likely to occur due to increased fire ignition sources (i.e., litter burning around housing developments; Sturtevant et al., 2009) compared to natural areas, and greater connectivity of fuels (vegetated areas and fire-prone native vegetation, such as chaparral (Syphard et al,. 2007) or fire-prone nonnative vegetation, such as cheat grass (Mack and D'Antonio, 1998) than found in the urban areas. There is also a synergy between landscape fragmentation and disturbed habitats, such as harvested forests (Franklin and Forman, 1987) and grazed pasturelands (Hobbs, 2001), that makes colonization by nonnative plants more likely. Likewise, nonnative invasive plant species may spread more easily through a fragmented landscape with greater connectivity of road corridors, emergent woodlots, and abandoned or disturbed fields and forests (Hobbs and Huenneke, 1992; Minor et al., 2009; Thiele et al., 2009).

More stressful habitats where there is competition for limited resources are less likely to be invaded (Alpert et al., 2000). However, what defines a stressful condition is species-specific, and several studies have shown no reduction in invasibility of a stressed site vs. a less stressed site (usually defined by degree of resource availability; MacDougall et al., 2006; Funk, 2008). It would appear that urban areas could be selecting for nonnative invasive plant species that are more tolerant of the unique urban environmental conditions, which could be stressful to previously abundant native plant species.

The sites least vulnerable to invasion should be those with strong biological legacies that make them resilient to perturbations as well as invasions (Franklin et al., 2002). Sites that recover after a disturbance by rapid colonization of compositionally and structurally complex native species assemblages, which follow predictable r (early successional or ruderal) to K (late successional) native species successional trajectories, are less likely to be invaded by nonnative plants. Such rapid colonization is usually possible because of the persistence of a native species seed and seedling bank as well as nearby native seed and pollinator sources (Krueger-Mangold et al., 2006; Swanson et al., 2011). Maintenance of these biological legacies is more likely to occur in larger forest patches with smaller edge/interior ratios. Zones with noted edge effects (presence of edge plant species) in northeastern deciduous forests of the United States have been estimated to be as large as 40 m wide (Matlack, 1994). Though nonnative invasive plant species are not likely to be found in the interior of a large forest patch with relatively little edge, forest interior species tend to be well represented in forest edges, as well as in forest interiors. Indeed, there may be few if any forest interior species that occur only in the forest interior (Godefroid and Koedam, 2003). Biological legacies may be easier to maintain with greater landscape connectivity of naturally vegetated areas (or less overall fragmentation) in addition to larger patch sizes. Greater landscape connectivity may ensure pollinator access as well as native seed dispersal over a larger area than the individual patches (Saunders et al., 1991; Hobbs and Yates, 2003).

Nonnative Invasive Plant Species Interactions with Native Flora as Barriers to Invasion

Species interactions involving plants can be organized into three main types: (i) pathogens and herbivores, (ii) mutualisms and facilitation, and (iii) competition, as well as combinations of these interaction types. The enemy release hypothesis is based on invasive plants' lack of interactions with pathogens and herbivores relative to associated native plants' interactions, giving the invasive nonnative a competitive advantage (Mitchell et al., 2006). The scientific literature contains examples of enemy release (Mitchell and Power, 2003; Maron et al., 2004), as well as examples of no significant release from herbivores and pathogens compared to associated native plants (Agrawal et al., 2005; Parker and Gilbert, 2007). Inconsistencies with this hypothesis may be due to how damage was measured (visible vs. invisible stress) and use of congeneric native species to make comparisons instead of any associated native competitor for a given site. Congeneric species are more likely to share herbivores and pathogens, possibly making this comparison overly conservative. Whether or not nonnative invasive plant species benefit from a release of enemies may also depend on the availability of resources. A nonnative invasive plant species competitive advantage may occur only when resource availability is high, as is true for many urban patches, including urban forest patches. A return to predisturbance conditions with lower resource availability may once again favor the native species (Daehler, 2003). (Box 5–4.)

Moreover, herbivores and pathogens of nonnative invasive plant species can accumulate over time, making this a form of biotic resistance; indeed, some native pathogens and herbivores may develop a preference for nonnative invasive plant species (Parker and Hay, 2005). However, Torchin and Mitchell (2004) argued that the number of new pests that accumulate on an invader is only a fraction of the number of old pests that were lost from their native range (up to 75%) for most plant invaders. Nonetheless, closer interactions with a diverse native species pool may increase the chances of pathogen and herbivore accumulation on nonnative invasive plant species over time. For example, several species have shown evidence of accumulating pathogens and herbivores, a few of which are severe in their impact and are postulated as possible biocontrols. These include rose rosette disease of *Rosa multiflora* Thunb. (multiflora rose; Tipping, 2000). Additionally, tree of heaven has shown significant mortality due to wilt caused by *Verticillium albo-atrum* Reinke & Berthier (Schall and Davis, 2009), and Japanese stiltgrass has shown 40% reduction of seed production in plants infected with the leaf blight fungus *Bipolaris* spp. (Kleczewski and Flory, 2010). Unfortunately, there are also examples of newly accumulating pathogens that not only limit the abundance of nonnative invasive plant species, but also negatively impact associated native species at a greater severity, which increases the nonnative invasive plant species' competitiveness. Eppinga et al. (2006) showed that *Ammophila arenaria* (L.) Link. (marram grass) in California accumulates local soil pathogens that affect associated species more negatively than they affect marram grass. Mangla and Callaway (2008) similarly showed that *Chromolaena odorata* (L.) R.M. King and H. Rob. (siam weed) in India accumulates the soil pathogen *Fusarium semitectum* Berkeley & Ravenel to the detriment of associated native species. Pathogens on nonnative invasive plant species that negatively impact an associated native species may be best described as novel weapons. Research has identified the use of allelopathy as a novel weapon by several nonnative invasive plant species, including *Alliaria petiolata* (M. Bieb.) Cavara and Grande (garlic mustard; Stinson et al., 2006), *Fallopia japonica* (Houtt.) Ronse Decr. (Japanese knotweed; Murrell et al., 2011), and tree of heaven (Gómez-Aparicio and Canham, 2008a). Allelopathic compounds can accumulate in soils over time if the nonnative invasive plant species populations are not removed, leading to costly restoration efforts that include not only adding seed or transplants but also removal or leaching out of the allelopathic compounds.

Shared mutualisms (i.e., with mycorrhizae, pollinators, and seed dispersers) between nonnative invasive plant species and associated native plants may increase competition for such interactions. Native species close to nonnative invasive plant species may initially help attract mycorrhizae, pollinators, or seed dispersers, which would be beneficial to nonnative invasive plant species and native species alike. If, however, nonnative invasive plant species dominate a site, the pollinators, seed dispersers, and mycorrhizae may grow to be too scarce to be beneficial to the associated native species (Traveset and Richardson, 2006). Conversely, nonnative invasive plant species could become so dependent on mutualisms that they become less competitive when the mutualisms are removed, especially at sites where resources may not be abundant. For instance, Marler et al. (1999) found that the invasive forb *Centaurea stoebe* ssp. *micranthos* (Gugler) Hayek (formerly C. *maculosa*; spotted knapweed) was more competitive against larger *Festuca idahoensis* Elmer (Idaho fescue) than smaller Idaho fescue, when arbuscular mycorrhizal fungi were present than when the fungi were absent. Moreover, neither species benefited significantly from the mycorrhizae without competition (Marler et al., 1999).

Box 5–4. Uniqueness of Urban Food Webs

Urban food webs, like urban species composition, also may be considered unique. A lack of large predators in urban areas has resulted in increased numbers of adult birds, while an abundance of feral cats has decreased the numbers of fledgling birds, although this situation may be changing as coyotes increase in abundance in urban areas (Faeth et al., 2005). An abundance of flowering ornamental plants has led to large numbers of generalist pollinators in urban areas. However, richness of pollinators has likely decreased because of less overall abundance of native species. Predation of insects by the abundant number of adult birds may have resulted in relatively low numbers of arthropods, including many pollinators, in cities (Faeth et al., 2005).

A nonnative invasive plant species surrounded by high native plant species diversity is more likely to encounter competition from native species, but only when there is a lack of resource or niche availability (Levine et al., 2004) and the nonnative invasive plant species does not possess a novel weapon (Cappuccino and Arnason, 2006) or other characteristics (lack of pathogens) that make it more competitive. Nonetheless, inherently stronger competitive abilities are often attributed to nonnative invasive plant species as opposed to associated native species, and these characteristics are not the result of a lack of enemies or possession of novel weapons. However, such innate competitive abilities are not supported well in the literature, possibly because the study designs have thus far been inadequate (Vilà and Weiner, 2004). Sher et al. (2000) found that the native *Populus deltoides* Bartr. ex Marsh (trembling aspen) grows faster than the nonnative *Tamarix ramosissima* Ledeb. (salt cedar) and could outcompete it if it reaches a site at the same time as or before salt cedar. Similarly, Huebner (2005) showed that the native *Rhus hirta* (L.) Sudworth (formerly *R. typhina*; staghorn sumac) could outgrow tree of heaven if seedlings were started at the same time. Not allowing invasive plants to colonize a disturbed site before native species appears to be an important strategy, which lends even more credence to having biological legacies of abundant native seeds in the seed banks.

Restoration, Rehabilitation, or Mitigation of Nonnative Invasive Plant Species

Examples of Positive Impacts of Removal or Eradication of Nonnative Invasive Plant Species

Restoration of invaded sites, such as remnant forests, in an urban area, as well as along the urban–rural–natural area gradient may be one way of slowing or even preventing homogenization and the spread of nonnative invasive plant species. Successful restoration is contingent on the degree (intensity and duration) of degradation and the time since invasion. Successful restoration of sites is more likely to occur in sites farther away from urban centers along the urban–rural–natural area gradient. Indeed, it is likely that only rehabilitation or reclamation or even just smaller mitigation efforts should be applied within urban areas; restoration may never be a realistic goal. There are some examples of successful restoration of remnant forests within the natural and rural portion of the urban–rural gradient. For instance, Hartman and McCarthy (2004) showed that removal of Amur honeysuckle from forested areas within a disturbed, regenerating forest in Ohio resulted in successful growth of planted 1-yr-old, native tree seedlings. Restoration success varied by native tree species as well as by climatic conditions during the 3 yr of measurements and microenvironmental differences within and between sites. Bakker et al. (2003) similarly showed that removal of *Agropyron cristatum* (L.) Gaertn. (crested wheatgrass) from grasslands planted in this perennial invasive grass 50 yr ago followed by broadcasting seeds of native grass species resulted in successful establishment of native grasses, but not complete elimination of the crested wheatgrass. They suggested that success is more likely when removal (via herbicide treatments) of the crested wheatgrass is done during dry years and seed broadcasting conducted during wet years (Bakker et al., 2003). Both of these examples involved active planting of native species. Ideally, we would like many sites to autogenically regenerate without seed addition because of existing biological legacies in the form of seed or seeding banks or nearby seed sources (Franklin et al., 2002). Donath et al. (2003) showed that successful re-establishment of native species in flood plain meadows of the Rhine valley in Germany without seed or seedling addition is limited by dispersal even under the most favorable environmental conditions.

Examples of Negative Impacts of Removal or Eradication of Nonnative Invasive Plant Species

We mentioned earlier that Hejda and Pyšek (2006) showed that Himalayan impatiens did not negatively impact the ecosystem when it took over the functional roles of dominant native species. Hulme and Bremner (2006) also found that removal of Himalayan impatiens led to increases in abundance of other nonnative species, indicating that this may be an instance where no control or management of a nonnative invasive plant may be the best strategy. Urban butterfly fauna in Davis, CA are dependent on nonnative plant species found in Davis. In fact, more than 40% of the butterflies have no known native hosts in urban–suburban areas of Davis (Shapiro, 2002). Because of the potential negative impact to native butterflies, Shapiro (2002) concluded that money spent on eradicating nonnative plants from urban areas would be better spent on buying and managing any remaining native habitat remnants within the urban area. We would predict that such impacts are more likely to occur closer to the urban core of the gradient, where interactions between native and nonnative species may have had more time to develop. This pattern may not always hold true. For instance, salt cedar removal has been stalled in several riparian areas because the endangered *Empidonax traillii extimus* A.R. Phillips (southwestern willow flycatcher) depends on it for nesting habitat (Zavaleta et al., 2001). It would be interesting to know if the interactions with the endangered flycatcher more commonly occur closer to urban areas where salt cedar was first introduced as an ornamental shade tree. Thus, without adequate planning, attempted eradications of nonnative invasive plant species could have detrimental impacts on other native species that have grown dependent on these nonnatives. These findings support the assertion of Davis et al. (2011) that we should no longer focus the origin (native vs.

nonnative) of a species but rather their function in a given ecosystem.

Moreover, nonnative invasive plant species could serve a temporary role in restoration, especially in sites that have been degraded to such an extent that soil fertility has been lost (D'Antonio and Meyerson, 2002; Lugo, 2004). For example, it has been suggested that *Acacia* spp. be planted after removal of *Imperata cylindrica* (L.) P. Beauv. (cogon grass) to promote more rapid native woody species colonization instead of re-establishment of cogon grass (Kuusipalo et al., 1995). Use of nonnative invasive plant species for rehabilitation is risky, but the risk may be worth it when human activity has severely modified environmental conditions (Ewel and Putz, 2004), such as in urban areas. Degraded site conditions that are physical modifications (loss of soil or soil fertility and increased heat due to a heat-island effect often associated with urban areas) may warrant the use of nonnative invasive plant species more than would sites degraded only biotically (Ewel and Putz, 2004). Indeed, some physically degraded sites in urban areas can support only particularly hardy nonnative invasive plant species, such as tree of heaven. Extreme degradation of sites is not limited to urban areas, but may also be found along the urban-rural-natural area gradient. For instance, even the mature forests of Puerto Rico show nearly equal nonnative invasive plant species and native species biomass and greater nonnative invasive plant species diversity than native species diversity. While urban forests of Puerto Rico have higher nonnative plant importance values (65%) than mature forests, the relatively undisturbed mature wet forests still have a nonnative plant importance value of 41% (Lugo 2004). It is unlikely to be cost-effective to restore forests in which the roles of nonnative invasive plant species clearly dominate, and such forests still play a valuable functional role, albeit as novel communities. These novel forests, which support wildlife, cycle nutrients, store carbon, accumulate species, and perform other valuable ecosystem functions, exist worldwide (Lugo, 2009). It may be that these novel mature forests may be the ultimate realistic goal for most urban forest remnants. Unfortunately, many urban forest remnants in the United States do not appear to be evolving into functional novel systems; rather, they seem to be degrading, with a loss of native tree species and potentially the eventual loss of all canopy trees, depending on the successional trajectory and remnant biological legacies. Reasons behind this change include the relatively small size of many urban forest patches, continual disturbance in such patches and adjacent patches, and minimal efforts (often budget related) to rehabilitate urban forest patches (McPherson et al., 1997). The rate of degradation of some remnant urban forests may also be influenced by nonnative insects and pathogen invaders, which may decimate entire populations of particular native tree species. Examples include *Agrilus planipenis* Fairmaire (emerald ash borer; Poland and McCullough, 2006) and *Lymantria dispar* L. (gypsy moth; Foss and Rieske, 2003). Tree cover in urban areas tends to decline as population density increases. As urban areas expand, however, the rate of conversion of once-forested land to fragmented urban forests also increases (Nowak et al., 2001). It is also important to distinguish potentially functional urban forest remnants from urban forest remnants that serve as ecological traps. For instance, several forest patches within the Allegheny National Forest in Pennsylvania, USA are now dominated by *Rhamnus cathartica* L. (common buckthorn), and common bird species may utilize this species for their nests (Schmidt and Whelan, 1999). Treatment of these populations of common buckthorn could have potential detrimental effects to birds. On the other hand, these birds could be experiencing high levels of nest predation because the structure of the shrub requires that the birds build their nests relatively close to the ground (Schmidt and Whelan, 1999).

Solutions

Spatially Explicit Land Use Planning and Management

At the risk of oversimplifying a complex problem, we have shown first that urban areas are a primary source of nonnative invasive plant species and that abandoned and developing lands along the urban–rural–natural areas gradient are the most susceptible to invasion. While the road corridors leading out of urban areas are unlikely to decrease or stop being sources of dispersal of nonnative invasive plant species, it may be possible to change land use in such a way that less susceptible land uses can serve as filters or barriers to reduce the spread of nonnative invasive plant species. For instance, placement of active agricultural or pastoral lands between urban areas and rural developments may slow the spread of nonnative invasive plant species. These agricultural lands may still harbor nonnative plants, but these plants tend not to be invasive (Williamson and Fitter, 1996). However, it is critical that such agricultural lands be allowed to go fallow for only short time periods. Instead of or in addition to agricultural land, it may be possible to retain or restore large, contiguous forested areas, which also serve to slow the spread of many species. However, these forested areas may be best managed as parks or harvested only under very controlled conditions, for example by using low-impact silvicultural methods, use of certified (cleaned) equipment, and use of certified (weed-free) seed. The size of the agricultural or forested buffer should be based on likely dispersal distances of known birds and mammals in the urban area. To reduce the potential for isolating some bird and insect populations within the urban areas, roadside corridors could be used. We could buffer the road corridors with native grass buffers that would make establishment of nonnatives more difficult and make the roads less of a disturbance corridor for the spread of nonnative invasive plant species.

A landscape design in which urban areas are linked to their own (well-managed) agricultural or natural area zones may lead to a lower agricultural carbon footprint as well as a lower urban carbon footprint, because there would be less need for intercity or interstate transport of food products and more local access to agricultural products and natural areas. Such easy access to fresh produce and other agricultural products as well as nature would add to the number of amenities already available in urban areas, including cultural amenities (e.g., theater, art, and music). Indeed, urban farming has recently increased in popularity as noted by recent books on the subject (e.g., *City Farmer* by L. Johnson, 2010; *Urban Agriculture* by D. Tracey, 2011). Perceived limitations of urban growth beyond the agricultural or forested zone are of concern. One option may be to include flexible or expanding buffers that can respond to an expanding urban area. Though we are not advocating a zero-growth policy, we are proposing urban sustainability, which may require that in response to increases in population, city planners and other decision-makers exercise some restraint on urban sprawl and focus on vertical growth in response to increases in populations instead of horizontal expansion (Wu, 2008). Increased communication among land managers, scientists, and urban planners may enable successful utilization of existing smart growth policies (Burchell et al., 2000). These policies focus on (i) use of urban growth boundaries that prevent expansion, (ii) increasing mixed land uses to minimize travel, (iii) charging impact fees on new developments that individual consumers pay rather than the general public, (iv) increasing residential densities, and (v) revitalizing older neighborhoods. Several of these principles have proven difficult to implement because they would likely lower property values or are more difficult to accomplish due to increased regulations (i.e., new developments in the city; Downs, 2005). Nonetheless, implementation of even just one of the smart growth policies, i.e., revitalization of older neighborhoods and vacant lots with urban gardens and small farming plots, could still have a significant impact on reducing the spread of nonnative invasive plant species along the urban–rural–natural area gradient.

Native and Nonnative Species Interactions within the Urban Core and the Urban–Rural Interface

Restoring and increasing the size of urban forest remnants or native grasslands (depending on the natural landscape of the urban area)—in other words, increasing the urban green space in the urban core and the urban–rural interface—will increase the number of native species present within the urban core and help maintain native species populations in the urban–rural interface. The native species associated with this green space will likely be coexisting with nonnative invasive plant species that may be adapted to the unique environmental conditions associated with urban areas. Having larger urban forest patches will not only increase the availability of native species' seed propagules relative to those of nonnative invasive plant species, but it will also increase the number of biotic interactions, perhaps reducing the time for herbivores or pathogens to find respective nonnative invasive plant species, which in turn could reduce the nonnative invasive plant species' competitive capacity over time. There is a risk that increasing such interactions could result in shared mutualisms with native plant species that could result in competition for pollinators or dispersal agents. If native species are kept at an appropriate population size, however, coexistence may be possible and may be the realistic goal. More research is needed to know what nonnative invasive plant species and native plant species population sizes will promote such coexistence in urban areas and lead to beneficial interactions with other trophic levels.

We have focused on relict or remnant original green space, but it is also possible to increase green space using built or rehabilitated parks and gardens. Indeed, the more fragmented and accessible these parks are throughout the urban core, the better it would be for biodiversity (Smith et al., 2006). The latter statement may hold true only if the parks or gardens are well-managed and are dominated by edible crops (Williamson and Fitter, 1996) or have a high degree of beta diversity across the urban area, comprising a variety of species (both native and nonnative), with few similarities in species composition among the green patches. This premise will not only help maintain high levels of biodiversity but may also prevent propagule buildup of potentially invasive species. Increasing the amount of green space in urban areas also decreases some of the negative environmental conditions associated with urban areas, which in turn may also reduce the likelihood of invasion by many nonnative invasive plant species. Such conditions that appear to promote plant invasions include the heat-island effect (Gill et al., 2007), water runoff, and contaminated storm water runoff that transports high levels of nutrients (Leishman and Thomson, 2005; Gill et al., 2007). Last, the perceived health of the people living in the city is also likely to improve with increased urban green space, especially for the less affluent areas within the urban area (Maas et al., 2006).

Manipulating the Nonnative Invasive Plant Species Propagule Pressure in Urban Areas

Educating buyers and sellers of horticultural plants not to buy or sell known invasive plant species has proven to be difficult and is primarily voluntary, but there has been some success. The U.S. National Invasive Species Council's 2008–2012 Invasive Species Management Plan calls for the Animal and Plant Health Inspection Service (APHIS) to develop screening protocols for invasive plants, but such protocols are not yet developed (National Invasive Species Council, 2011). There are a number of suggested protocols in the literature (Tucker and Richardson, 1995; Reichard and Hamilton, 1997; Maillet and Lopez-Garcia, 2000) that have, thus far, proven to be inadequate for scientific or economic reasons. Nationally, several ornamental horticulture organizations have endorsed the Voluntary Codes of Conduct, which states that the signers of the document will decrease the use of known nonnative invasive plant species (Niemiera and Von Holle, 2009). In Florida, growers voluntarily agreed to stop growing 45 known nonnative invasive plant species, but faced with an economic analysis that showed a potential loss of $59 million, they could not agree to stop growing 14 other known nonnative invasive plant species (Wirth et al., 2004). A greater challenge is with the new horticultural species of which there is likely to be a steady supply, especially in the more affluent urban sectors. Educating or training home owners and landscapers to understand the ecological impacts of known plant invaders and to value variety by not purchasing the most popular landscape plants is a start. Incentives to purchase native species or less popular and less aggressive nonnative plants instead of known nonnative invasive plant species could be made available through local, state, or federal subsidies. Cities could also set an example by promoting the planting of native and noninvasive nonnative tree species along public right-of-ways and using a variety of species instead of many of the same species both along roadsides as well as in city parks and near city-owned buildings. For example, New York City has a program providing incentives to increase urban tree canopy cover by 30% by the year 2030 (Grove et al., 2006a). Use of such models as the Urban Forest Effect (UFORE) model enables cities to monitor tree composition within urban areas with minimal effort as well as monitor potential ecosystems services of the trees and urban forest remnants (Nowak et al., 2008). Perhaps more importantly, such species lists should be considered dynamic, keeping climate change in mind. Moreover, use of a variety of noninvasive plant species spatially as well as temporally not only reduces the potential loading of propagules from any one plant species but will also reduce the impacts of any associated pathogens or insects that may be inadvertently introduced into the area.

Conclusions

We conclude that nonnative invasive plant species associated with urbanization can negatively impact exurban and urban remnant natural areas, but these impacts can be avoided with various planning and management measures that include strategic placement of barriers to invasion and leaving larger buffers around the urban core. In addition, increasing green space within the urban core and urban–rural interface will promote novel yet functional plant communities. Such novel communities will not only provide positive environmental benefits to the urban area, but also increase biotic interactions with potential herbivores and pathogens that could reduce their invasive potential; these communities thereby act as barriers to invasion. Diverse novel communities with large areas dominated by native species should also reduce the propagule pressure of any known nonnative invasive plant species as well as potential future nonnative invasive plant species, thus decreasing the likelihood of establishment and spread of non-native invasive plant species along the urban–rural–natural area gradient. These changes would still allow for urban growth but in a more sustainable direction.

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References

Agrawal, A.A., P.M. Kotanen, C.E. Mitchell, A.G. Power, W. Godsoe, and J. Klironomos. 2005. Enemy release? An experiment with congeneric plant pairs and diverse above- and belowground enemies. Ecology 86(11):2979–2989. doi:10.1890/05-0219

Alig, R.J., J.D. Kline, and M. Lichtenstein. 2004. Urbanization on the U.S. landscape: Looking ahead in the 21st century. Landscape Urban Plan. 69:219–234. doi:10.1016/j.landurbplan.2003.07.004

Alpert, P., E. Bone, and C. Holzapfel. 2000. Invasiveness, invasibility and the role of environmental stress in the spread of non-native plants. Perspect. Plant Ecol. Evol. Syst. 3(1):52–66. doi:10.1078/1433-8319-00004

Alston, K.P., and D.M. Richardson. 2006. The roles of habitat features, disturbance, and distance from putative source populations in structuring alien plant invasions at the urban/wildland interface on the Cape Peninsula, South Africa. Biol. Conserv. 132:183–198. doi:10.1016/j.biocon.2006.03.023

Alvey, A.A. 2006. Promoting and preserving biodiversity in the urban forest. Urban For. Urban Green. 5:195–201. doi:10.1016/j.ufug.2006.09.003

Bakker, J.D., S.D. Wilson, J.M. Christian, X. Li, L.G. Ambrose, and J. Waddington. 2003. Ecol. Appl. 13(1):137–153. doi:10.1890/1051-0761(2003)013[0137:COGROY]2.0.CO;2

Bartuszevige, A.M., R.L. Hrenko, and D.L. Gorchov. 2007. Effects of leaf litter on establishment, growth and survival of invasive plant seedlings in a deciduous forest. Am. Midl. Nat. 158(2):474–477.

Belnap, J., S.L. Phillips, S.K. Sherrod, and A. Moldenke. 2005. Soil biota can change after exotic plant invasion: Does this effect ecosystem processes? Ecology 86(11):3007–3017. doi:10.1890/05-0333

Bolund, P., and S. Hunhammar. 1999. Ecosystem services in urban areas. Ecol. Econ. 29:293–301. doi:10.1016/S0921-8009(99)00013-0

Botkin, D.B., and C.E. Beveridge. 1997. Cities as environments. Urban Ecosyst. 1:3–19. doi:10.1023/A:1014354923367

Burchell, R., D. Listokin, and C.C. Galley. 2000. Smart growth: More than a ghost of urban policy past, less than a bold new horizon. Hous. Policy Debate 11:821–879. doi:10.1080/10511482.2000.9521390

Burton, M.L., S.J. Samuelson, and S. Pan. 2005. Riparian woody plant diversity and forest structure along an urban-rural gradient. Urban Ecosyst. 8:93–106. doi:10.1007/s11252-005-1421-6

California Invasive Species Advisory Committee. 2010. The California Invasive Species List. http://www.iscc.ca.gov/docs/CaliforniaInvasiveSpeciesList.pdf. (accessed June 2011).

Callaway, R.M., and J.L. Maron. 2006 What have exotic plant invasions taught us over the past 20 years? Trends Ecol. Evol. 21(7):369–374. doi:10.1016/j.tree.2006.04.008

Cappuccino, N., and J.T. Arnason. 2006. Novel chemistry of invasive exotic plants. Biol. Lett. 2:189–193. doi:10.1098/rsbl.2005.0433

Carreiro, M.M. 2005. Effects of urban sprawl on decomposer communities and soil processes in forest remnants. In: E.A. Johnson and M.W. Klemens, editors, Nature in fragments: The legacy of sprawl. Columbia Univ. Press, New York.

Carreiro, M.M., R.V. Pouyat, C. Tripler, and W. Zhu. 2009. Carbon and nitrogen cycling in soils of remnant forests along urban–rural gradients: Case studies in the New York metropolitan area and Louisville, Kentucky. In: M.J. McDonnell, A. Hahs, and J. Breuste, editors, Ecology of cities and towns: A comparative approach. Cambridge Univ. Press, Cambridge, UK. p. 308–328.

Celesti-Grapow, L., and C. Blasi. 1998. A comparison of the urban flora of different phytoclimatic regions in Italy. Global Ecol. Biogeogr. Lett. 7:367–378. doi:10.2307/2997684

Celesti-Grapow, L., P. Pyšek, V. Jaro◎ík, and C. Blasi. 2006. Determinants of native and alien species richness in the urban flora of Rome. Divers. Distrib. 12:490–501. doi:10.1111/j.1366-9516.2006.00282.x

Claridge, K., and S.B. Franklin. 2002. Compensation and plasticity in an invasive plant species. Biological Invas. 4:339–347. doi:10.1023/A:1023671006342

Clemants, S.E., and G. Moore. 2003. Patterns of species richness in eight northeastern United States cities. Urban Habitats 1:4–15.

Clemants, S.E., and G. Moore. 2005. The changing flora of the New York Metropolitan Region. Urban Habitats 3(1):192–210.

Cohen, B. 2004. Urban growth in developing countries: A review of current trends and a caution regarding existing forecasts. World Dev. 32(1):23–51. doi:10.1016/j.worlddev.2003.04.008

Cohen, B. 2006. Urbanization in developing countries: Current trends, future projections, and key challenges for sustainability. Technol. Soc. 28:63–80. doi:10.1016/j.techsoc.2005.10.005

Colautti, R.I., I.A. Grigorovich, and H.J. MacIsaac. 2006. Propagule pressure: A null model for biological invasions. Biol. Invas. 8:1023–1037. doi:10.1007/s10530-005-3735-y

Collins, M.D., D.P. Vázquez, and N.J. Sanders. 2002. Species-area curves, homogenization and the loss of global diversity. Evol. Ecol. Res. 4:457–464.

Cramer, V.A., R.J. Hobbs, and R.J. Standish. 2008. What's new about old fields: Land abandonment and ecosystem assembly. Trends Ecol. Evol. 23(2):104–112. doi:10.1016/j.tree.2007.10.005

Crooks, J.A. 2005. Lag times and exotic species: The ecology and management of biological invasions in slow-motion. Ecoscience 12(3):316–329. doi:10.2980/i1195-6860-12-3-316.1

Daehler, C.C. 2001. Darwin's naturalization hypothesis revisited. Am. Nat. 158(3):324–330. doi:10.1086/321316

Daehler, C.C. 2003. Performance comparisons of co-occuring native and alien invasive plants: Implications for conservation and restoration. Annu. Rev. Ecol. Evol. Syst. 34:183–211. doi:10.1146/annurev.ecolsys.34.011802.132403

D'Antonio, C., and L.A. Meyerson. 2002. Exotic plant species as problems and solutions in ecological restoration: A synthesis. Restor. Ecol. 10(4):703–713. doi:10.1046/j.1526-100X.2002.01051.x

Darwin, C. 1859. The origin of species. John Murray, London.

Davies, T.J., G.F. Smith, D.U. Bellstedt, J.S. Boatwright, B. Bytebier, R.M. Cowling, F. Forest, L.J. Harmon, A. M. Muasya, B.D. Schrire, Y. Steenkamp, M. van der Bank, and V. Savolainen. 2011. Extinction risk and diversification are linked in a plant biodiversity hotspot. PLoS 9(5):1–9.

Davis, M.A. 2003. Biotica globalization: Does competition from introduced species threaten biodiversity? BioScience 53(5):481–489. doi:10.1641/0006-3568(2003)053[0481:BGDCFI]2.0.CO;2

Davis, M.A., M.K. Chew, R.J. Hobbs, A.E. Lugo, J.J. Ewel, G.J. Vermeij, J.H. Brown, M.L. Rosenzweig, M.R. Gardener, S.P. Carroll, K. Thompson, S.T.A. Pickett, J.C. Stromberg, P.D. Tredici, K. N. Suding, J.G. Ehrenfeld, J.P. Grime, J. Mascaro, and J.C. Briggs. 2011. Don't judge species on their origins. Nature 474:153–154. doi:10.1038/474153a

DeCandido, R. 2004. Recent changes in plant species diversity in urban Pelham Bay Park, 1947–1198. Biol. Conserv. 120:129–136. doi:10.1016/j.biocon.2004.02.005

Dehnen-Schmutz, K., J. Touza, C. Perrings and M. Williamson. 2007. A century of the ornamental plant trade and its impact on invasion success. Diversity Distrib. 13:527–534. doi:10.1111/j.1472-4642.2007.00359.x

Didham, R.K., J.M. Tylianakis, M.A. Hutchinson, R.M. Ewers and N.J. Gemmell. 2005. Are invasive species the drivers of ecological change? Trends Ecol. Evol. 20(9):470–474. doi:10.1016/j.tree.2005.07.006

Dirr, M.A. 1998. Manual of woody landscape plants. Stipes Publ., LLC, Champaign, IL.

Donath, T.W., N. Hotzel, and A. Otte. 2003. The impact of site conditions and seed dispersal on restoration success in alluvial meadows. Appl. Veg. Sci. 6:13–22. doi:10.1111/j.1654-109X.2003.tb00560.x

Downs, A. 2005. Smart growth: Why we discuss it more than we do it. J. Am. Plan. Assoc. 71(4):367–380. doi:10.1080/01944360508976707

Duggan, I.C., C.A.M. Rixon, and H.J. MacIsaac. 2006. Popularity and propagule pressure: Determinants of introduction and establishment of aquarium fish. Biol. Invas. 8:377–382. doi:10.1007/s10530-004-2310-2

Duguay, S., F. Eigenbrod, and L. Fahrig. 2007. Effects of surrounding urbanization on non-native flora in small forest patches. Landscape Ecol. 22:589–599. doi:10.1007/s10980-006-9050-x

Duncan, R.P., and P.A. Williams. 2002. Darwin's naturalization hypothesis challenged. Nature 417:608–609. doi:10.1038/417608a

Ehrenfeld, J.G. 2003. Effects of exotic plant invasions on soil nutrient cycling processes. Ecosystems 6:503–523. doi:10.1007/s10021-002-0151-3

Ellis, E.C., H. Wang, H.S. Xiao, K. Peng, X. P. Liu, S.C. Li, H. Ouyang, X. Cheng, and L.Z. Yang. 2006. Measuring long-term ecological changes in densely populated landscapes using current and historical high resolution imagery. Remote Sens. Environ. 100:457–473. doi:10.1016/j.rse.2005.11.002

Eppinga, M.B., M. Rietkerk, S.C. Dekker, and P.C. De Ruiter. 2006. Accumulation of local pathogens: Anew hypothesis to explain exotic plant invasions. Oikos 114(1):168–176. doi:10.1111/j.2006.0030-1299.14625.x

Ewel, J.J., and F.E. Putz. 2004. A place for alien species in ecosystem restoration. Frontiers in Ecol. Environ. 2(7):354–360. doi:10.1890/1540-9295(2004)002[0354:APFASI]2.0.CO;2

Faeth, S.H., P.S. Warren, E. Shochat, and W.A. Marussich. 2005. Trophic dynamics in urban communities. BioScience 55(5):399–407. doi:10.1641/0006-3568(2005)055[0399:TDIUC]2.0.CO;2

Fargione, J., C.S. Brown, and D. Tilman. 2003. Community assembly and invasion: An experimental test of neutral versus niche processes. Proc. Natl. Acad. Sci. 100(15):8916–8920.

Foss, L.K., and L.K. Rieske. 2003. Species-specific differences in oak foliage affect preference and performance of gypsy moth caterpillars. Entomol. Exp. Appl. 108:87–93. doi:10.1046/j.1570-7458.2003.00067.x

Franklin, J. 2007. Recovery from clearing, cyclone and fire in rain forests of Tonga, South Pacific: Vegetation dynamics 1995–2005. Austral Ecol. 32:789–797. doi:10.1111/j.1442-9993.2007.01766.x

Franklin, J.F., and R.T.T. Forman. 1987. Creating landscape pattern by forest cutting: Ecological consequences and principles. Landscape Ecol. 1:5–18. doi:10.1007/BF02275261

Franklin, J.F., T.A. Spies, S. Van Pelt, A.B. Carey, D. A. Thornburgh, D. R. Berg, D.B. Lindenmayer, M.E. Harmon, W.S. Keeton, D.C. Shaw, K. Bible, and J. Chen. 2002. Disturbances and structural development of natural forest ecosystems with silvicultural implications, using Douglas-fir forests as an example. For. Ecol. Manage. 155:399–423. doi:10.1016/S0378-1127(01)00575-8

Franks, S.J., and A.E. Weis. 2009. Climate change alters reproductive isolation and potential gene flow in an annual plant. Evol. Appl. 2(4):481–488. doi:10.1111/j.1752-4571.2009.00073.x

Funk, J.L. 2008. Differences in plasticity between invasive and native plants from a low resource environment. J. Ecol. 96:1162–1173. doi:10.1111/j.1365-2745.2008.01435.x

Gavier-Pizarro, G.I., V.C. Radeloff, S.I. Stewart, C.D. Huebner, and N.S. Keuler. 2010a. Housing is positively associated with invasive exotic plant species richness in New England, USA. Ecol. Appl. 20(7):1913–1925. doi:10.1890/09-2168.1

Gavier-Pizarro, G.I., V.C. Radeloff, S.I. Stewart, C.D. Huebner, and N.S. Keuler. 2010b. Rural housing is related to plant invasions in forests of southern Wisconsin, USA. Landscape Ecology 25:1505–1518. doi:10.1007/s10980-010-9516-8

Gilbert, B., and M.J. Lechowicz. 2005. Invasibilty and abiotic gradients: The positive correlation between native and exotic plant diversity. Ecol. 86(7):1848–1855. doi:10.1890/04-09997

Gill, S.E., J.F. Handley, A.R. Ennos, and S. Pauleit. 2007. Adapting cities for climate change: The role of the green infrastructure. Built Environ. 33(1):115–133. doi:10.2148/benv.33.1.115

Given, D. 1990. Conserving botanical diversity on a global scale. Annu Missouri Bot. Gardens 77:48–62. doi:10.2307/2399624

Godefroid, S., and N. Koedam. 2003. Distribution pattern of the flora in a peri-urban forest: An effect of the city-forest ecotone. Landscape Urban Plan. 65:169–185. doi:10.1016/S0169-2046(03)00013-6

Gómez-Aparicio, L., and C.D. Canham. 2008a. Neighborhood analyses of the allelopathic effects of the invasive tree *Ailanthus altissima* in temperate forests. J. Ecol. 96:447–458. doi:10.1111/j.1365-2745.2007.01352.x

Gómez-Aparicio, L., and C.D. Canham. 2008b. Neighborhood models of the effects of invasive tree species on ecosystem processes. Ecol. Monogr. 78(1):69–86. doi:10.1890/06-2036.1

Gosper, C.R., C.D. Stansbury, and G. Vivian-Smith. 2005. Seed dispersal of fleshy-fruited invasive plants by birds: Contributing factors and management options. Divers. Distrib. 11:549–558. doi:10.1111/j.1366-9516.2005.00195.x

Grimm, N.B., S.H. Faeth, N.E. Golubiewski, C.L. Redman, J. Wu, X. Bai, and J.M. Briggs. 2008. Global change and the ecology of cities. Science 319:756–760. doi:10.1126/science.1150195

Grove, J.M., J. O'Neil-Dunne, K. Pelletier, D. Nowak, and J. Walton. 2006a. A report on New York City's present and possible urban tree canopy. Forestry and Horticulture, Dep. of Parks and Recreation, New York City, NY.

Grove, J.M., A.R. Troy, J.P.M. O'Neil-Dunne, W.R. Burch Jr., M.L. Cadenasso, and S.T.A. Pickett. 2006b. Characterization of households and its implications for the vegetation of urban ecosystems. Ecosystems 9:578–597. doi:10.1007/s10021-006-0116-z

Guo, Q., H. Qian, R.E. Ricklefs, and W. Xi. 2006. Distributions of exotic plants in eastern Asia and North America. Ecol. Lett. 9:827–834. doi:10.1111/j.1461-0248.2006.00938.x

Gurevitch, J., and D.K. Padilla. 2004. Are invasive species a major cause of extinctions? Trends Ecol. Evol. 19(9):470–474. doi:10.1016/j.tree.2004.07.005

Hahs, A.K., M.J. McDonnell, M.A. McCarthy, P.A. Vesky, R.T. Corlett, B.A. Norton, S.E. Clements, R.P. Duncan, K. Thompson, M.W. Schwartz, and N.S.G. Williams. 2009. A global synthesis of plant extinction rates in urban areas. Ecol. Lett. 12:1165–1173. doi:10.1111/j.1461-0248.2009.01372.x

Hammer, R.B., S.I. Stewart, and V.C. Radeloff. 2009. Demographic trends, the wildland–urban interface, and wildfire management. Soc. Nat. Resour. 22:777–782. doi:10.1080/08941920802714042

Hanski I., and O. Ovaskainen. 2003. Metapopulation theory for fragmented landscapes. Theoretical Population Biology 64:119–127. doi:10.1016/S0040-5809(03)00022-4

Hartman, K., and B.C. McCarthy. 2004. Restoration of a forest understory after the removal of an invasive shrub, Amur honeysuckle (*Lonicera maackii*). Restor. Ecol. 12(2):154–165. doi:10.1111/j.1061-2971.2004.00368.x

Haas, C.A. 1995. Dispersal and use of corridors by birds in wooded patches on an agricultural landscape. Conserv. Biol. 9(4):845–854. doi:10.1046/j.1523-1739.1995.09040845.x

Hejda, M., and P. Pyšek. 2006. What is the impact of *Impatiens glandulifera* on species diversity of invaded riparian vegetation? Biol. Conserv. 132:143–152. doi:10.1016/j.biocon.2006.03.025

Hess, G.R. 1994. Conservation corridors and contagious disease: A cautionary note. Conserv. Biol. 8(1):256–262. doi:10.1046/j.1523-1739.1994.08010256.x

Hobbs, R.J. 2001. Synergisms among habitat fragmentation, livestock grazing, and biotic invasions in Southwestern Australia. Conserv. Biol. 15(6):1522–1528. doi:10.1046/j.1523-1739.2001.01092.x

Hobbs, R.J., S. Arico, J. Aronson, J. S. Baron, P. Bridgewater, V. A. Cramer, P.R. Epstein, J.J. Ewel, C. A. Klink, a. E. Lugo, D. Norton, D. Ojima, D. M. Richardson, R.W. Sanderson, F. Valladoares, M. Vilà, R. Zamora, and M. Zobel. 2006. Novel ecosystems: Theoretical and management aspects of the new ecological order. Global Ecol. Biogeogr. 15:1–7. doi:10.1111/j.1466-822X.2006.00212.x

Hobbs, R.J., and L.F. Huenneke. 1992. Disturbance, diversity, and invasion: Implications for conservation. Conserv. Biol. 6(3):324–337. doi:10.1046/j.1523-1739.1992.06030324.x

Hobbs, R.J., and C.J. Yates. 2003. Impacts of ecosystem fragmentation on plant populations: Generalising the idiosyncratic. Aus. J. Bot. 51:471–488. doi:10.1071/BT03037

Holdaway, R.J., and A.D. Sparrow. 2006. Assembly rules operating along a primary riverbed-grassland successional sequence. J. Ecol. 94:1092–1102. doi:10.1111/j.1365-2745.2006.01170.x

Hope, D., C. Gries, W. Zhu, W.F. Fagan, C.L. Redman, N.B. Grimm, A.L. Nelson, C. Martin, and A. Kinzig. 2003. Socioeconomics drive urban plant diversity. Proc. Natl. Acd. Sci.100 (15):8788–8792. doi:10.1073/pnas.1537557100

Huebner, C.D. 2005. Competitive ability of *Ailanthus altissima* and an overview of other RWU-4557 invasive plant studies. In: Proc. 16th USDA interagency research forum gypsy moth and other invasive species. GTR-NE-337. p. 45.

Huebner, C.D., and P.C. Tobin. 2006. Invasibility of mature and 15-year-old deciduous forests by exotic plants. Plant Ecol. 186:57–68. doi:10.1007/s11258-006-9112-9

Huebner, C.D., C. Olson, and H. Smith. 2007. Invasive plants field and reference guide: An ecological perspective of plant invaders of forests and woodlands and supplements 1 and 2. NA-TP-05-04. USDA Forest Service, Northern Area State and Private Forestry, Newtown Square, PA.

Huebner, C.D. 2011. Seed mass, viability, and germination of Japanese stiltgrass (*Microstegium vimineum*) under variable light and moisture conditions. Invas. Plant Sci. Manage. 4:274–283. doi:10.1614/IPSM-D-10-00090.1

Hulme, P.E., and E.T. Bremner. 2006. Assessing the impact of *Impatiens glandulifera* on riparian habitats: Partitioning diversity components following species removal. J. Appl. Ecol. 43:43–50. doi:10.1111/j.1365-2664.2005.01102.x

Hutchinson, T.F., and J.I. Vankat. 1998. Landscape structure and spread of the exotic shrub *Lonicera maackii* (Amur honeysuckle) in southwestern Ohio forests. Am. Midl. Nat. 139:383–390. doi:10.1674/0003-0031(1998)139[0383:LSASOT]2.0.CO;2

Jablonski, D. 1986. Mass extinctions: New answers, new questions. In: L. Kaufman and K. Mallory, editors, The last extinction. MIT, Cambridge, MA. p. 43–62.

Johnson, L. 2010. City farmer. Graystone Books, Vancouver, BC, Canada. p. 1–256.

Kagata, H., and T. Ohgushi. 2006. Bottom-up tropic cascades and material transfer in terrestrial food webs. Ecol. Res. 21:26–34. doi:10.1007/s11284-005-0124-z

Kareiva, P., S. Watts, R. McDonald, and T. Boucher. 2007. Domesticated nature: Shaping landscapes and ecosystems for human welfare. Science 316:1866–1869. doi:10.1126/science.1140170

Kennedy, T.A., S. Naeem, K.M. Howe, J.M.H. Knops, D. Tilman, and P. Reich. 2002. Biodiversity as a barrier to ecological invasion. Nature 417:636–638. doi:10.1038/nature00776

Kleczewski, N.M., and S.L. Flory. 2010. Leaf blight disease on the invasive grass *Microstegium vimineum* caused by a *Bipolaris* sp. Plant Dis. 94:807–811. doi:10.1094/PDIS-94-7-0807

Kostel-Hughes, F., T.P. Young, and M.M. Carreiro. 1998a. Forest leaf litter quantity and seedling occurrence along an urban–rural gradient. Urban Ecosyst. 2:263–278. doi:10.1023/A:1009536706827

Kostel-Hughes, F., T.P. Young, and M.J. McDonnell. 1998b. The soil seed bank and its relationship to the aboveground vegetation in deciduous forests in New York City. Urban Ecosystems 2:43–59. doi:10.1023/A:1009541213518

Kowarik, I. 1995. Time lags in biological invasions with regards to the success and failure of alien species. In: P. Pyšek et al., editors, Plant invasions: General aspects and special problems. SPB Academic Publ., Amsterdam. p. 85–103.

Kowarik, I. 2008. On the role of alien species in urban flora and vegetation. In: J.M. Marzluff et al., editors, Urban ecology. Springer, New York. p. 321– 338.

Kowarik, I. 2011. Novel urban ecosystems, biodiversity, and conservation. Environ. Pollut. 159:1974–1983. doi:10.1016/j.envpol.2011.02.022

Křivánek, M., P. Pyšek, and V. Jarošík. 2006. Planting history and propagule pressure as predictors of invasion by woody species in a temperate region. Conserv. Biol. 20(5):1487–1498. doi:10.1111/j.1523-1739.2006.00477.x

Krueger-Mangold, J.M., R.L. Sheley, and T.J. Svejcar. 2006. Toward ecologically-based invasive plant management on rangeland. Weed Science 54:597–605. doi:10.1614/WS-05-049R3.1

Kuhman, T.R., S.M. Pearson, and M.G. Turner. 2011. Agricultural land-use history increases non-native plant invasion in a southern Appalachian forest a century after abandonment. Can. J. For. Res. 41:920–929. doi:10.1139/x11-026

Kühn, I., and S. Klotz. 2006. Urbanization and homogenization– comparing the floras of urban and rural areas in Germany. Biol. Conserv. 127: 292–300. doi:10.1016/j.biocon.2005.06.033

Kumar, S., T.J. Stohlgren, and G.W. Chong. 2006. Spatial heterogeneity influences native and non-native plant species richness. Ecology 87(12):3186–3199. doi:10.1890/0012-9658(2006)87[3186:SHINAN]2.0.CO;2

Kuusipalo, J., G. Adjers, Y Jafarsidik, A. Otasamo, K. Tuomela, and R. Vuokko. 1995. Restoration of natural vegetation in degraded *Imperata cylindrica* grassland: Understorey development in forest plantations. J. Veg. Sci. 6:205–210. doi:10.2307/3236215

La Sorte, F.A., M.L. McKinney, and P. Pyšek. 2007. Compositional similarity among urban floras within and across continents: Biogeographical consequences of human-mediated biotic interchange. Global Change Biol. 13:913–921. doi:10.1111/j.1365-2486.2007.01329.x

Lambdon, P.W., and P.E. Hulme. 2006. How strongly do interactions with closely-related native species influence plant invasions? Darwin's naturalization hypothesis assessed on Mediterranean islands. J. Biogeogr. 33:1116–1125. doi:10.1111/j.1365-2699.2006.01486.x

Lambrinos, J.G. 2000. The impact of invasive alien grass *Cortaderia jubata* (Lemoine) Stapf. on an endangered Mediterranean-type shrubland in California. Divers. Distrib. 6:217–231. doi:10.1046/j.1472-4642.2000.00086.x

Lavergne, S., W. Thuiller, J. Molina, and M. Debussche. 2005. Environmental and human factors influencing rare plant local occurrence, extinction and persistence: A 115 year study in the Mediterranean region. J. Biogeogr. 32:799–811. doi:10.1111/j.1365-2699.2005.01207.x

Leishman, M.R., and V.P. Thomson. 2005. Experimental evidence for the effects of additional water, nutrients and physical disturbance on invasive plants in low fertility Hawkesbury Sandstone soils, Sydney. Aust. J. Ecol. 93: 38–49.

Levine, J.M., P.B. Adler, and S.G. Yelenik. 2004. A meta-analysis of biotic resistance to exotic plant invasions. Ecol. Lett. 7:975–989. doi:10.1111/j.1461-0248.2004.00657.x

Levine, J.M., M. Vilà, C.M. D'Antonio, J.S. Dukes, K. Grigulis, and S. Lavorel. 2003. Mechanisms underlying the impacts of exotic plant invasions. Proc. R. Soc. Lond. B 270:775–781. doi:10.1098/rspb.2003.2327

Lockwood, J.L., P. Cassey, and T. Blackburn. 2005. The role of propagule pressure in explaining species invasions. Trends Ecol Evol 20(5):223–228. doi:10.1016/j.tree.2005.02.004

Lockwood, J.L., P. Cassey, and T.M. Blackburn. 2009. The more you introduce the more you get: The role of colonization pressure and propagule pressure in invasion ecology. Divers. Distrib. 15:904–910. doi:10.1111/j.1472-4642.2009.00594.x

Loewenstein, N.J., and E.F. Loewenstein. 2005. Non-native plants in the understory of riparian forests across a land use gradient in the Southeast. Urban Ecosyst. 8:79–91. doi:10.1007/s11252-005-1420-7

Long, J.D., G.C. Trussell, and T. Elliman. 2009. Linking invasions and biogeography: Isolation differentially affects exotic and native plant diversity. Ecology 90(4):863–868. doi:10.1890/08-1337.1

Lovett, G.M., M.M. Traynor, R.V. Pouyat, M.M. Carreiro, W.X. Zhu, and J.W. Baxter. 2000. Atmospheric deposition to oak forests along an urban–rural gradient. Environ. Sci. Technol. 34(20):4294–4300. doi:10.1021/es001077q

Luck, G.W., L.T. Smallbone, and R. O'Brien. 2009. Socio-economics and vegetation change in urban ecosystems: Patterns in space and time. Ecosystems 12: 604–620. doi:10.1007/s10021-009-9244-6

Lugo, A.E. 2004. The outcome of alien tree invasions in Puerto Rico. Front. Ecol. Environ. 2(5):265–273. doi:10.1890/1540-9295(2004)002[0265:TOOATI]2.0.CO;2

Lugo, A.E. 2009. The emerging era of novel tropical forests. Biotropica 41(5):589–591. doi:10.1111/j.1744-7429.2009.00550.x

Maas, J., R.A. Verheij, P.P. Groenewegen, S. de Vries, and P. Spreeuwenberg. 2006. Green space, urbanity, and health: How strong is the relation? J. Epidemiol. Community Health 60:587–592. doi:10.1136/jech.2005.043125

MacDougall, A.S., and R. Turkington. 2005. Are invasive species the drivers or passengers of change in degraded ecosystems. Ecology 86(1):42–55. doi:10.1890/04-0669

MacDougall, A.S., J. Boucher, R. Turkington, and G.E. Bradfield. 2006. Patterns of plant invasion along an environmental stress gradient. J. Veg. Sci. 17:47–56. doi:10.1111/j.1654-1103.2006.tb02422.x

Maestas, J. D., R.L. Knight, and W.C. Gilgert. 2003. Biodiversity across a rural land-use gradient. Conserv. Biol. 17(5):1425–1434. doi:10.1046/j.1523-1739.2003.02371.x

Maillet, J., and C. Lopez-Garcia. 2000. What criteria are relevant for predicting the invasive capacity of a new agricultural weed? The case of invasive American species in France. Weed Res. 40:11–26. doi:10.1046/j.1365-3180.2000.00171.x

Mack, M.C., and C.M. D'Antonio. 1998. Impacts of biological invasions on disturbance regimes. Trends Ecol. Evol. 13(5):195–198.

Mangla, S. I., and R.M. Callaway. 2008. Exotic invasive plant accumulates native soil pathogens which inhibit native plants. J. Ecol. 96:58–67.

Marler, M.J., C.A. Zabinski, and R.M. Callaway. 1999. Mycorrhizae indirectly enhance competitive effects of an invasive forb on a native bunchgrass. Ecology 80:1180–1186. doi:10.1890/0012-9658(1999)080[1180:MIECEO]2.0.CO;2

Maron, J.L., M. Vilà, and J. Arnason. 2004. Loss of enemy resistance among introduced populations of St. John's Wort (*Hypericum perforatum*). Ecology 85:3243–3253. doi:10.1890/04-0297

Marshall, J.M., and D.S. Buckley. 2008. Effects of microsites created by selective harvesting on growth of *Microstegium vimineum* in a central hardwood forest. For. Sci. 54(5):534–542.

Martin, C.A., P.S. Warren, and A.P. Kinzig. 2004. Neighborhood socioeconomic status is a useful predictor of perennial landscape vegetation in residential neighbourhoods and embedded small parks of Phoenix, AZ. Landscape Urban Plan. 69:355–368. doi:10.1016/j.landurbplan.2003.10.034

Martin, P.H., C.D. Canham, and P.L. Marks. 2009. Why forests appear resistant to exotic plant invasions: Intentional introductions, stand dynamics, and the role of shade tolerance. Front. Ecol. Environ. 7(3):142–149. doi:10.1890/070096

Martin, P.H., and P.L. Marks. 2006. Intact forests provide only weak resistance to a shade-tolerant invasive Norway Maple (*Acer platanoides* L.). J. Ecol. 94:1070–1079. doi:10.1111/j.1365-2745.2006.01159.x

Matlack, G.R. 1994. Vegetation dynamics of the forest edge–trends in space and successional time. J. Ecol. 82:113–123. doi:10.2307/2261391

McDonald, R.I., P. Kareiva, and R.T.T. Forman. 2008. The implications of current and future urbanization for global protected areas and biodiversity conservation. Biol. Conserv. 141:1695–1703. doi:10.1016/j.biocon.2008.04.025

McDonnell, M.J., S.T.A. Pickett, P. Groffman, P. Bohlen, R.V. Pouyat, W. Zipperer, R.W. Parmelee, M.M. Carreiro, and K. Medley. 1997. Ecosystem processes along an urban-to-rural gradient. Urban Ecosyst. 1:21–36. doi:10.1023/A:1014359024275

McKinney, M.L. 2004. Measuring floristic homogenization by non-native plants in North America. Global Ecol. Biogeogr. 13:47–53. doi:10.1111/j.1466-882X.2004.00059.x

McKinney, M.L. 2005. Species introduced from nearby sources have a more homogenizing effect than species from distance sources: Evidence from plants and fishes in the USA. Divers. Distrib. 11:367–374. doi:10.1111/j.1366-9516.2005.00181.x

McKinney, M.L. 2006. Urbanization as a major cause of biotic homogenization. Biol. Conserv. 127:247–260. doi:10.1016/j.biocon.2005.09.005

McKinney, M.L., and J.L. Lockwood. 1999. Biotic homogenization: A few winners replacing many losers in the next mass extinction. Trends Ecol. Evol. 14(11):450–453. doi:10.1016/S0169-5347(99)01679-1

McPherson, E.G., D. Nowak, G. Heisler, S. Grimmond, C. Souch, R. Grant, and R. Rowntree. 1997. Quantifying urban forest structure, function, and value: The Chicago urban forest climate project. Urban Ecosyst. 1:49–61. doi:10.1023/A:1014350822458

Minor, E.S., S.M. Tessel, K.A.M. Engelhardt, and T.R. Lookingbill. 2009. The role of landscape connectivity in assembling exotic plant communities: A network analysis. Ecology 90(7):1802–1809. doi:10.1890/08-1015.1

Mitchell, C.E., A.A. Agrawal, J.D. Bever, G.S. Gilbert, R.A. Hufvauer, J.N. Klironomos, J. L. Maron, W.F. Morris, I.M. Parker, A.G. Power, E.W. Seabloom, M.E. Torchin, and D.P. Vazquez. 2006. Biotic interactions and plant invasions. Ecol. Lett. 9:726–740. doi:10.1111/j.1461-0248.2006.00908.x

Mitchell, C.E., and A.G. Power. 2003. Release of invasive plants from fungal and viral pathogens. Nature 421:625–627. doi:10.1038/nature01317

Moffatt, S.F., and S.M. McLachlan. 2004. Understorey indicators of disturbance for riparian forests along an urban-rural gradient in Manitoba. Ecol. Indicators 4:1–16. doi:10.1016/j.ecolind.2003.08.002

Moffatt, S.F., S.M. McLachlan, and N.C. Kenkel. 2004. Impacts of land use on riparian forest along an urban– rural gradient in southern Manitoba. Plant Ecol. 174:119–135. doi:10.1023/B:VEGE.0000046055.27285.fd

Moles, A.T., M.A.M. Gruber, and S.P. Bonser. 2008. A new framework for predicting invasive plant species. J. Ecol. 96:13–17.

Montgomery, M.R. 2008. The urban transformation of the developing world. Science 319: 761–764. doi:10.1126/science.1153012

Murrell, C., E. Gerber, C. Krebs, M. Parepa, U. Schaffner, and O. Bossdorf. 2011. Invasive knotweed affects native plants through allelopathy. Am. J. Bot. 98(1):38–43. doi:10.3732/ajb.1000135

Naeem, S., J.M.H. Knops, D. Tilman, K.M. Howe, T. Kennedy, and S. Gale. 2000. Plant diversity increases resistance to invasion in the absence of covarying extrinsic factors. Oikos 91:97–108. doi:10.1034/j.1600-0706.2000.910108.x

National Invasive Species Council. 2011. National Invasive Species Management Plan 2008–2012. http://www.invasivespecies.gov (accessed October 2011).

New York State Department of Environmental Conservation. 2011. Interim Invasive Species Plant List. http://www.dec.ny.gov/animals/65408.html (accessed June 2011).

Niemelä, J. 1999. Is there a need for a theory of urban ecology? Urban Ecosyst. 3:57–65. doi:10.1023/A:1009595932440

Niemiera, A.X., and B. Von Holle. 2009. Invasive plant species and the ornamental horticultural industry. In: Inderjit, editor, Management of invasive weeds. Springer, Center for Environmental Management of Degraded Ecosystems, University of Delhi, Delhi, India. p. 167–187.

Nowak, D.J. 2010. Urban biodiversity and climate change. In: N. Muller, P. Werner, and J.G. Kelcey, editors, Urban biodiversity and design. Wiley-Blackwell, Hoboken, NJ. p. 101–117.

Nowak, D.J., D.E. Crane, J.C. Stevens, R.E. Hoehn, J.T. Walton, and J. Bond. 2008. A ground-based method of assessing urban forest structure and ecosystem services. Arboric. Urban For. 34(6):347–358.

Nowak, D.J., D.E. Crane, J.C. Stevens, and M. Ibarra. 2002. Brooklyn's urban forest. General Tech. Rep. NE-290. USDA Forest Service, Northern Research Station, Newtown Square, PA.

Nowak, D.J., M.H. Noble, S.M. Sisinni, and JF. Dwyer. 2001. People & trees: Assessing the U.S. urban forest resource. J. For. 99(3):37–42.

Nowak, D.J., and J.T. Walton. 2005. Projected urban growth (2000–2050) and its estimated impact on the U.S. forest resource. J. For. 103(8):383–389.

Oke, T.R. 1995. The heat island of the urban boundary layer: Characteristics, causes, and effects. In: J.E. Cermak et al., editors, Wind climate in cities. Kluwer Academic Publishers, Amsterdam, the Netherlands. p. 81–107.

Olden, J.D., N. LeRoy, and M.L. McKinney. 2006. Forecasting faunal and floral homogenization associated with human population geography in North America. Biol. Conserv. 127: 261–271. doi:10.1016/j.biocon.2005.04.027

Olden, J.D., and T.P. Rooney. 2006. On defining and quantifying biotic homogenization. Global Ecol. Biogeogr. 15:113–120. doi:10.1111/j.1466-822X.2006.00214.x

Parker, I.M., and G.S. Gilbert. 2007. When there is no escape: The effects of natural enemies on native, invasive, and noninvasive plants. Ecology 88:1210–1224. doi:10.1890/06-1377

Parker, J.D., and M.E. Hay. 2005. Biotic resistance to plant invasions? Native herbivores prefer non-native plants. Ecol. Letters 8:959–967. doi:10.1111/j.1461-0248.2005.00799.x

Pauchard, A., M. Aguayo, E. Peña, and R. Urrutia. 2006. Multiple effects of urbanization on the biodiversity of developing countries: The case of a fast-growing metropolitan area (Concepción, Chile). Biol. Conserv. 127:272–281. doi:10.1016/j.biocon.2005.05.015

Pearman, P.B., A. Guisan, O. Broennimann, and C.F. Randin. 2008. Niche dynamics in space and time. Trends Ecol. Evol. 23(3):149–158. doi:10.1016/j.tree.2007.11.005

Pemberton, R.W, and H. Liu. 2009. Marketing time predicts naturalization of horticultural plants. Ecology 90:69–80. doi:10.1890/07-1516.1

Pickett, S.T.A., W.R. Burch, Jr., S.E. Dalton, T.W. Foresman, J. M. Grove, and R. Rowntree. 1997. A conceptual framework for the study of human ecosystems in urban areas. Urban Ecosyst. 1:185–199. doi:10.1023/A:1018531712889

Pickett, S.T.A., M.L. Cadenasso, J. M. Grove, P.M. Groffman, L.E. Band, C.G. Boone, W.R. Burch, Jr., S.B. Grimmond, J. Hom, J.C. Jenkins, N.L. Law, C.H. Nilon, R.V. Pouyat, K. Szlavecz, P.S. Warren, and M.A. Wilson. 2008. Beyond urban legends: An emerging framework of urban ecology, as illustrated by the Baltimore ecosystem study. BioSci. 58(2):139–150. doi:10.1641/B580208

Pickett, S.T.A., M.L. Cadenasso, J.M. Grove, C.H. Nilon, R.V. Pouyat, W.C. Zipperer, and R. Costanza. 2001. Urban ecological systems: Linking terrestrial ecological, physical, and socioeconomic components of metropolitan areas. Annu. Rev. Ecol. Syst. 32:127–157. doi:10.1146/annurev.ecolsys.32.081501.114012

Pilgrim, E.S., M.J. Crawley, and K. Dolphin. 2004. Patterns of rarity in the native British flora. Biol. Conserv. 120:161–170. doi:10.1016/j.biocon.2004.02.008

Pokorny, M.L., R.L. Shelley, C.A. Zabinski, R.E. Engel, T.J. Svejcar, and J.J. Borkowski. 2005. Plant functional group diversity as a mechanism for invasion resistance. Restor. Ecol. 13(3):448–459. doi:10.1111/j.1526-100X.2005.00056.x

Poland, T.M, and D.G. McCullough. 2006. Emerald ash borer: Invasion of the urban forest and the threat to North America's ash resource. J. For. 104(3):118–124.

Polasky, S., E. Nelson, D. Pennington, and K.A. Johnson. 2011. The impact of land-use change on ecosystem services, biodiversity, and returns to landowners: A case study in the state of Minnesota. Environ. Res. Econ. 48:219–242. doi:10.1007/s10640-010-9407-0

Pouyat, R.V., and M.J. McDonnell. 1991. Heavy metal accumulations in forest soils along an urban-rural gradient in southeastern New York, USA. Water Air Soil Pollut. 57–58:797–807. doi:10.1007/BF00282943

Pouyat, R.V., M.J. McDonnell, and S.T.A. Pickett. 1997. Litter decomposition and nitrogen mineralization in oak stands along an urban-rural land use gradient. Urban Ecosyst. 1:117–131. doi:10.1023/A:1018567326093

Pretto, F., L. Celesti-Grapow, E. Carli, and C. Blasi. 2010. Influence of past land use and current human disturbance on non-native plant species on small Italian islands. Plant Ecol. 210:225–239. doi:10.1007/s11258-010-9751-8

Radeloff, V.C., R.B. Hammer, S.I. Stewart, J.S. Fried, S.S. Holcomb, and J.F. McKeefry. 2005. The wildland-urban interface in the United States. Ecol. Appl. 15(3):799–805. doi:10.1890/04-1413

Ravallion, M., S. Chen, and P. Sangraula. 2007. New evidence on the urbanization of global poverty. Popul. Dev. Rev. 33(4):667–701. doi:10.1111/j.1728-4457.2007.00193.x

Rebele, F. 1994. Urban ecology and special features of urban ecosystems. Global Ecol. Biogeogr. Lett. 4:173–187. doi:10.2307/2997649

Reichard, S.H., and C.W. Hamilton. 1997. Predicting invasions of woody plants introduced into North America. Conserv. Biol. 11(1):193–203. doi:10.1046/j.1523-1739.1997.95473.x

Ricotta, D., M. DiNepi, D. Guglietta, and L. Celesti-Grapow. 2008. Exploring taxonomic filtering in urban environments. J. Veg. Sci. 19:229–238. doi:10.3170/2008-8-18363

Robinson, G.R., and S.N. Handel. 1993. Forest restoration on a closed landfill: Rapid addition of new species by bird dispersal. Conserv. Biol. 7(2):271–278. doi:10.1046/j.1523-1739.1993.07020271.x

Rosenzweig, M.L. 2001. The four questions: What does the introduction of exotic species do to diversity? Evol. Ecol. Res. 3: 361–367.

Saunders, D.A., R.J. Hobbs, and C.R. Margules. 1991. Biological consequences of ecosystem fragmentation: A review. Conserv. Biol. 5(1):18–32. doi:10.1111/j.1523-1739.1991.tb00384.x

Schall, M.J., and D.D. Davis. 2009. *Ailanthus altissima* wilt and mortality: Etiology. Plant Disease 93:747–751. doi:10.1094/PDIS-93-7-0747

Schmidt, K.A., and C.J. Whelan. 1999. Effects of exotic *Lonicera* and *Rhamnus* on songbird nest predation. Conserv. Biol. 13(6):1502–1506. doi:10.1046/j.1523-1739.1999.99050.x

Schwartz, M.W., and D. Simberloff. 2001. Taxon size predicts rates of rarity in vascular plants. Ecol. Lett. 4: 464–469. doi:10.1046/j.1461-0248.2001.00241.x

Schwartz, M.W., J.H. Thorne, and J.H. Viers. 2006. Biotic homogenization of the California flora in urban and urbanizing regions. Biol. Conserv. 127:282–291. doi:10.1016/j.biocon.2005.05.017

Shapiro, A.M. 2002. The California urban butterfly fauna is dependent on alien plants. Divers. Distrib. 8:31–40. doi:10.1046/j.1366-9516.2001.00120.x

Sher, A.A., D.I. Marshall, and S.A. Gilbert. 2000. Competition between native *Populus deltoids* and invasive *Tamarix ramosissima* and the implications for re-establishing flooding disturbance. Conserv. Biol. 14(6):1744–1754. doi:10.1046/j.1523-1739.2000.99306.x

Sieving, K.E., M.F. Wilson, and T. L. De Santo. 1996. Habitat barriers to movement of understory birds in fragmented south-temperate rain-forest. The Auk 113(4):944–949.

Simberloff, D. 2009. The role of propagule pressure in biological invasions. Ann. Rev. Ecol. Evol. Syst. 40:81–102. doi:10.1146/annurev.ecolsys.110308.120304

Smith, R.M., K. Thompson, J.G. Hodgson, P.H. Warren, and K.J. Gaston. 2006. Urban domestic gardens (IX): Composition and richness of the vascular flora, and implications for native biodiversity. Biol. Conserv. 129:312–322. doi:10.1016/j.biocon.2005.10.045

Stehlik, I., J.P. Caspersen, L. Wirth, and R. Holderegger. 2007. Floral free fall in the Swiss lowlands: Environmental determinants of local plant extinction in a peri-urban landscape. J. Ecol. 95:734–744. doi:10.1111/j.1365-2745.2007.01246.x

Steinberg, D.A., R.V. Pouyat, R.W. Parmelee, and P.M. Groffman. 1997. Earthworm abundance and nitrogen mineralization rates along an urban–rural land use gradient. Soil Biol. Biochem. 29(3–4):427–430. doi:10.1016/S0038-0717(96)00043-0

Stewart, S.I., V.C. Radeloff, and R.B. Hammer. 2007. Defining the wildland urban interface. J. For. 105(4):201–207.

Stinson, K.A., S.A. Campbell, J.R. Powell, B.E. Wolfe, R.M. Callaway, G.C. Thelen, S.G. Hallett, D. Prati, and J.N. Klironomos. 2006. Invasive plant suppresses the growth of native tree seedlings by disrupting belowground mutualisms. PLoS Biol. 4(5):e140. doi:10.1371/journal.pbio.0040140

Stohlgren, T.J., D. Binkley, G.W. Chong, M.A. Kalkhan, L.D. Schell, K.A. Bull, Y. Otsuki, G. Newman, M. Bashkia, and Y. Son. 1999. Exotic plant species invade hot spots of native plant diversity. Ecol. Monogr. 69:25–46. doi:10.1890/0012-9615(1999)069[0025:EPSIHS]2.0.CO;2

Strauss, S.Y., C.O. Webb, and N. Salamin. 2006. Exotic taxa less related to native species are more invasive. Proc. Natl. Acad. Sci. 103(15):5841–5845. doi:10.1073/pnas.0508073103

Sturtevant, B.R., B.R. Miranda, J. Yang, H.S. He, E.J. Gustafson, and R.M. Scheller. 2009. Studying fire mitigation strategies in multi-ownership landscapes: Balancing the management of fire-dependent ecosystems and fire risk. Ecosystems 12:445–461. doi:10.1007/s10021-009-9234-8

Sullivan, J.J., S.M. Timmins, and P.A. Williams. 2005. Movement of exotic plants into coastal native forests from gardens in northern New Zealand. N.Z. J. Ecol. 29(1):1–10.

Swanson, M.E., J. F. Franklin, R. L. Beschta, C.M. Crisafulli, D.A. DellaSala, R.L. Hutto, D.B. Lindenmayer, and F.J. Swanson. 2011. The forgotten stage of forest succession: Early-successional ecosystems on forest sites. Front. Ecol. Environ. 9(2):117–125. doi:10.1890/090157

Syphard, A.D., K.C. Clarke, and J. Franklin. 2007. Simulating fire frequency and urban growth in southern California coastal shrublands, USA. Landscape Ecol. 22:431–445. doi:10.1007/s10980-006-9025-y

Theobald, D.M. 2004. Placing exurban land-use change in a human modification framework. Frontiers Ecol. Environ. 2(3):139–144. doi:10.1890/1540-9295(2004)002[0139:PELCIA]2.0.CO;2

Theobald, D.M., and W.H. Romme. 2007. Expansion of the U.S. wildland-urban interface. Landscape Urban Plan. 83:340–354. doi:10.1016/j.landurbplan.2007.06.002

Theoharides, K.A., and J.S. Dukes. 2007. Plant invasion across space and time: Factors affecting nonindigenous species success during four stages of invasion. New Phytol. 176:256–273. doi:10.1111/j.1469-8137.2007.02207.x

Thiele, J., J. Kollmann, and U.R. Anderson. 2009. Ecological and socioeconomic correlates of plant invasions in Denmark: The utility of environmental assessment data. Ambio 38(2):89–94. doi:10.1579/0044-7447-38.2.89

Tilman, D. 1994. Competition and biodiversity in spatially structured habitats. Ecol. 75(1):2–16. doi:10.2307/1939377

Tipping, P.W. 2000. Natural and augmented spread of rose rosette disease of multiflora rose in Maryland. Plant Disease 84(12):1344. doi:10.1094/PDIS.2000.84.12.1344C

Torchin, M.E., and C.E. Mitchell. 2004. Parasites, pathogens, and invasions by plants and animals. Front. Ecol. Environ. 2(4):183–190. doi:10.1890/1540-9295(2004)002[0183:PPAIBP]2.0.CO;2

Tracey, D. 2011. Urban agriculture. New Society Publ., Gabriola Island, BC, Canada. p. 1–256.

Traveset, A., and D.M. Richardson. 2006. Biological invasions as disruptors of plant reproductive mutualisms. Trends Ecol. Evol. 21(4):208–216. doi:10.1016/j.tree.2006.01.006

Tucker, K.C., and D.M. Richardson. 1995. An expert system for screening potentially invasive alien plants in South African fynbos. J. Environ. Manage. 44:309–338. doi:10.1016/S0301-4797(95)90347-X

Turner, I.M., and R.T. Corlett. 1996. The conservation value of small, isolated fragments of lowland tropical rain forest. Trends Ecol. Evol. 11(8):330–333. doi:10.1016/0169-5347(96)10046-X

United Nations Population Division. 2006. World urbanization prospects: The 2005 revision. United Nations, New York.

University of Georgia, Georgia Exotic Pest Plant Council. 2006. List of Non-native Invasive Plants in Georgia. http://www.gaeppc.org/list.cfm (accessed June 2011).

University of Georgia, Center for Invasive Species and Ecosystem Health. Illionois Invasive plant List 2011. http://www.invasive.org/species/list.cfm?id=152 (accessed June 2011).

University of Georgia, Center for Invasive Species and Ecosystem Health. 2010. Plant Species Reported to be Invasive in Natural Areas. Invasive Plant Atlas of the United States. http://www.invasiveplantatlas.org/index.html (accessed June 2011).

U.S. Bureau of the Census. 2011a. Population distribution and change: 2000 to 2010. U.S. Department of Commerce, Economics and Statistics Administration. http://www.census.gov/prod/cen2010/briefs/c2010br-01.pdf (accessed Aug. 2011).

U.S. Bureau of the Census. 2011b. Urban area criteria for the 2010 census. Federal Register 76(164):53030–53043.

U.S. Department of the Interior, Bureau of Land Management. 2008. BLM National List of Invasive Weed Species of Concern. http://www.blm.gov/co/st/en/BLM_Programs/botany/invasiweed.html (accessed June 2011).

USDA Forest Service, Fire Effects Information System. 2011. FEIS Invasive Plants List. http://www.fs.fed.us/database/feis/plants/weed/index.html (accessed June 2011).

Vermeij, G.J. 2005. Invasion as expectation: A historical fact of life. In: D.F. Sax, J.J. Stachowicz, and S.D. Gaines, editors, Species invasions: Insights into ecology, evolution, and biogeography. Sinauer Associates, Inc., Sunderland, MA. p. 315–339.

Vilà, M., J. Pino, and X. Font. 2007. Regional assessment of plant invasions across different habitat types. J. Veg. Sci. 18:35–42. doi:10.1111/j.1654-1103.2007.tb02513.x

Vilà, M., and J. Weiner. 2004. Are invasive plant species better competitors than native plant species?—evidence from pair-wise experiments. Oikos 105:229–238. doi:10.1111/j.0030-1299.2004.12682.x

von der Lippe, M., and I. Kowarik. 2008. Do cities export diversity? Traffic as dispersal vector across urban-rural gradients. Divers. Distrib. 14:18–25. doi:10.1111/j.1472-4642.2007.00401.x

Von Holle, B., and D. Simberloff. 2005. Ecological resistance to biological invasion overwhelmed by propagule pressure. Ecology 86(12):3212–3218. doi:10.1890/05-0427

Walker, J.S., N.B. Grimm, J.M. Briggs, C. Gries, and L. Dugan. 2009. Effects of urbanization on plant species diversity in central Arizona. Front. Ecol. Environ. 7(9):465–470. doi:10.1890/080084

Wania, A., I. Kühn, and S. Klotz. 2006. Plant richness patterns in agricultural and urban landscapes in Central Germany–spatial gradients of species richness. Landscape Urban Plan. 75:97–110. doi:10.1016/j.landurbplan.2004.12.006

Weng, Y-C. 2007. Spatiotemporal changes of landscape pattern in response to urbanization. Landscape Urban Plan. 81:341–353. doi:10.1016/j.landurbplan.2007.01.009

Westphal, J.M. 2001. Managing agricultural resources at the urban–rural interface: A case study of the Old Mission Peninsula. Landscape Urban Plan. 57:13–24. doi:10.1016/S0169-2046(01)00185-2

Wilcove, D.S., D. Rothstein, J. Dubow, A. Phillips, and E. Losos. 1998. Quantifying threats to imperiled species in the United States. Bioscience 48(8):607–615. doi:10.2307/1313420

Williams, N.S.G., J.W. Morgan, M.J. McDonnell, and M.A. McCarthy. 2005. Plant traits and local extinctions in natural grasslands along an urban–rural gradient. J. Ecol. 93:1203–1213. doi:10.1111/j.1365-2745.2005.01039.x

Williams, N.S.G., M.W. Schwartz, P.A. Vesk, M.A. McCarthy, A.K. Hahs, S.E. Clements, R.T. Corlett, R.P. Duncan, B.A. Norton, K. Thompson, and M.J. McDonnell. 2009. A conceptual framework for predicting the effects of urban environments on floras. J. Ecol. 97:4–9. doi:10.1111/j.1365-2745.2008.01460.x

Williamson, M., and A. Fitter. 1996. The varying success of invaders. Ecology 77:1661–1666. doi:10.2307/2265769

Willis, C.G., B.R. Ruhfel, R.B. Primack, A.J. Miller-Rushing, J.B. Losos, and C.C. Davis. 2010. Favorable climate change response explains non-native species' success in Thoreau's Woods. PLoS One 5(1):E8878. doi:10.1371/journal.pone.0008878

Wilson, J.R.U., E. E. Dormontt, P.J. Prentis, A.J. Lowe, and D.M. Richardson. 2009. Something in the way you move: Dispersal pathways affect invasion success. Trends Ecol Evol. 24(3):136–44.

Wirth, F.F., K.J. Davis, and S.B. Wilson. 2004. Florida nursery sales and economic impacts of 14 potentially invasive landscape plant species. J. Environ. Hort. 22(1):12–16.

With, K.A. 2002. The landscape ecology of invasive spread. Conserv. Biol. 16:1192–1203. doi:10.1046/j.1523-1739.2002.01064.x

Wittig, R. 2004. The origin and development of the urban flora of Central Europe. Urban Ecosyst. 7:323–339. doi:10.1007/s11252-005-6833-9

Wu, J. 2008. Making a case for landscape ecology: An effective approach to urban sustainability. Landscape J. 27:41–50. doi:10.3368/lj.27.1.41

Zavaleta, E.S., R.J. Hobbs, and H.A. Mooney. 2001. Viewing invasive species removal in a whole-ecosystem context. Trends Ecol. Evol. 16(8):454–459. doi:10.1016/S0169-5347(01)02194-2

Zipperer, W.C. 2002. Species composition and structure of regenerated and remnant forest patches within an urban landscape. Urban Ecosyst. 6:271–290. doi:10.1023/B:UECO.0000004827.12561.d4

Zipperer, W.C. 2010. Factors influencing non-native tree species distribution in urban landscapes. In: N. Muller, P. Werner, and J.G. Kelcey, editors, Urban biodiversity and design. Blackwell, Hoboken, NJ. p. 243–251.

Zipperer, W.C., J. Wu, R.V. Pouyat, and S.T.A. Pickett. 2000. The application of ecological principles to urban and urbanizing landscapes. Ecol. Appl. 10(3):685–688. doi:10.1890/1051-0761(2000)010[0685:TAOEPT]2.0.CO;2

Ziska, L.H., J.A. Bunce, and E.W. Goins. 2004. Characterization of an urban-rural CO_2/temperature gradient and associated changes in initial plant productivity during secondary succession. Oecologia 139:454–458. doi:10.1007/s00442-004-1526-2