

Exotic invasive species in urban wetlands: environmental correlates and implications for wetland management

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Summary

1. Wetlands in urban regions are subjected to a wide variety of anthropogenic disturbances, many of which may promote invasions of exotic plant species. In order to devise management strategies, the influence of different aspects of the urban and natural environments on invasion and community structure must be understood.

2. The roles of soil variables, anthropogenic effects adjacent to and within the wetlands, and vegetation structure on exotic species occurrence within 21 forested wetlands in north-eastern New Jersey, USA, were compared. The hypotheses were tested that different vegetation strata and different invasive species respond similarly to environmental factors, and that invasion increases with increasing direct human impact, hydrologic disturbance, adjacent residential land use and decreasing wetland area. Canonical correspondence analyses, correlation and logistic regression analyses were used to examine invasion by individual species and overall site invasion, as measured by the absolute and relative number of exotic species in the site flora.

3. Within each stratum, different sets of environmental factors separated exotic and native species. Nutrients, soil clay content and pH, adjacent land use and canopy composition were the most frequently identified factors affecting species, but individual species showed highly individualistic responses to the sets of environmental variables, often responding in opposite ways to the same factor.

4. Overall invasion increased with decreasing area but only when sites > 100 ha were included. Unexpectedly, invasion decreased with increasing proportions of industrial/commercial adjacent land use.

5. The hypotheses were only partially supported; invasion does not increase in a simple way with increasing human presence and disturbance.

6. *Synthesis and applications.* The results suggest that a suite of environmental conditions can be identified that are associated with invasion into urban wetlands, which can be widely used for assessment and management. However, a comprehensive ecosystem approach is needed that places the remediation of physical alterations from urbanization within a landscape context. Specifically, sediment, inputs and hydrologic changes need to be related to adjoining urban land use and to the overlapping requirements of individual native and exotic species.

Key-words: forested wetlands, human impacts, land use, nutrients, soils, species richness

Introduction

Forested wetlands in developed landscapes are subject to a large number of stressors that alter their structure and function (Pickett *et al.* 2001; Ehrenfeld *et al.* 2003; Ehrenfeld 2004; Meyer, Paul & Taulbee 2005). These stressors include hydrological changes, inputs of nutrients from both aqueous and atmospheric sources, high frequencies of physical disturbance within sites, large propagule sources of exotic

species from adjacent development, and enhanced dispersal of propagules from human and animal traffic on trails. Invasive and non-native species are likely to establish within such wetlands as a result of these stresses, as frequently demonstrated in comparisons of urban and non-urban landscapes (Kowarik 1995; Borgmann & Rodewald 2005). However, recent studies of urban ecology point out that urban landscapes are themselves highly heterogeneous (McGranahan & Satterthwaite 2003; Clergeau, Jokimäki & Snep 2006; Grove *et al.* 2006). This variability is not surprising, as 'urban development' is actually a very heterogeneous category of

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land use and includes a large range of conditions. In this study the importance of heterogeneity in environmental conditions was evaluated as an explanation for patterns of diversity and abundance of invasive species in urban forested wetlands.

Developed landscapes may affect wetland plant communities through impacts emanating from the surrounding uplands. The types of adjacent land use (e.g. residential, commercial and industrial), road density and human population density in the surrounding region all affect water flow into and through the wetland (Booth & Jackson 1997; Reinelt & Taylor 2000; Paul & Meyer 2001; Allan 2004). These factors also influence nutrient and pollutant inputs, through both water and atmospheric deposition (Lovett *et al.* 2000; Brabec, Schulte & Richards 2002; Connor & Thomas 2003). Area and the amount of habitat edge are well-known correlates of species richness (Harper *et al.* 2005) and most sites in developed regions are small fragments of initially larger habitat. These factors generate other processes influencing invasion; for example, residential development may be a source of propagules from ornamental plants that are also commonly invasive in natural communities, such as Japanese barberry *Berberis thunbergii* DC, burning bush *Euonymus alata* (Thunb.) Sieb. and privet *Ligustrum vulgare* L.

Direct impacts result from the presence of people within wetlands and involve a separate set of factors that can promote exotic invasions. These include: (i) dredging of channels and ditches within the wetland; (ii) presence of formally established or informally created paths, with concomitant disturbance from foot and vehicular traffic (e.g. bicycles and all-terrain vehicles); (iii) presence of pet animals that may serve as dispersers of seeds or as predators of native seed dispersers; (iv) frequent use of wetland edges as dumping sites for rubbish, garden waste, etc., all of which may enhance propagule transport into the wetlands or create disturbed areas; (v) other types of physical disturbance that are frequently observed, including excavations and earth mounds, often reflecting past abuse of the wetland for the disposal of material from adjacent development; (vi) erosional reductions of stream channel elevations (Booth & Jackson 1997; Groffman *et al.* 2003) that lowers the water table in the adjacent wetland surface.

Urban disturbances also may modify the physical environment within wetlands. Soils may be enriched with nutrients, arriving in both soluble form (in floodwater and precipitation) and through deposition of sediments. In wetlands affected by ditches and eroded streams, formerly hydric soils may lose their distinctive properties if they are predominantly dry. Because the large majority of invasive species in these sites are understorey herbs and shrubs, invasion may also reflect the structural properties of vegetation, as canopy cover and shrub density will control light regimes, and plant densities will affect competitive interactions (Alston & Richardson 2006). Physical disturbances to both canopy and shrub strata may enhance invasion by permitting more light penetration and reducing competition from native species.

This study used information on a previously described set of wetlands in the New Jersey section of the metropolitan area around New York City, USA (Ehrenfeld 2000, 2004, 2005;

Ehrenfeld *et al.* 2003), to explore the relative importance of three sets of variables in explaining the degree of exotic invasion. These were (i) soil properties; (ii) descriptors of human impact, including adjacent land use and evidence of direct human disturbance within the wetlands; and (iii) descriptors of vegetation structure. Based on the considerations above, it was hypothesized that the diversity and abundance of exotic species will increase with (i) increasing evidence of direct human presence, (ii) increasing hydrologic disturbance, (iii) increasing residential development in the area surrounding the wetland, and decreasing area of the wetland, and (iv) disrupted canopies, evidenced by low tree densities and/or basal areas.

Methods

SITES AND DATA COLLECTION METHODS

Sites were located throughout north-eastern New Jersey, which is part of the New York–Newark metropolitan urban region of 18.5 million people, the third-largest such agglomeration in the world (United Nations 2004). Sites were chosen following criteria described in Ehrenfeld (2000); briefly, all sites supported mature deciduous forested wetlands as mapped by the New Jersey Wetland Inventory maps (www.statc.nj.us/dep/gis/wetshp.html) and were distributed through the region by selecting one site per US Geological Survey 7.5° quadrangle maps (21 quadrangles). In each site, 10 circular plots, each 10 m in radius (314 m²), were distributed on transects orientated to cover the longest dimensions of each site. Data on vegetation, soils, hydrology and indicators of human disturbance were collected within each plot, as described more fully in Ehrenfeld (2004, 2005) and Ehrenfeld *et al.* (2003). Plants were separated into herbaceous (forbs, graminoids and pteridophytes), woody understorey (shrubs and woody vines), and trees for separate analyses, to test the hypothesis that the different strata are responding to different environmental factors. Taxonomy follows Kartesz & Meacham (1999).

The soils data set included data that were averages of either samples collected at five of the 10 sample points of the top 20 cm of soil (pH, organic matter and texture) or randomly chosen samples from two points that were submitted to the Rutgers University Soil Testing Laboratory, New Brunswick, NJ, for analysis (Mehlich III extractable P, extractable cations and micronutrients). A separate set of eight samples per site was utilized for measurements of extractable inorganic nitrogen (NH_4^+ , NO_3^- + NO_2^-), 2 M KCl extractions following standard methods, and 10-day incubations in the laboratory to determine potential net N mineralization and nitrification rates, normalized to the organic matter content, following standard protocols (Sollins *et al.* 1999). In addition, at each sample point field measurements were made of the depth of the organic layer, percentage of samples ($n = 40$ per site) with Munsell chromas of 2 or less, and percentage of samples with redoximorphic concentrations and depletions present in the top 30 cm of soil (Vepraskas 1996; Vepraskas & Faulkner 2001).

Land-use data were based on measurements made using ARCInfo software. A buffer area of 300 m from the mapped wetland edge was analysed to determine the amount of residential development, a combination of industrial and commercial land use, and naturally vegetated area. These areas were then converted to percentages of the total buffer area for each site. Road density was quantified as

kilometre of road surface (all road size categories) per km² of buffer area. Population density of the surrounding municipality of each site (from census data for the year 2000 (<http://www.census.gov>, accessed July 2006) was used as an indicator of adjacent human population. The area of each wetland site (hectares), was determined from the New Jersey GIS file (<http://www.state.nj.us/Department/gis/wetshp.html>) based on contiguous polygons of forested wetlands at each site. The frequencies of occurrence at the 10 sample points of rubbish (e.g. fast food containers, plastic bags, shopping trolleys and broken furniture), ditches and trails were calculated as indicators of direct human impact.

Descriptors of plant community structure included the mean diameter breast height (cm) of trees ($n = 40$ per site); tree density (number ha⁻¹); shrub density (number of stems ha⁻¹); basal area (m² ha⁻¹); an index of vegetation density [rank order observations of the density (absent, low and high) of four understorey strata, low herbaceous (< 0.5 m), tall herbaceous (0.5–1 m), low woody vegetation (1–3 m) and tall woody understorey vegetation (3–5 m)]; the total number of native species; and a measure of microtopographic heterogeneity (SD of six measures of height from a standard horizontal bar to the ground around a 2-m diameter circle). Shrubs included all species that had multiple woody stems originating from a single root base, whereas trees included stems of at least 2.5 cm d.b.h. of species that have a single main unbranched stem or trunk. Density of trees was calculated from point-quarter measurements made at the centre point of each of the 10 plots. Density of shrubs was determined as the average over the 10 plots of stem counts in a 5-m radius sample area at each point.

STATISTICAL ANALYSES

Canonical correspondence analyses (CCA) were conducted to explore the relationships between species occurrences and the three sets of environmental factors (all analyses conducted in PC-ORD version 5.07; McCune & Mefford 1999). This method was chosen because it specifically and directly tests the importance of explanatory environmental variables in explaining the variance in species composition of a sample of sites (McCune & Grace 2002). In this study, the method was used to test the responses of groups of species (each stratum) to each set of environmental variables. This approach allowed both the important variables within each type of environmental data to be identified and permitted comparisons of the relative importance of the different types of environmental variables in explaining species composition.

Species occurring in fewer than three of the 21 sites were eliminated from the analyses, leaving 105 herbaceous, 38 shrub and vine, and 42 tree species in the three data sets, respectively. Species were represented by their frequency of occurrence at the 10 sample points in each site. Most of the exotic species retained in the analyses were ranked as moderately to highly invasive and damaging to natural communities (NatureServe database; <http://www.natureserve.org/explorer/index.htm>, accessed July 2006). Results of each ordination are displayed as a graph of the species' locations with respect to the first two axes and a listing of factor loadings for the three axes identified by the ordination analysis. Exotic species are identified on each figure (Figs 1–3). Initial data sets including a larger number of variables were pruned to remove variables highly correlated with each other, so that each of these data sets included only variables with correlations of ≤ 0.50 . When variables had correlations > 0.50 , the variable with the largest number of correlations over 0.50 to other variables was dropped. All variables used in the ordinations are described in Table 1.

In order to test whether exotic species as a class were responding to environmental factors differently from native species, the ordination axis scores were compared using a *t*-test for each of the ordination analyses. Equality of variances of the two classes (exotics and natives) was tested and the appropriate *F*-statistic used to evaluate the results of each test. As a second test of the hypothesis that exotic and native species respond uniformly to environmental conditions, overall site invasion was indexed by (i) the total number of exotic species per site and (ii) the proportion of the site flora that was exotic; these two measures were then correlated with the environmental variables.

The behaviour of individual exotic species relative to specific environmental variables was further examined by pooling data for the entire set of 210 plot measurements and using logistic regression to determine whether and how the probability of occurrence of each species was related to those environmental variables measured at each plot. Only exotic species that occurred in at least 20 plots were used for these analyses (12 species). While the 10 points within each site were not technically independent, they reflected a range of physical conditions (varying soil, hydrology, native plant diversity, proximity to boundaries, trails, streams, etc., within each site). For example, the range of diversities within sites (21.3 ± 2.1) was comparable with the mean diversity among sites (25.1 ± 1.6). Moreover, the average frequency of each species within sites was 32% (maximum 47%), indicating that no exotic occurred at all points within a site. The low frequencies of occurrences within sites suggested that spatial correlation of occurrence within sites was low or absent. Therefore, these analyses are presented as providing an indication of the behaviour of each exotic. All statistical tests other than the ordination analyses were conducted in SAS version 9.1 (SAS Institute Inc. 2002).

Results

SPECIES' ORDINATIONS

The environmental variables against which the species were ordinated all covered a wide range of absolute values (Table 1). Canonical correspondence analyses of the three vegetation strata revealed environmental correlates of community composition for each of the sets of factors (Figs 1–3; Table 2). The ordinations all explained about one-third of the variance in the species matrices, suggesting that the three sets of environmental variables were similar in their influence on community structure. On only a few of the ordination axes were native and exotic species significantly different in their mean axis scores (Table 2).

Ordination of the three vegetation strata with respect to soil variables (Fig. 1) showed that the species of each stratum responded to the soil factors differently, as did native and exotic groups of species (Table 2). For herbaceous species (Fig. 1a), gradients of nutrient availability and soil clay content distinguished exotic (higher nutrient availability and pH) and native species (lower nutrient availability, lower pH and higher clay content). Shrubs and vines, in contrast, were primarily arrayed along pH and calcium gradients, with lesser effects of soil texture and nutrient availability; pH was the primary factor separating native and exotic species (Fig. 1b). For the tree species, a combination of nutrients and pH, but also the redox status of the soil (as indicated by reduced chromas), was important in separating native and exotic

Table 1. Environmental variables included in the ordination analyses. For each, the abbreviation used in the ordination diagrams, a description of the units or method of determination, the mean \pm SE and the range for the entire data set (21 sites) are given

Data set	Variable	Units	Abbreviation	Mean \pm SE	Range
Human impact	Ditches	Frequency (of 10 points site ⁻¹)	DITCH	1.5 \pm 0.3	0–5
	Trash	Frequency (of 10 points site ⁻¹)	TRASH	3.6 \pm 0.6	0–8
	Trails	Frequency (of 10 points site ⁻¹)	TRAIL	1.2 \pm 0.3	0–4
	Population density	Number km ⁻² , 2000 census	POPDEN	789.5 \pm 106.2	261–2304
	Area	ha of forested wetland	AREA	71.9 \pm 23.7	5.2–488.6
	Open area	% of buffer in unplanted vegetation	OPEN	61 \pm 6	19–100
	Residential	% of buffer in residential land use	RES	29 \pm 6	0–81
	Industrial	% of buffer in industrial–commercial land use	IND	8 \pm 3	0–47
	Roads	km roads/km ² total buffer area	ROADS	4.3 \pm 0.6	0–10.5
Soil	Organic horizon	Thickness of organic horizon*	OM	16.7 \pm 4.7	0–70
	cm pH	pH units*	pH	5.13 \pm 0.10	4.3–6
	Extractable NO ₃	mg NO ₃ kg organic matter ⁻¹ †	NO3	8.07 \pm 1.7	0–35.4
	Nitrification rate	mg NO ₃ kg organic matter ⁻¹ †	NITR	3.5 \pm 0.5	0–7.44
day ⁻¹	% clay	% clay fraction‡	CLAY	16.5 \pm 3.0	0–45.5
	% reduced chroma	% of soil samples with chroma < 2§	REDCHR	64.7 \pm 7.8	0–100
	P	kg P _{ext} ha ⁻¹ §	P	97.2 \pm 11.24	27.0–227.4
	Zn	mg Zn _{ext} kg soil ⁻¹ †	Zn	17.3 \pm 6.2	2.4–136.7
Vegetation	Tree density	Number stems ha ⁻¹	TREES	596.9 \pm 81.0	231–1864
	Shrub density	Number stems ha ⁻¹	SHRUBS	5863.6 \pm 690.4	51–12942
	Diameter at breast height	cm	DBH	25.8 \pm 1.23	14.7–35.1
	Native richness	Number species	NATIVES	68.2 \pm 5.1	26–110
	Understorey density	Values of 1–8	UND	0.71 \pm 0.02	0.56–0.9
	Microtopography	Coefficient of variation	MIC	6.64 \pm 0.60	1.6–11.1
	Basal area	m ² ha ⁻¹	BA	30.5 \pm 2.22	13.6–44.7

**n* = 40 per site; surface soil to 20 cm depth.†*n* = 8 per site, top 20 cm of soil.‡*n* = 10 per site, top 30 cm of mineral soil.§*n* = 40 per site, top 30 cm of mineral soil.

species and in structuring the tree communities in general (Fig. 1c).

Similarly, ordination of the three vegetation data sets with respect to the human environmental factors suggested that different sets of factors structured each of the strata (Fig. 2). Herbaceous species were most strongly related to a combination of population density, roads and residential land use outside the wetlands and the presence of rubbish within the sites, and these factors accounted for significant differences in the occurrence of exotic and native species. Herb communities were also affected by a separate gradient of industrial land use adjacent to the wetlands and ditches within the wetlands, but this gradient did not separate exotic from native species. For the shrubs and vines, only the presence of rubbish (an internal factor) and residential housing adjacent to the wetlands (an external factor) accounted for differences both between native and exotic species (Table 2). Other external (population density and industrial land use) and internal (ditches and trails) factors differentiated species' occurrences but did not distinguish exotic from native species. For trees, only within-wetland factors, the presence of rubbish and ditches, affected the occurrence of native and exotic species; adjacent land use affected community composition but did not distinguish exotic and native species presence.

The influence of stand structure on the composition of the vegetation was more similar among the three strata (Fig. 3).

For all three layers, tree size and density were a primary factor that both structured communities and accounted for differences in occurrence between native and exotic species. Microtopography influenced community composition of all strata, and contributed to an axis that was marginally significant in separating exotics and natives. Unexpectedly, the diversity of native species was not important in the distribution of exotic herbs but did significantly affect the distribution of exotic trees (Table 2).

In all of the ordinations, most species clustered around the centres of the ordination spaces and did not form obvious clusters. In all cases, exotic species were prominently among those that were outliers at the ends of the various gradients (Figs 1–3). Certain exotics, notably *Allium vineale* L., *Hemerocallis fulva* (L.) L., *Artemisia vulgaris* L. and *Polygonum cuspidatum* Sieb. & Zucc., were frequently the outliers in several or all of the ordinations, whereas other exotics, such as *Microstegium vimineum* (Trin.) A. Camus, *Solanum dulcamara* L. and *Polygonum hydropiper* L., occurred near the centre of all of the ordinations, overlapping with many of the native species in response to the environmental gradients.

SITE-BASED PATTERNS

Overall amount of invasion was measured by the absolute number of exotic species (species richness) and the relative

Table 2. Variables with correlations over ± 0.35 with each of the three axes of within each CCA (intraspecific correlations) and *P*-values of two-tailed *t*-test comparing mean values for exotics and natives (NS, not significantly different). (–) A negative correlation with the axis. Factors are listed in descending order of correlation coefficient. See Table 1 for factor abbreviations. The total percentage of variation explained is given for each ordination

Stratum	Soil axes	Human axes	<i>P</i>	Vegetation axes	<i>P</i>
Herbs	1: (–) Zn, (–) P, CLAY, (–) NITR 2: (–) CLAY, (–) pH 3: (–) OM, (–) Ca, (–) pH 26.1	1: (–) POPDEN, (–) TRASH, RES 2: ROADS, (–) OPEN, RES, (–) AREA 3: IND, DITCH 25.9	0.019 0.038 NS	1: (–) DBH, TREES 2: (–) NATIVES, MIC, UND 3: BA, MIC, (–) UND 26.8	0.012 NS 0.056
% variance					
Shrubs and vines	1: (–) pH 2: (–) pH, (–) Ca, (–) OM, CLAY, NITR 3: Zn, P, NITR 28.4	1: (–) TRASH, RES 2: (–) RES, DITCH, (–) TRAILS, TRASH, IND 3: (–) IND, (–) POPDEN, (–) RES 31.5	0.004 0.042 NS	1: TREES, (–) d.b.h., MIC 2: MIC, (–) Natives 3: UND 31.7	0.060 NS 0.030
% variance					
Trees	1: (–) pH, (–) NITR, Zn, REDCHR 2: (–) pH, (–) Zn, NITR, (–) NO3 3: P, Zn, NITR, (–) clay 32.3	1: (–) TRASH, (–) DITCH 2: DITCH 3: POPDEN, IND, OPEN 31.5	0.015 NS NS	1: (–) d.b.h., TREES, SHRUBS 2: (–) NATIVES, UND 3: MIC, (–) SHRUBS 32.1	0.001 0.039 NS
% variance					

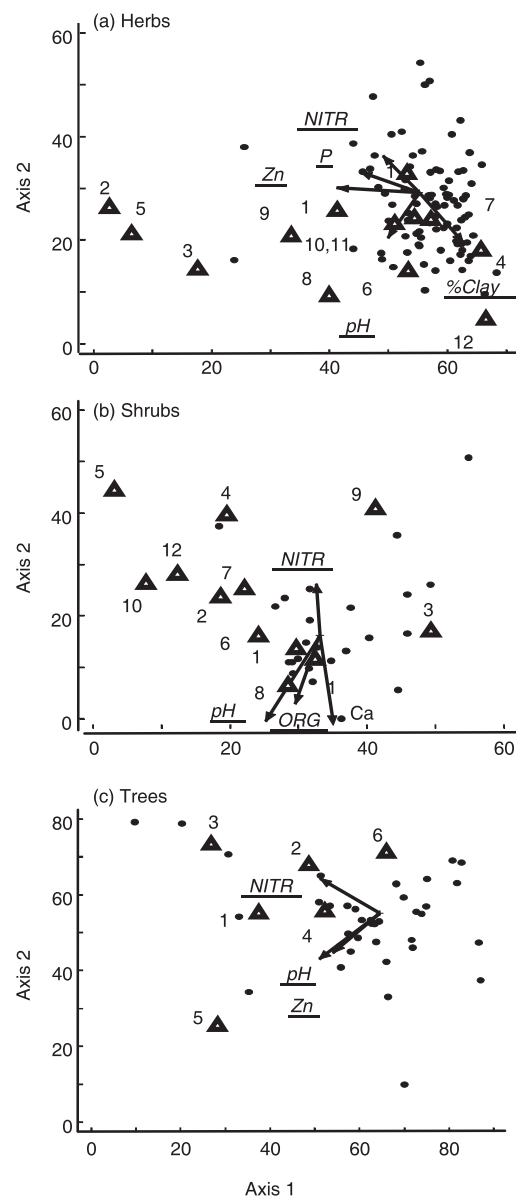


Fig. 1. CCA of vegetation strata with respect to soil factors. Native species are indicated by filled circles and exotic species are indicated by triangles. Bi-plot arrows indicate environmental factors with correlation coefficients > 0.2; factor abbreviations are given in Table 1. Authorities for all names follow Kartesz & Meacham (1999). Exotic species are identified by numbers. (a) Herbs: 1, *Alliaria petiolata*; 2, *Allium vineale*; 3, *Artemisia vulgaris*; 4, *Chenopodium album*; 5, *Hemerocallis fulva*; 6, *Lysimachia nummularia*; 7, *Microstegium vimineum*; 8, *Plantago major*; 9, *Polygonum cuspidatum*; 10, *Polygonum hydropiper*; 11, *Poa pratensis*; 12, *Prunella vulgaris*; 13, *Solanum dulcamara*. (b) Shrubs: *Celastrus orbiculatus*; 2, *Berberis thunbergii*; 3, *Euonymus alata*; 4, *Forsythia viridissima*; 5, *Humulus japonicus*; 6, *Ligustrum vulgare*; 7, *Lonicera japonica*; 8, *Lonicera tatarica*; 9, *Rhamnus cathartica*; 10, *Ribes rubrum*; 11, *Rosa multiflora*; 12, *Rubus phoenicolasius*. (c) Trees: 1, *Acer platanoides*; 2, *Ailanthus altissima*; 3, *Gleditsia triacanthos*; 4, *Malus pumila*; 5, *Morus rubra*; 6, *Prunus avium*.

fraction of the site flora represented by exotics. These two metrics may respond differently to environmental factors than the patterns of community composition captured by the ordination analyses.

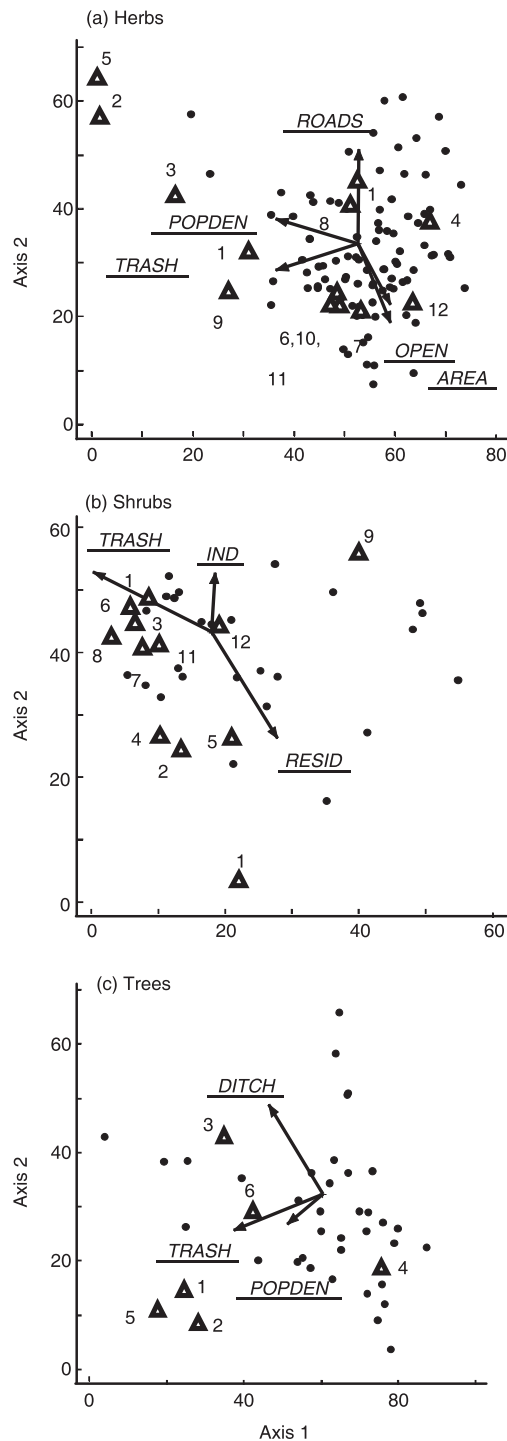


Fig. 2. CCA of vegetation strata with respect to human factors. Species symbols and numbers and bi-plot arrows as in Fig. 1.

The total number of exotic species was responsive to wetland area and adjoining land use but the effects were mostly seen only when large sites (> 100 ha) were included in the analysis (Table 3 and Fig. 4). Surprisingly, the presence of adjacent industrial land reduced the number of exotic species over all sizes of wetlands. The fraction of the flora that was exotic was more strongly affected by area than absolute richness, as the relationship held for the set of small wetlands as well as the entire set

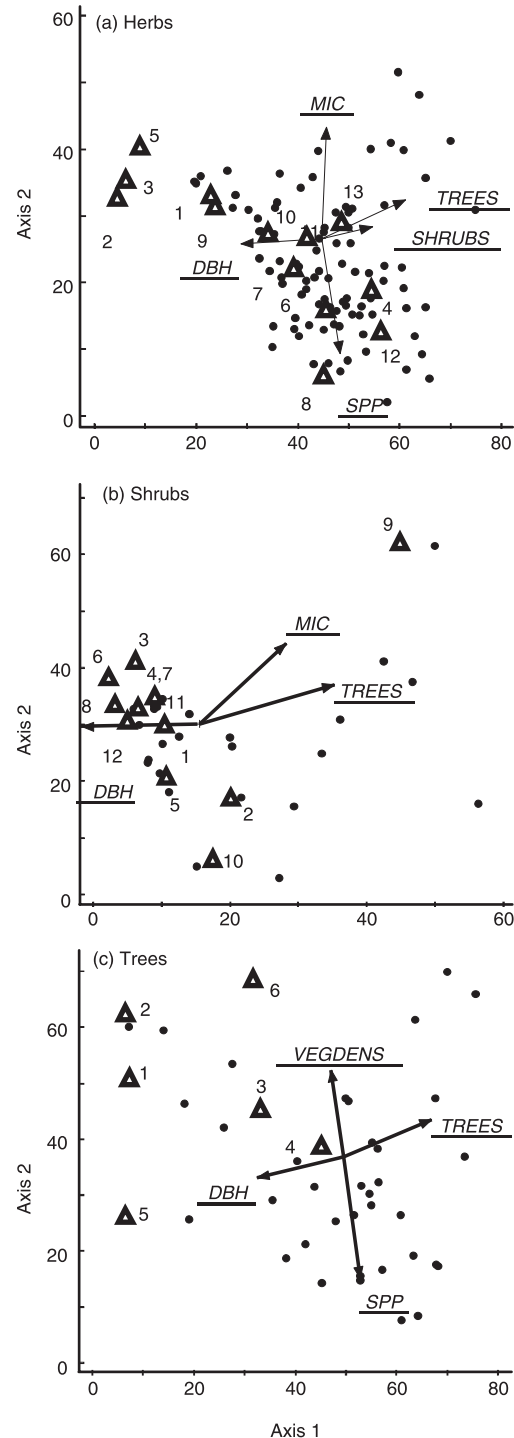


Fig. 3. CCA of vegetation strata with respect to vegetation structural factors. Species symbols and numbers and bi-plot arrows as in Fig. 1.

of sites. In addition, the presence of vegetated upland adjacent to the wetland reduced relative invasion over all wetland sizes.

Soil texture affected the fraction of the flora that was exotic but not the absolute number of exotic species. In contrast, both soil texture and site area affected the number of native species over the range of site areas. Soil texture had contrasting effects on native and exotic species. Native species increased with increasing clay and decreasing sand content, probably

Table 3. Spearman correlation coefficients (rho) and significance level (probability) between measures of species composition and environmental descriptors of the sites

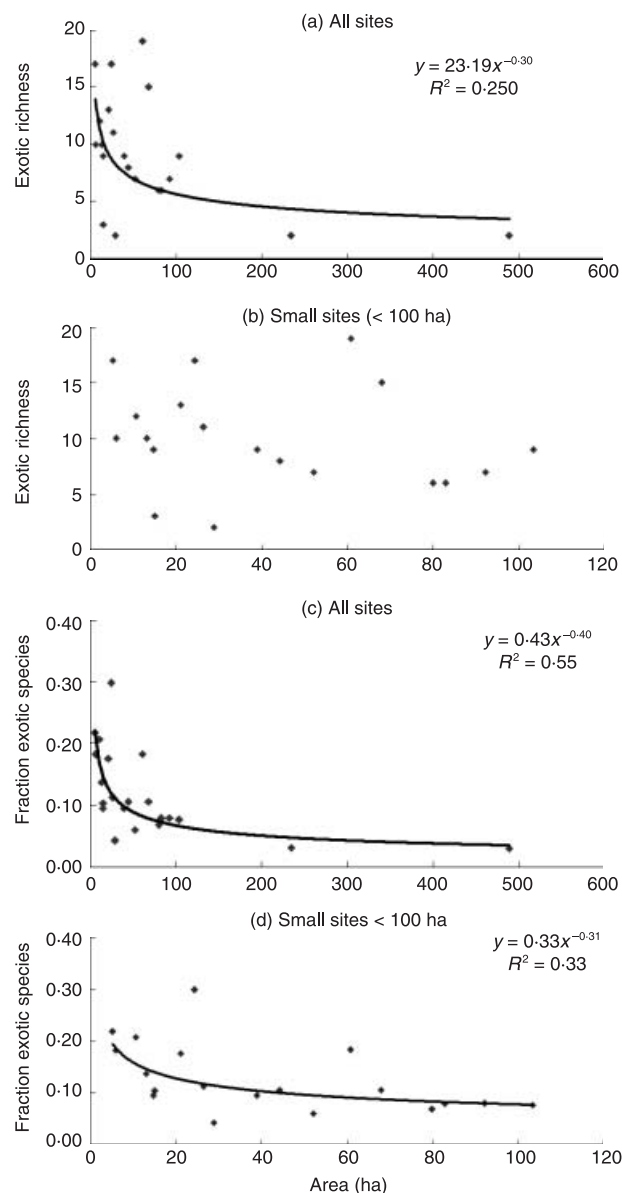
Invasion indicator	Environmental factor	Rho	Probability
Exotic richness	Area (all sites)	-0.503	0.02
	Area (sites < 100 ha)	NS	
	Industrial land use (all sites)	-0.503	0.02
	Industrial land use (sites < 100 ha)	-0.462	0.05
	Open land use (all sites)	-0.530	0.014
Fraction exotic	Open land use (sites < 100 ha)	NS	
	Area (all sites)	-0.721	0.002
	Area (sites < 100 ha)	-0.623	0.004
	% sand	0.559	0.012
	Open land use (all sites)	-0.700	0.0004
Native richness	Open land use (sites < 100 ha)	-0.623	0.004
	% sand	-0.405	0.042
	% clay	0.610	0.009
	Area (all sites)	0.484	0.026
	Area (sites ≤ 100 ha)	0.600	0.007

reflecting the increased presence of wetland-dependent plants such as sedges and rushes, whereas exotic species increased with increasing sand content, probably reflecting the better drainage in sandy soils and the fact that most of the exotics were only moderately to slightly tolerant of wetland conditions (Ehrenfeld *et al.* 2003).

Notably, neither the total number of exotic species nor the fraction of exotics in the flora was significantly correlated with the number of native species. Analyses by vegetation stratum also failed to find any relationship between either measure of invasion and native species richness. In addition, neither measure of invasion was related to indicators of direct human presence (either adjacent population density or the frequency of trails within the sites).

SPECIES' RESPONSES TO ENVIRONMENTAL FACTORS

In striking contrast to the results of measures of overall site invasion (Table 3), the probability of occurrence of eight of the 12 species for which logistic regressions could be calculated were significantly related to the native richness of the sample plots (312 m²) (Table 4). However, the species differed in their response: *Alliaria petiolata* (Bieb.) Cavara & Grande and *Acer platanoides* L. increased in occurrence as native richness decreased, while the other species either increased with increasing native richness or did not respond to native richness. Regressions against soil factors showed equally heterogeneous results (Table 4). A few species were less likely to be present as the clay content of the soil increased, but most showed no response. Conversely, most species showed a small but significant response to the sand fraction of the soil but, again, individual species were both more likely [e.g. *Solanum dulcamara* and *Paulownia tomentosa* (Thunb.) Sieb. & Zucc. ex Steud.] and less likely (e.g. *Microstegium vimineum* and *Rosa multiflora* Thunb. ex Murr.) to occur on such soils. Odds ratios for the relationships were mostly close to one, indicating relatively small differences in the probabilities of occurrence

**Fig. 4.** Relationship of exotic species richness (number of species in 10 312-m² plots site⁻¹) and fraction of flora that is exotic with site area, for (a) and (c) all sites, and (b) and (d) sites of less than 100 ha in extent.

for most species. The notable exception to this pattern was pH, for which the odds ratios indicated that pH strongly influenced the probabilities of occurrence of the four species for which this factor was significant, with three of the four of the exotics strongly associated with non-acidic soil (Table 4). Other factors for which plot-level data were available (microtopography, mean tree diameter and shrub density) were not significant predictors of presence of any exotic species.

Discussion

This study clearly demonstrates that the distribution of exotic species within urban wetlands is highly variable, reflecting strongly individualistic responses of different exotic species to physical, ecological and human environmental factors. Plants

Table 4. Logistic regressions of exotic species presence/absence as a function of selected soil and vegetation variables. For significant regressions, the regression coefficient is given, with the *P*-value of Wald's test of $H_0: \beta = 0$ and the odds ratio in parentheses. All cells marked '–' were not significant. *n* is the number of occurrences of each species in the sample of 210 plots

Species	<i>n</i>	Native spp.	Clay	Sand	Loss-on-ignition	pH
<i>Microstegium vimineum</i>	79	0.062 (0.004, 1.06)	–	–0.067 (0.001, 0.94)	–	–0.66 (0.035, 0.52)
<i>Alliaria petiolata</i>	52	–0.048 (0.016, 0.95)	–0.024 (0.04, 0.98)	–	–	0.69 (0.029, 2.0)
<i>Polygonum hydropiper</i>	27	–	–	–0.04 (0.03, 0.96)	–	–
<i>Solanum dulcamara</i>	22	–	–	0.03 (0.064, 1.03)	–	–
<i>Berberis thunbergii</i>	32	0.08 (0.0005, 1.08)	–	–0.04 (0.006, 0.96)	–	0.70 (0.063, 2.02)
<i>Ligustrum vulgare</i>	35	–	–	–0.06 (0.001, 0.94)	–	–
<i>Lonicera tatarica</i>	28	0.105 (< 0.0001, 1.11)	–	–	–	–
<i>Rosa multiflora</i>	75	0.11 (< 0.0001, 1.11)	–	–0.08 (0.003, 0.97)	0.02 (0.006, 1.02)	–
<i>Celastrus orbiculatus</i>	33	–	–0.058 (0.013, 0.944)	–	–	–
<i>Lonicera japonica</i>	32	0.083 (0.002, 1.09)	–	–0.05 (0.001, 0.95)	–0.03 (0.035, 0.97)	–
<i>Acer platanoides</i>	16	–0.058 (0.044, 0.93)	–0.06 (0.065, 0.94)	–	–	0.86 (0.064, 2.35)
<i>Paulownia tomentosa</i>	19	–	–0.09 (0.01, 0.91)	0.07 (0.001, 1.07)	–	–

of each stratum, both native and exotic, responded differently to both environmental and human-related factors, emphasizing the individualistic nature of species' responses to the environment (Gleason 1926). Furthermore, the results belie the widely accepted notion that all natural areas within urbanized regions are highly invaded (Hoehne 1981; Moffatt, McLachlan & Kenkel 2004; Borgmann & Rodewald 2005; Hansen *et al.* 2005; Kowarik 2005; McKinney 2006). Rather, patterns of invasion appear to reflect combinations of particular environmental conditions and human influences at individual sites and the ecological characteristics of individual species, such that some sites within this highly urban region were not heavily invaded. Finally, exotic species overlap with native species in their responses to both natural and anthropogenic environmental factors; few environmental factors separate exotic species as a group from native species.

The original hypotheses were only partially supported by the results. Exotic invasion does increase with increasing human presence in the region, as measured by the surrounding population density and the presence of rubbish, but the presence of trails, which bring people directly into the wetlands, was not a factor in the distribution of either herbs or trees. Contrary to expectation, hydrologic disturbances, as indexed by the presence of ditches and evidence of oxic conditions in soils, have little effect on the extent of invasion and, indeed, are surprisingly unimportant in structuring any component of the vegetation. As expected, adjacent residential development was associated with higher abundance of exotic herbs and woody understorey.

In contrast, and unexpectedly, the presence of adjoining industrial land reduced the overall amount of invasion, as measured by the number of exotic species (Table 4). Also unexpectedly, the presence of naturally vegetated upland adjacent to the wetland (open area) also decreased the overall amount of invasion (Table 4). This result was particularly surprising because this adjoining upland habitat was sometimes itself heavily dominated by weedy and invasive exotic species, including several of the species that were common within the wetlands. Finally, the relationship of invasion to wetland area was only partially supported: the relationship depends on the

measure of invasion used and the size range of the wetland population. Large sites (relative to the median size of patches in urban areas (Ehrenfeld 2000)) are less invaded than small sites, but within the set of small sites the amount of invasion is highly variable and not clearly related to area. These results suggest that the assessment of invasion depends, in part, on the metric used to measure invasion. Exotic richness, native richness and the fraction of the flora that is exotic are all associated with different environmental conditions; a relative measure of invasion (fraction of the flora) will thus reflect the separate factors that affect native as well as exotic species.

The differential effects of residential, industrial and vegetated adjacent land on both species associations and metrics of overall invasion emphasize the importance of variation in the structure of urban regions. In other urban regions, variability in structure within the urban environment has proved important in explaining stream biota (Alberti 2005) as well as terrestrial communities, although the mechanisms of these effects are as yet not well understood (Clergeau, Jokimäki & Snep 2006; Grove *et al.* 2006). The differential effect of industrial/commercial and residential land use on many of the exotic species supports the need for greater fine-scale study of heterogeneity within urban land-use categories.

It is not clear why industrial land use would have the surprising effect of decreasing invasions by shrubs and vines and decreasing the overall representation of exotics in site vegetation. One factor might be the lack of horticultural planting in these areas; many of the species associated with residential and not industrial land (e.g. *Forsythia viridissima* Lindl., *Berberis thunbergii* and *Ribes rubrum* L.) are common ornamental plants. Residential areas have several other features that may make wetlands embedded within them more prone to invasion than wetlands within industrial areas. The use of the wetlands for dumping of homeowner garden waste, the presence of pet animals as dispersers, and the presence of deer *Odocoileus virginianus* (which are over-abundant in residential areas throughout the study region but absent from industrial areas) are factors that may enhance propagule availability and dispersal in residential but not industrial areas. This result strongly suggests that general statements

about high invasion in urban areas may not be reliable, and should be re-evaluated with respect to different specific types of urban land use.

All three vegetation strata responded strongly to both pH and nutrients. Zinc (Zn) concentrations were well within the concentration ranges reported for unpolluted soils (Kabata-Pendias & Pendias 1984; Pouyat & McDonnell 1991; Doichinova, Sokolovska & Velizarova 2006), as were the concentrations of copper (highly correlated with Zn and therefore deleted from the ordination data sets). These results suggest that the metal concentrations are not high enough to be a direct cause of stress for the vegetation. The close association of phosphorus (P) and Zn vectors in all ordination analyses suggests, rather, that both elements are associated with sediment deposition. P in wetlands is frequently associated with sediments and deposition during flood events, as P is typically tightly adsorbed to iron oxides within the mineral soil matrix (Mitsch & Gosselink 2000; Olde Venterink *et al.* 2003). Zn is probably an indicator of mineral sediment influx as well. Sediment deposition may increase the sand fraction of the surface soil, also a factor associated with increased overall invasion and presence of some species. Thus these results suggest that sediment deposition during flood events may facilitate invasion of many exotics, particularly the herbs.

Nitrogen availability has frequently been associated with exotic invasion (Ostertag & Verville 2002; Brooks 2003; Ehrenfeld 2003). Indeed, nitrification rate (but not extractable nitrate concentration) was an important factor in both separating exotic and native species of all strata and structuring the communities of native species in these wetlands. However, no nutrient factor emerged as a significant correlate of overall site invasion (number and percentage of species). This contrast supports the conclusion that overall site patterns are a result of the individualistic behaviour of the particular species present in a site.

The minimal association of trails with invasion was also contrary to expectation. In other regions, trails and trail use have been associated with exotic invasion (Larson 2003; Alston & Richardson 2006). In this study, only a few woody understorey exotic species, including *Forsythia viridissima*, *Berberis thunbergii* and *Humulus japonicus* Sieb. & Zucc., were clearly associated with trails. The partial association of trails with particular invasive species suggests that the decision to enhance public utilization of these sites as an ecosystem service (Bolund & Hunhammar 1999) may need to be balanced with management goals for particular invasive species.

Finally, the relationship of exotic richness to native species richness was complex. While the ordination analyses showed that, in all vegetation strata, many exotic species were associated with sites with low native diversity, there were no significant relationships between either the absolute or relative number of exotic species and native species richness. This result may be explained by the logistic regressions: because some exotic species increase in abundance with increasing native richness, while others decrease or have no relationship to native richness, there is no overall relationship between exotic richness and native richness. This individualistic response of exotic species

to native richness may help to explain the continuing controversy about the association of native richness with increased or decreased invasion (Levine 2000; Shea & Chesson 2002; Stohlgren *et al.* 2002; Brown & Peet 2003; Fargione, Brown & Tilman 2003; Richardson *et al.* 2005).

In summary, exotic species invade urban wetlands as a result of a complex mixture of influences that include intrinsic site properties such as soils, anthropogenic effects both within and surrounding the wetlands, and the individualistic response of species to all factors. This result supports the contention of Hulme (2006) that invasion must be understood with respect to a synthetic, ecosystem approach to characterizing the environment (both physical and human) and the landscape within which specific invasion events occur. A single approach to wetland management, such as altering hydrology, reducing nutrient inputs or enhancing native diversity, may enhance population growth of some invasive species while reducing others. Management plans should instead be developed for individual sites that take into account their particular constellation of invasive and native species, the size of the wetlands and the nature of their surrounding urban matrix, the particular forms of urban impact that are important at the sites, and the interest of the surrounding human community in their wetlands.

Exotic species in urban wetlands have individualistic responses to a range of physical and human environmental factors, suggesting that management strategies may need to be tailored for specific species at a given site. Nevertheless, several general conditions enhancing invasion can be managed to reduce invasion. These include the reduction of sediment deposition (reducing nutrient and sand inputs), filling of ditches and maintenance of a vegetated upland border along the wetland edge. Wetlands within industrial areas may be subject to less invasion, especially by woody species; they should be carefully considered for conservation and restoration. Soil textures should be considered in evaluating sites for conservation, as clay soils have more native species and sandy soils enhance invasion.

There is little relationship between size and invasion among smaller sites (< 100 ha), suggesting that even small parcels within urban landscapes may have few non-native species in the flora. This finding suggests that small wetlands should not be eliminated from priority rankings for preservation or protection simply on the basis of size. The results support an ecosystem approach to invasive species management in urban environments, in which human and physical aspects of the wetland environment and the nature and impacts of the surrounding urban landscape are integrated with the ecological requirements of both invasive and native species.

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References

- Alberti, M. (2005) The effects of urban patterns on ecosystem function. *International Regional Science Review*, **28**, 168–192.
- Allan, J.D. (2004) Landscapes and riverscapes: the influence of land use on stream ecosystems. *Annual Review of Ecology and Systematics*, **35**, 257–284.
- Alston, K.P. & Richardson, D.M. (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. *Biological Conservation*, **132**, 183–198.
- Bolund, P. & Hunhammar, S. (1999) Ecosystem services in urban areas. *Ecological Economics*, **29**, 293–301.
- Booth, D.B. & Jackson, C.R. (1997) Urbanization of aquatic systems: degradation thresholds, stormwater detention and the limits of mitigation. *Journal of the American Water Resources Association*, **33**, 1077–1090.
- Borgmann, K.L. & Rodewald, A.D. (2005) Forest restoration in urbanizing landscapes: interactions between land uses and exotic shrubs. *Restoration Ecology*, **13**, 334–340.
- Brabec, E., Schulte, S. & Richards, P.L. (2002) Impervious surfaces and water quality: a review of current literature and its implications for watershed planning. *Journal of Planning Literature*, **16**, 499–514.
- Brooks, M.L. (2003) Effects of increased soil nitrogen on the dominance of alien annual plants in the Mojave Desert. *Journal of Applied Ecology*, **40**, 344–353.
- Brown, R.L. & Peet, R.K. (2003) Diversity and invasibility of southern Appalachian plant communities. *Ecology*, **84**, 32–39.
- Clergeau, P., Jokimäki, J. & Snep, R. (2006) Using hierarchical levels for urban ecology. *Trends in Ecology and Evolution*, **21**, 660–661.
- Connor, S.E. & Thomas, I. (2003) Sediments as archives of industrialisation: evidence of atmospheric pollution in coastal wetlands of southern Sydney, Australia. *Water, Air and Soil Pollution*, **149**, 189–210.
- Doichinova, V., Sokolovska, M. & Velizarova, E. (2006) Heavy metals contamination of soils under oak ecosystems in the Sofia region. *Environmental Chemistry Letters*, **4**, 101–105.
- Ehrenfeld, J.G. (2000) Evaluating wetlands within an urban context. *Urban Ecosystems*, **4**, 69–85.
- Ehrenfeld, J.G. (2003) Effect of exotic plant invasions on soil nutrient cycling processes. *Ecosystems*, **6**, 503–523.
- Ehrenfeld, J.G. (2004) The expression of multiple functions in urban forested wetlands. *Wetlands*, **24**, 719–733.
- Ehrenfeld, J.G. (2005) Vegetation of forested wetlands of urban and suburban landscapes in New Jersey. *Journal of the Torrey Botanical Society*, **132**, 262–279.
- Ehrenfeld, J.G., Cutway, H.B., Hamilton, R.I.V. & Stander, E. (2003) Hydrologic description of forested wetlands in northeastern New Jersey, USA: an urban/suburban region. *Wetlands*, **23**, 685–700.
- Fargione, J., Brown, C.S. & Tilman, D. (2003) Community assembly and invasion: an experimental test of neutral versus niche processes. *Proceedings of the National Academy of Sciences USA*, **100**, 8916–8920.
- Gleason, H.A. (1926) The individualistic concept of the plant association. *Bulletin of the Torrey Botanical Club*, **53**, 7–26.
- Groffman, P.M., Bain, D.J., Band, L.E., Belt, K.T., Brush, G.S., Grove, J.M., Pouyat, R.V., Yesilonis, I.C. & Zipperer, W.C. (2003) Down by the riverside: urban riparian ecology. *Frontiers in Ecology and the Environment*, **1**, 315–321.
- Grove, J.M., Cadenasso, M.L., Burch, W.R., Pickett, S.T.A., Schwarz, K., O'Neil-Dunne, J., Wilson, M., Troy, A. & Boone, C. (2006) Data and methods comparing social structure and vegetation structure of urban neighborhoods in Baltimore, Maryland. *Society and Natural Resources*, **19**, 117–136.
- Hansen, A.J., Knight, R.L., Marzluff, J.M., Powell, S., Brown, K., Gude, P.H. & Jones, A. (2005) Effects of exurban development on biodiversity: patterns, mechanisms, and research needs. *Ecological Applications*, **15**, 1893–1905.
- Harper, K.A., Macdonald, S.E., Burton, P.J., Chen, J.Q., Broszofski, K.D., Saunders, S.C., Euskirchen, E.S., Roberts, D., Jaiteh, M.S. & Esseen, P.A. (2005) Edge influence on forest structure and composition in fragmented landscapes. *Conservation Biology*, **19**, 768–782.
- Hoehne, L.M. (1981) The groundlayer vegetation of forest islands in an urban-suburban matrix. *Forest Island Dynamics in Man-Dominated Landscapes* (eds R.L. Burgess & D.M. Sharpe), pp. 45–54. Springer-Verlag, New York, NY.
- Hulme, P.E. (2006) Beyond control: wider implications for the management of biological invasions. *Journal of Applied Ecology*, **43**, 835–847.
- Kabata-Pendias, A. & Pendias, H. (1984) *Trace Elements in Soils and Plants*. CRC Press Inc., Boca Raton, FL.
- Kartesz, J.T. & Meacham, C.A. (1999) *Synthesis of the North American Flora*, Version 1.0. University of North Carolina Botanical Garden, Chapel Hill, NC.
- Kowarik, I. (1995) On the role of alien species in urban flora and vegetation. *Plant Invasions: General Aspects and Special Problems* (eds P. Pysek, K. Prach, M. Rejmanek & M. Wade), pp. 85–103. SPB Academic Publishing, Amsterdam, the Netherlands.
- Kowarik, I. (2005) Wild urban woodlands: towards a conceptual framework. *Wild Urban Woodlands* (eds I. Kowarik & S. Körner), pp. 1–32. Springer-Verlag, Heidelberg, Germany.
- Larson, D.L. (2003) Native weeds and exotic plants: relationships to disturbance in mixed-grass prairie. *Plant Ecology*, **169**, 317–333.
- Levine, J.M. (2000) Species diversity and biological invasions: relating local process to community pattern. *Science*, **288**, 852–854.
- Lovett, G.M., Traynor, M.M., Pouyat, R.V., Carreiro, M.M., Zhu, W.-X. & Baxter, J.W. (2000) Atmospheric deposition to oak forests along an urban-rural gradient. *Environmental Science and Technology*, **34**, 4292–4300.
- McCune, B. & Grace, J. (2002) *Analysis of Ecological Communities*. MjM Software Design, Gleneden Beach, OR.
- McCune, B. & Mefford, M.J. (1999) *PC-ORD. Multivariate Analysis of Ecological Data*. MjM Software, Gleneden Beach, OR.
- McGranahan, D. & Satterthwaite, D. (2003) Urban centers: an assessment of sustainability. *Annual Review of Ecology and Systematics*, **28**, 243–274.
- McKinney, M.L. (2006) Urbanization as a major cause of biotic homogenization. *Biological Conservation*, **127**, 247–260.
- Meyer, J.L., Paul, M.J. & Taulbee, W.K. (2005) Stream ecosystem function in urbanizing landscapes. *Journal of the North American Benthological Society*, **24**, 602–612.
- Mitsch, W. & Van Gosselink, J.G. (2000) *Wetlands*, 3rd edn. Nostrand Reinhold, New York, NY.
- Moffatt, S.F., McLachlan, S.M. & Kenkel, N.C. (2004) Impacts of land use on riparian forest along an urban-rural gradient in southern Manitoba. *Plant Ecology*, **174**, 119–135.
- Olde Venterink, H., Wiegman, F., Van der Lee, G.E.M. & Vermaat, J.E. (2003) Role of active floodplains for nutrient retention in the River Rhine. *Journal of Environmental Quality*, **32**, 1430–1435.
- Ostertag, R. & Verville, J.H. (2002) Fertilization with nitrogen and phosphorus increases abundance of non-native species in Hawaiian montane forests. *Plant Ecology*, **162**, 77–90.
- Paul, M.J. & Meyer, J.L. (2001) Streams in the urban landscape. *Annual Review of Ecology and Systematics*, **32**, 333–366.
- Pickett, S.T.A., Cadenasso, M.L., Grove, J.M., Nilon, C.H., Pouyat, R.V., Zipperer, W.C. & Costanza, R. (2001) Urban ecological systems: linking terrestrial, ecological, physical and socioeconomic components of metropolitan areas. *Annual Review of Ecology and Systematics*, **32**, 127–157.
- Pouyat, R.V. & McDonnell, M.J. (1991) Heavy metal accumulations in forest soils along an urban-rural gradient in southeastern New York, USA. *Water, Air and Soil Pollution*, **57–58**, 797–807.
- Reinelt, L.E. & Taylor, B.L. (2000) Effects of watershed development on hydrology. *Wetlands and Urbanization: Implications for the Future* (eds A.L. Azous & R.R. Horner), pp. 221–235. Lewis Publishers, Boca Raton, FL.
- Richardson, D.M., Rouget, M., Ralston, S.J., Cowling, R.M., Van Rensburg, B.J. & Thuiller, W. (2005) Species richness of alien plants in South Africa: environmental correlates and the relationship with indigenous plant species richness. *Ecoscience*, **12**, 391–402.
- SAS Institute Inc. (2002) SAS System version 9.1. SAS Institute Inc., Cary, NC.
- Shea, K. & Chesson, P. (2002) Community ecology theory as a framework for biological invasions. *Trends in Ecology and Evolution*, **17**, 170–176.
- Sollins, P., Glassman, C., Paul, E.A., Swanston, C., Lajtha, K., Heil, J.W. & Elliott, E.T. (1999) Soil carbon and nitrogen pools and fractions. *Standard Soil Methods for Long-Term Ecological Research* (eds G.P. Robertson, D.C. Coleman, C.S. Bledsoe & P. Sollins), pp. 89–105. Oxford University Press, New York, NY.
- Stohlgren, T.J., Chong, G.W., Schell, L.D., Rimar, K.A., Otsuki, Y., Lee, M., Kalkhan, M.A. & Villa, C.A. (2002) Assessing vulnerability to invasion by nonnative plant species at multiple spatial scales. *Environmental Management*, **29**, 566–577.
- United Nations (2004) *World Urbanization Prospects. The 2003 Revision Data Tables and Highlights*. Report ESA/P/WP.190. United Nations Department of Economic and Social Affairs, Population Division, New York, NY.
- Vepraskas, M.J. (1996) *Redoximorphic Features for Identifying Aquic Conditions*. Technical Bulletin 301. North Carolina Agricultural Research Service, North Carolina State University, Raleigh, NC.
- Vepraskas, M.J. & Faulkner, S.P. (2001) Redox chemistry of hydric soils. *Wetland Soils* (eds J.L. Richardson & M.J. Vepraskas), pp. 85–105. Lewis Publishers, Boca Raton, FL.

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