Plant invasion along an urban-to-rural gradient in northeast Connecticut

Carolyn Ariori,* Matthew E. Aiello-Lammens, and John A. Silander, Jr

Department of Ecology and Evolutionary Biology, University of Connecticut, Storrs, CT 06269-4210, USA
*Corresponding author. Ecology & Evolutionary Biology, 75 N. Eagleville Road, Unit 3043, Storrs, CT 06269-3043, USA. E-mail: carolyn.ariori@gmail.com

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Abstract

Humans are the most important drivers of global invasive species introduction and natural habitat transformation. An understanding of the relationships between these impacts is needed to understand how we may prevent future species invasions. We explored the ecological differences between areas of dense human habitation and minimally managed natural habitats across an urban-to-rural gradient of land use in southern New England. Urban habitats were significantly different environmentally from rural habitats. Urban soils were more alkaline and coarse textured and had higher lead concentrations than rural soils. Urban habitats had more open canopies, impervious surface, patch forests and induced edge habitats than rural habitats. We also examined differences in presence/absence patterns and leaf functional traits for a set of invasive species across an urban to rural environmental gradient. Some species were more restricted to urban or rural sites than others along this gradient. A priori urban-classified species tended to show trait values associated with drought tolerance, including higher leaf length-to-width ratio, greater leaf thickness, higher leaf dry matter content and lower specific leaf area. Our findings suggest that urban environmental conditions contribute to an ‘urban drought island’ syndrome that favors drought-tolerant species.

Key words: urban ecology, invasive species, urbanization, New England

Introduction

Urbanization is a pervasive form of land-use change characterized by increased human impacts, fragmentation of natural habitats, intensive land transformation and an increase in impervious surface land cover (Vitousek et al. 1997; Irwin and Bockstael 2007; Angel et al. 2011; Williams et al. 2009). Urban populations have increased as cities became centers of employment, habitation, transportation, culture and trade. Although cities cover only 0.5% of the Earth’s surface (Schneider et al. 2009; Angel et al. 2011), they contain >50% of the world’s population (United Nations 2015) and account for a disproportionately large amount of the world’s resources consumption (Kareiva et al. 2007). Urban growth is expected to continue—the US population is projected to be urban by 2050 (United Nations 2015). As of the 2010 decennial census, 80.7% of the US population lives in an urban setting (US Census 2012). Because of this growth, urban services are vital for supporting modern human life. However, the resources required for these services, combined with the impacts of land-use change associated with urbanization, can have detrimental effects on the persistence of naturally occurring biota. To understand these effects, it is necessary to compare patterns of species abundance and functional trait values in areas with greater and lesser amounts of human impact associated with urbanization. McDonnell and Pickett (1990) introduced the concept of an urban-to-rural ecological gradient, in part, as a way to quantify these impacts (McDonnell and Pickett 1990; Gagné 2013).

Several factors contribute to the differences in ecological conditions observed in urban areas compared to more natural areas. Impervious surface cover is frequently used as a proxy for urban...
land use (Lu and Weng 2006) along rural-to-urban gradients, and it plays a large role in shaping the biogeochemical conditions in urban soils and streams (Arnold and Gibbons 1996; Cicco et al. 2002). Previous research indicates urban soils are more alkaline than rural soils due to leaching from calcareous concrete and mortar comprising built structures (Jim 1998). These structures, and other remnants of human activity, are worn down over time and contribute particulate matter to urban soils (Jim 1998; Lehmann and Stahr 2007). Heavy metal pollution due to outputs from road traffic and industries or erosion of construction materials also leads to notable differences between urban and natural soils (Lehmann and Stahr 2007; Calace et al. 2012). Atmospheric N inputs (NOx gases), and other inputs (e.g. lawn fertilization or sewage), may also affect urban soil nutrients (Pickett and Cadenasso 2009), contributing to eutrophication of some urban habitats. Soil compaction can occur in parks, yards and urban forest remnants from trampling and development (Scharenbroch et al. 2005; Edmondson et al. 2011). High densities of roads, sidewalks and buildings also contribute to changes in rainwater runoff patterns to urban streams and soils. These impacts contribute to lowered water tables in urban riparian habitats, causing ‘hydrological drought’ in soils (Groffman et al. 2003). Further, urban soils overall tend to be drier than rural soils (Pickett and Cadenasso 2009). These altered hydrological regimes make water less available for plants, even when rainfall is plentiful (Paul and Meyer 2001; Pickett and Cadenasso 2009). Finally, urban regions often have elevated temperatures compared to surrounding rural areas (i.e. urban heat island effect; Pickett et al. 2011) because solar radiation absorbed by impervious surface creates elevated nighttime temperatures (Parlow 2011). The associated higher evapotranspiration may also contribute to urban areas as ‘drought islands’.

Urbanization may also have effects on the biotic composition of ecosystems. Several studies have suggested that invasive plant distributions are closely tied to anthropogenic influences, including housing development, proximity to roads, agriculture and socioeconomic factors such as income (Mosher et al. 2009; Allen et al. 2013; Kuhman et al. 2011; Santos et al. 2011; González-Moreno et al. 2013; Ripplinger et al. 2016). In New England, edges created by forest fragmentation during urban growth and development are known to promote the spread of certain woody invasive species. Factors like road density and housing are positive correlates of invasive species richness (Mosher et al. 2009; Gavier-Pizarro et al. 2010; Allen et al. 2013), as are linear edge-creating features such as roads and trails, which may act as disturbed dispersal corridors (Cilliers and Bredenkamp 2000; Nemec et al. 2011; von der Lippe et al. 2013). As sites of both disturbed edge habitats and species introductions, urban areas seem primed to promote the spread of invasive species. Plants have adapted physiological features that allow them to tolerate a range of environmental challenges. These features can be quantified by measuring plant functional traits (PFTs) as physiological proxies (Westoby et al. 2002; Donovan et al. 2011; Garnier and Navas 2012). PFTs are defined as any measurable aspect of a plant with some direct or indirect effect on plant performance and fitness (Viole et al. 2007) and can be divided into ‘hard’ and ‘soft’ traits. Soft traits are quickly and easily measured and are often correlated with ‘hard’ traits, which are more direct measures of ecological significance and plant functioning (Cornelissen et al. 2003). For example, the soft trait specific leaf area (SLA), the ratio of leaf area to leaf dry mass, is positively correlated to plant relative growth rate and photosynthetic capacity (Cornelissen et al. 2003). Given environmental stresses and limited energy budgets, plants must invest resources in a way that maximizes their success under different environmental conditions (Orians and Solbrig 1977). Suites of similar trait responses to similar environments have been noted—for example, leaves from arid regions tend to be thick, small and tough with low photosynthetic rates (Orians and Solbrig 1977, Reich et al. 1999, Wright et al. 2004). But traits within a species can also be plastic, or change in response to different environmental conditions (Chapin et al. 1993).

Associations between PFTs and environmental conditions are likely the result of environmental filters (Diaz et al. 1998). That is, environmental conditions may be conducive for survival of species that have certain trait values (e.g. dry environments being conducive for plants with succulent leaves). Williams et al. (2009) describe four urban environmental filters that can increase or decrease the probability of plant species occurring in urban areas: (i) habitat transformation, (ii) habitat fragmentation, (iii) human species planting preferences and (iv) the unique soils and climates associated with cities. To become established naturally in an urbanizing landscape, species must have a combination of attributes that allow them to pass through these filters (Duncan et al. 2011). Habitat transformation will likely remove species associated with natural habitats from the urban species pool. Landscape fragmentation creates high habitat heterogeneity in cities and patches and edges in natural habitats, as well as altering metapopulation connectivity and dispersal corridors (Irwin and Bockstael 2007; Shrestha et al. 2012). Human planting preferences lead to new plant introductions, frequently through the horticultural trade (Dolan et al. 2011) and weeding of ‘undesirable’ species (Walker et al. 2009; Gulezian and Nyberg 2010). Some patterns in urban plant traits have been observed that may be the result of environmental filtering. For example, a study of urban and rural forests in France found that urban forests were more likely to contain short-lived species with a higher SLA (Vallet et al. 2010). In Germany, urban areas have higher proportions of wind-pollinated plants, plants with scleromorphic leaves and leaves with a higher SLA and lower leaf dry matter content (LDMC), and plants that prefer warm climates (Knapp et al. 2008, 2009). Based on their results, Knapp et al. (2008) described an additional set of critical filters in urban environments with respect to plant traits: the urban heat island should favor drought-adaptive traits; intense and irregular disturbance patterns should favor high SLA and low LDMC; and urban spatial heterogeneity should favor plants with strong dispersal abilities, mostly by animals.

In this study, we examined the relationships between environmental conditions and invasive species occurrence and traits along an urban-to-rural gradient. Twenty-five species were surveyed across an urban-to-rural gradient in central Connecticut based on their previously known presence and prevalence in urban areas or their inclusion on the Invasive Plant Atlas of New England (IPANE) list of invasive and potentially invasive species. Using methodology adapted from the IPANE protocol (Mehrhoff et al. 2003; Bois et al. 2011), we aimed to answer the following questions: (i) What growing conditions does the urban environment provide to invasive plant species in Southern New England, USA? (ii) Are there differences in invasive species distribution along an urban-to-rural gradient in southern New England? (iii) Are invasive species distributions associated with any socioeconomic variables that vary along urban-to-rural gradients? (iv) Finally, are there differences in functional traits among invasive species that could account for differences in species distribution along these gradients?
Study area

This study took place in southern New England, primarily in Connecticut (Fig. 1). The initial urban-to-rural gradient ranged from Hartford and surrounding inner suburbs to forested rural areas 30-km east; however, supplemental sampling extended further east to parts of metropolitan Boston, MA. Across this geographic range, mean annual temperature and annual precipitation (Hijmans et al. 2005) show only minor variations of about 1°C and 100 mm, respectively; therefore, climate conditions were not included as predictor variables in this study.

Methods

Delineation of sampling area into urban, suburban and rural grid squares

Housing, population, and per capita income data from the 2010 Census (www.census.gov) and the 2011 5-year American Community Survey were accessed from the National Historical Geographic Information System (Minnesota Population Center 2011) at the block group level. A block group is a geographical division used by the US Census Bureau and is the smallest available geography used by the American Community Survey. Percent impervious cover information, available as a 30-m resolution raster dataset from 2006, was downloaded from the National Land Cover Database (Fry et al. 2011). A grid of 1-km² cells covering Connecticut and eastern Massachusetts was created using Geospatial Modelling Environment (Beyer 2012) and ArcGIS 10 (ESRI 2010). Within each grid cell, we calculated the area-weighted mean of per capita household income, the area-weighted sum of the number of housing units and total population and the percent impervious land cover. Area-weighted mean and area-weighted sums are means and sums calculated using a multiplier (weight), where the weight is the proportion of the total area of a given block group within the grid cell.

Population density in each grid cell was used to define rural, suburban and urban land-use a priori. A cell with <500 people mi⁻² (193 people km⁻²) was defined as rural, based on the minimum value for inclusion in an urban cluster of blocks and tracts for the 2000 US Census. Urban was defined as an area with a minimum of 2500 people mi⁻² (965 people km⁻²), based on overall current population densities for the USA and previous definitions of urban areas (Urban and Rural Classification, US Census Bureau). Suburban grid cells had population densities that fell between those of urban and rural grid cells. To express urbanization as an alternative continuous value, a GIS raster layer of square meters of impervious surface per person per block group for Connecticut and the Boston metro area was created in ArcGIS 10. We used this layer to define our urbanization metric. Mean values of this metric peaked in suburban sites, reflecting more area of impervious surface cover per person in suburbs relative to densely populated urban sites or lightly inhabited rural sites (Supplementary Material S1 for the distribution of population densities and urbanization metric values in this study.) We created a raster layer of edge, patch and core forest, with the Landscape Fragmentation Tool (LFT) v2.0 (Parent and Hurd 2010). Edge distance was defined as 30 m, based on prior definitions and studies of edges in this region (Allen et al. 2013). Land-use data from the Center for Land Use Education and Research (CLEAR) and from MassGIS (http://www.mass.gov/ant/research-and-tech/it-serv-and-support/application-serv/office-of-geographic-information-massgis/) were used as tool
inputs and proportional cover of edge, patch and core forest was calculated for each grid cell.

**Sampling methods**

Grid cells were randomly selected to stratify sampling among the three neighborhood types and across the urban-to-rural gradient. A total of 1101-km² grid cells were visited, of which 36 were classified as urban, 40 suburban and 34 rural. Five 5-m radius circular sample plot locations were randomly placed in each grid cell at a minimum distance of 100 m apart (cf. Fig. 1). Plot points were navigated to using GPS units and coordinates were taken at the center of every plot. Plots were moved if the pre-selected coordinates fell in a location that could not be sampled, such as a building or road. In these cases, sampling took place in the nearest available space occupied by plants. Opportunistic plots were also sampled as encountered throughout the study region; these plots were included to supplement data from the original sampling scheme and to sample as widely as possible. All plots were visited between May and September in 2012 and 2013. Additional observations were collected in the Boston metro region by a collaborator using the same methodology.

Data collection within each plot was adapted from the IPANE surveying methodology. Early investigation of IPANE data collected prior to this survey revealed under-sampling in urban areas. Using IPANE methods allowed us to both answer research questions and improve the spatial coverage of the IPANE dataset. We estimated the abundance, percent plot cover and distribution of 25 nonnative species within each plot (Supplementary Material S1, Table S1A-1). Species selected were a subset of common invasive species from the IPANE list, and species with a known presence in urban areas. In addition, we quantified categorical and ordinal measures of plot environment, including habitat type, surrounding land use, and plot canopy cover (Supplementary Material S1, Table S1A-2). Habitat type was classified as four aggregated categories of habitat characteristics: ‘induced edges’ included fragmented habitats with surrounding human influences (e.g. sidewalks and roadsides), ‘natural edges’ included areas where two or more naturally occurring habitats met, ‘induced habitats’ included large areas of habitat influenced by human management (e.g. lawns, gardens and abandoned lots) and ‘natural habitats’ included naturally occurring habitats. The six categories of land use were commercial, residential, agricultural, industrial, forested and mixed-use, where the mixed-use category described multiple categories of land uses in adjacent properties. Plot canopy cover was measured in four ordinal categories, ‘0–25%’, ‘26–50%’, ‘51–75%’ and ‘76–100%’.

**Species trait sampling**

Two species of five growth forms (trees, shrubs, vines, forbs and grasses) were selected from the full set of 25 species. One species in each pair was classified as an urban-associated species, while the other was classified as a rural-associated species. Species that preferred open canopy edge habitats were classified as urban, whereas species that preferred closed canopy forested habitats were classified as rural. Preference was indicated by observed differences in species frequency across the urban-to-rural gradient and habitat preferences as listed on the IPANE website (Figs 3 and 4). A description of the species pairs is included in Supplementary Material S3.

Leaf samples for PFT analysis were collected for each species from populations in two urban and two rural sites, where possible. Populations were selected for sampling from plots that had been visited in 2012 and from recorded IPANE point locations. The standardized procedures for measuring PFTs followed Cornelissen et al. (2003). Two fully expanded, representative sun-exposed leaves were selected from five individuals that were regularly spaced apart. In the shade adapted species Alliaria petiolata, Berberis thunbergii and Microstegium vimineum, leaves were selected that were obviously receiving sun exposure from canopy gaps. Leaves were stored in sealable plastic bags with a damp piece of paper towel inside a cooler to minimize water loss during storage and transport and measured on the day of collection.

In the lab, leaf lamina thickness was measured with digital calipers. The petiole was removed and wet mass was obtained. A Li-COR Model LI-3000 A portable leaf area meter (LI-COR, Lincoln, NE) was used to obtain leaf area, leaf length, maximum leaf width and average leaf width. Leaves were then oven dried to a constant dry mass. From these measurements SLA, leaf water content, leaf mass per area, length-width ratio (LWR) and LDMC were calculated as per calculations outlined in Cornelissen et al. (2003). (See Supplementary Material S3 and Table S3A-1 for a list of all measurements and measurement units.)

**Soil sampling**

We collected soil samples from 22 representative urban and rural sites that we had sampled for invasive species. Soil sampling took place in October and November of the 2012 and 2013 field season. Two samples each were taken at 11 rural and 11 urban sites, respectively. Leaf matter and surface detritus were cleared from the sampling area, and a soil sample was taken at a depth of 15 to 20 cm with a spade, stored in sealable plastic bags and transported on ice to a refrigerator to halt any soil biological processes. Half of the samples were taken to the Soil Nutrient Analysis Laboratory at the University of Connecticut (http://www.soiltest.uconn.edu/). Soil macronutrients were measured using the Modified Morgan extraction technique and potassium, calcium and magnesium were measured using an Inductively Coupled Plasma Optical Emission Spectrometry machine (Spectro Ciros Vision model). A Technicon Autoanalyzer II and a Scientific AC 200 colorimeter were used to measure phosphorus and nitrate concentrations. The lab also measured soil pH levels and lead content and estimated soil texture and organic matter content. The other half was retained for estimation of soil nitification rates. These were bagged and incubated at room temperature (22°C) for 31 days and subsequently analyzed for nitrogen. Net nitrification rates were calculated as the difference in soil nitrate between initial measurements and the incubated soils measured at the end of the 31 days, divided by the total amount of time passed (Robertson et al. 1999).

**Statistical analysis**

GPS positions were uploaded to Pathfinder Office and differentially corrected before being converted into shapefiles and merged into a single file. Each GPS point was associated with the continuous socioeconomic data from the 1-km grid into which it fell. Subsequent analyses were done in R version 3.0.0 (R Core Team 2013). To address the first research question regarding urban environmental growing conditions, several statistical tests were employed to determine environmental
differences between plots. We determined if there were differences between urban and rural soil sample nutrient content using two-tailed t-tests. Data from the two paired samples were averaged together for the t-test, and a log transformation was applied to address deviations from normality. Categorical measures of soil texture and soil organic content were tested using Fisher’s exact test on a 2 × 4 contingency table of the four types of soil texture (high organic content, loamy sand, sand and sandy loam) and a 2 × 3 contingency table with counts of the three types of organic content categories in urban and rural soil samples. χ² tests were performed on contingency tables of categorical plot data. Differences between continuous socioeconomic and forest cover site information were tested using a one-way analysis of variance (ANOVA) with a Tukey honestly significant difference test for determining individual comparisons while accounting for multiple comparisons.

Pearson’s χ² test was performed on 3 × 2 contingency tables of counts of species across the three types of plots. Species encountered fewer than five times total were excluded. Fisher’s exact test was employed where any contingency tables contained zeros. These tests were intended to determine if the observed distribution of species across urban, suburban and rural plot types occurred due to chance, addressing the second research question.

To examine and explore associations between different measures of urbanization, including socioeconomic variables, and species presence/absence across the urban-to-rural gradient, two multivariate methods were employed. Canonical correspondence analysis (CCA) was used to assess the relationships between invasive species presence/absence and categorical and continuous environmental variables (Ter Braak 1986; Palmer 1993) using the function ‘cca’ from the R package vegan (Oksanen et al. 2016). Categorical environmental variables were transformed into dummy variables and a matrix of plot by species presence/absence was created for entry into the function, excluding null plots. The significance of the environmental constraints used in the CCA models was assessed using ‘ANOVA-like’ permutation tests (Oksanen et al. 2016). The strength of the species/environment relationship was assessed with correlations of the weighted average scores and linear combination scores.

The woody invasives B. thunbergii, Solanum dulcamara and Celastrus orbiculatus were selected for use in logistic regression models, to explore influences of a subset of environmental variables on species presences. These species were selected as a priori representatives of rural-associated, urban-associated and generalist species. B. thunbergii was most frequent in rural plots, S. dulcamara was most frequent in urban plots, and C. orbiculatus was present at high frequencies across all three plot types. Grid cell-level per capita income, average impervious surface cover per person and proportion of core forest were chosen for continuous explanatory values in a full model, representing socio-economic status, degree of development intensity and population and forest cover, respectively. Values of these variables were applied to each plot falling within the grid cell. Other variables—population, housing and two fragmentation variables—were excluded from the full model due to strong collinearity with either the income metric or other fragmentation measures. Additionally, plot-level information on urban/suburban/rural grid cell classification, land use, canopy cover, number of invasive species in a plot (excluding the response species) and habitat type were included in the full models. A reference category was used for the categorical variables: for grid cell classification, it was ‘suburban’; for land use, ‘mixed-use’; for canopy cover, ‘51–75%’ and for habitat type, ‘natural edge’. Income and the urbanization metrics were log transformed. Forward and backward stepwise regression based on Akaike’s Information Criterion was used to select the optimal combination of explanatory variables. Model residuals were checked to account for potential spatial autocorrelation (Supplementary Material S4).

To address the final study question, we employed two-factor ANOVA models to determine if the trait means of an urban-classified species differed significantly from the trait means of the corresponding rural-classified species. The two leaf trait values from the same individual were averaged, as suggested by Cornelissen et al. (2003), for all PFT analyses. SLA, LDMC, LWR, leaf thickness and leaf area were selected for consideration. Each trait was selected for its ability to reveal aspects of plant investment strategy. Untransformed traits were examined for correlation using a scatterplot matrix and correlation coefficients. No strong correlations were graphically revealed and no correlation was greater than 0.7. One ANOVA model was fit for each of the five traits. A log transformation was applied to all variables to meet assumptions of normality and homoscedasticity. Tukey’s honestly significant difference test was used to determine significance of specific comparisons.

Results

Environmental differences between urban and rural sites

Soil nutrient means and standard errors are reported in Table 1. There were significant differences between urban and rural soil lead content and pH levels (Fig. 2a, b). Lead is a heavy metal that historically was commonly used as an additive component in gasoline and paint. Its use was phased out in the 1970s due to lead’s toxicity to humans, but it remains prevalent in urban areas. No rural site had lead levels above 100 ppm, which is considered within the normal range of lead content for New England soils by UCONN’s Soil Analysis Laboratory, while urban soils ranged from 108 to 1388 ppm. Per US EPA guidelines, soil lead levels above 400 ppm are considered of concern, while soil levels above 1200 are cause for soil remediation (USEPA 2012). There were significant differences between urban and rural soils in content of calcium, aluminum, zinc, copper and iron. Levels of calcium (t = −2.9, df = 15.1, P < 0.05), aluminum (t = −5.0, df = 12.3, P < 0.001), zinc (t = −3.3, df = 10.1, P < 0.01) and copper (Wilcoxon test, P < 0.01) were greater in urban sites. Iron levels were higher in the acidic soils of rural sites (t = 3.0, df = 10.4, P < 0.05). Nitrogen, a critical element for plants, was not significantly different between urban and rural sites (t = 0.9, df = 17.9, P = 0.389), nor was the nitrification rate (t = 1.2, df = 17.9, P = 0.286). There was a significant difference between the four soil textures of urban versus rural soils (Fisher’s exact test, P < 0.001). Most rural soils were sandy loams, while most urban soils were loamy sands or just sands, indicating a greater prevalence of coarse texture in urban soils (Fig. 2c). Soil organic content was not significantly different between urban and rural sites (Fisher’s test, P = 0.460, Fig. 2d).

While all the soils sampled in this study were acidic (pH < 7), urban soils were significantly less acidic than rural soils (t = −6.6, df = 19.61, P < 0.005, Fig. 2b). This difference is the most likely cause of observed nutrient differences between urban and rural soils; soil pH impacts nutrient solubility in the soil (Jim 1998) and therefore nutrient availability to plants. For
example, uptake rates for the essential nutrient phosphorus are highest at a pH level between 5.0 and 6.0 (Schachtman et al. 1998), which corresponds to the range of observed acidity for urban soils. Phosphorus was observed at higher concentrations in urban soils ($t = -2.7$, $df = 15.9$, $P < 0.05$).

Per capita income and proportion of core forest declined from rural to urban grid cells (Fig. 3a and f), although average per capita income was not significantly different between suburban and urban sites. The number of housing units, percent impervious surface and proportion of patch forest in a grid cell increased from rural and suburban to urban grid cells (Fig. 3b–d). The number of housing units and proportion of patch forest in urban sites was more variable than in rural and suburban grid cells. The proportion of edge forest (Fig. 3e) was greatest in suburban grid cells and not significantly different between rural and urban grid cells.

### Table 1. Means and standard errors for soil nutrient contents

| Nutrient | Rural Mean ± SE | Urban Mean ± SE |
|----------|-----------------|-----------------|
| Aluminum (ppm) | 321.77 ± 35.57 | 66.95 ± 14.72 |
| Boron (ppm) | 0.09 ± 0.02 | 0.35 ± 0.09 |
| Calcium (kg/ha) | 1000.92 ± 252.59 | 2227.84 ± 310.43 |
| Copper (ppm) | 0.30 ± 0.05 | 3.30 ± 1.19 |
| Iron (ppm) | 80.55 ± 15.05 | 16.31 ± 3.03 |
| Lead (ppm) | 74.36 ± 2.50 | 213.77 ± 58.20 |
| Magnesium (kg/ha) | 30.75 ± 200.53 | 200.22 ± 23.46 |
| Manganese (ppm) | 9.00 ± 1.64 | 19.61 ± 6.58 |
| Nitrification rate (mg N kg$^{-1}$ day$^{-1}$) | 4.57 ± 0.09 | 5.59 ± 0.09 |
| Phosphorus (kg/ha) | 5.66 ± 1.58 | 16.86 ± 3.06 |
| Potassium (kg/ha) | 1.75 ± 0.23 | 14.34 ± 3.20 |
| Zinc (ppm) | 0.09 ± 5.59 | 3.20 ± 15.05 |

Plot-level environmental information revealed differing trends across the three urbanization zones. Land-use categories for all plots were significantly different across the three zones ($\chi^2 = 199.1$, $df = 10$, $P < 0.001$). Rural plots were overwhelmingly located in or surrounded by areas of forested (60%) and residential (26.5%) land use. Agricultural land use was the least frequently encountered out of the six land-use categories. Only 8% of rural plots were in agricultural areas, followed by 0.9% of suburban plots and 0.4% of urban plots. Both urban and suburban plots were mostly located in areas of residential land use (57% and 58%), while urban plots had a greater proportion of mixed use plots than suburban plots. Canopy cover was also significantly different across the three zones ($\chi^2 = 82.7$, $df = 6$, $P < 0.001$). Half of all urban plots had the lowest of the four categories of canopy cover and half of rural plots had the highest category of canopy cover. Finally, the frequency of the four habitat types was also significantly different across the three neighborhood types ($\chi^2 = 118.1$, $df = 6$, $P < 0.001$). The ‘natural habitat’ classification, including deciduous, evergreen and mixed forests, and wetlands comprised 57% of rural plots. The ‘induced edge’ classification included linear patches of unmanaged wild vegetation persistent in small patches, created by sidewalks, roads, parking lots, walls, fences and rail-yards, and comprised about 50% of all urban plots.

### Patterns of species occurrences

Overall, the most commonly encountered invasive species of interest was the woody vine C. orbiculatus, followed by Rosa multiflora and B. thunbergii (Fig. 4). But relative frequency of some species clearly differed across urban, suburban and rural plots. Differences in associations between species presence and plot urbanization category were tested using two-tailed Pearson’s $r^2$ test or Fisher’s exact test. Acer platanoides, A. altissima, Bromus tectorum, Ligustrum spp., Robinia pseudoacacia and S. dulcamara.
were most frequently encountered in urban plots (Fig. 5). *Frangula alnus* and *Lonicera* shrub species were most frequent in suburban plots. *R. multiflora* and the grass *M. vimineum* were most frequently encountered in rural plots. For other species, urban, suburban or rural plot classification had no effect on the species’ frequency. The presence of *A. petiolata*, *Artemisia vulgaris*, *Catapla spp.*, *C. orbiculatus*, *Cynanchum louiseae*, *Euonymus alatus*, *Lonicera japonica* and *Rhamnus cathartica* and *Wisteria* spp. was independent of the three plot types.

Results of the CCA analysis are shown as a biplot (Fig. 6), where arrows represent direction and magnitude of environmental gradients. Species are plotted with respect to their relationship to these gradients. For example, the presence of *Elaeagnus angustifolium* was strongly influenced by induced habitat. *Acer platanoides*, *Ligustrum spp.*, *S. dulcamara*, *R. cathartica* and *Catalpa* spp. were associated with impervious surface cover and proportional cover of patch and edge forest types. Greater induced edge habitat and lower levels of canopy cover influenced the presence of *A. altissima*, *B. tectorum* and *A. vulgaris*, while natural habitats and core forest influenced *E. umbellata*, *R. multiflora*, *Lythrum salicaria*, *B. thunbergii* and *M. vimineum*. Finally, income and intermediate levels of canopy cover had a weak influence on *Wisteria* spp and *Lonicera* spp., respectively. *Celastrus orbiculatus* was not strongly influenced by any of the environmental gradients.

The first axis in the CCA analysis separated impervious surface cover, induced edge habitats, low levels of canopy cover and higher proportions of patch and edge forest from high proportions of core forest, high levels of canopy cover, natural habitat types and income; separating strongly urban-associated measures from rural-associated measures. This axis had a species–environment correlation of 0.6539. The second axis separated induced habitat types, intermediate and low levels of canopy cover, and proportion cover of edge forests from high levels of canopy cover and core forest, with a species–environment correlation of 0.4298. All model constraints were found to be significant using a permutation test ($P = 0.005$).

**Modeling species occurrences**

Three separate logistic regression models were fit for the species *B. thunbergii*, *S. dulcamara* and *C. orbiculatus*, representing a
rural, urban, and generalist species, respectively. Model diagnostic tests showed that all three models fit the assumptions of logistic regression. Spatial autocorrelation was measured using bubble plots, variograms and the Moran’s I test on model residuals; no evidence of spatial autocorrelation in the models was detected (Supplementary Material S4). Different explanatory variables were significant in explaining the presences of the three species (Table 2). Presences for all three species were significantly positively associated with invasive species richness. The presence of B. thunbergii, the a priori identified rural-associated species, was significantly positively associated with rural sites and higher canopy closure (76–100%). It was also significantly negatively associated with urban-classified sites. The urbanization metric was a significant predictor of the a priori urban-associated species, S. dulcamara. Distribution of this species was significantly positively associated with urban-classified sites and negatively associated with rural sites compared to suburban sites, though the latter relationship was not significant. Its presence was also negatively associated with all levels of canopy closure compared to the base level of 0–25%. Solanum dulcamara was influenced differently by all of the land-use categories compared to mixed-use, the base level. The strongest significant positive relationship was with agricultural land use, which was marginally significant. On the other hand, commercial, forested and industrial land classifications were all negatively associated with S. dulcamara presence, compared to the base level of mixed land-use. Considering the model explaining C. orbiculatus presence, other than a positive association with invasive species richness, it was also significantly negatively associated with both urban- and rural-classified sites. Land-use classification was included in the model, with different classifications having different associations with the presence of C. orbiculatus, but no relationship was significant. Nagelkerke’s pseudo-$R^2$ values were calculated for the three models and were universally relatively low, between 0.31 and 0.37; however, area under the receiver operator curve values were high for all three models, ca. 0.80, suggesting good model fits, although the models only explain about one-third of the variation in the data.

ANOVA models for trait data

Two-way ANOVA models using the a priori species classification and growth form revealed significant differences between urban and rural species with regard to plant traits (Supplementary Material S3). Trees, forbs and grasses had contrasting patterns in trait values between urban and rural species, with urban-classified species having a lower SLA, higher leaf thickness, higher LWR and lower leaf area compared to rural species. For shrubs and forbs LDMC was higher for the urban species. Vines showed the opposite trend for thickness and no significant trend for SLA and LWR. The urban-classified shrub species, E. umbellata, was lower for SLA and LWR and not significantly
different from *B. thunbergii* in leaf thickness. Leaf area was significantly smaller for urban-associated trees, vines, forbs and grasses compared to the rural-associated species.

Additional ANOVA models explored the effect of site and urban- or rural-species association, as well as individual models for each growth form (Supplementary Material S3). While there were significant differences between many mean trait values for paired urban and rural species, these differences did not coincide with consistent differences between species trait values for samples from species that occurred in both urban sites and rural sites within the five growth forms in most cases. Overall, differences in trait values among species and growth forms were more important than differences within species between sites in explaining trait values, indicating little consistent evidence for phenotypic plasticity or genotypic variation within species among contrasting sites.

### Discussion

**The urban environment**

Urban plots had more open canopy, induced habitats, and induced edges than rural plots. Closed canopy and natural habitats were less common, as were core forests. Induced habitats, patch forests and open canopies reflect the forest fragmentation and habitat conversion that occurred as a result of urbanization. Urbanization is also reflected in the increasing average percent impervious surface cover and number of housing units from rural to urban sites (Fig. 3).

Levels of soil nutrients and contaminants varied between urban and rural soil samples. Lead content was significantly higher in urban soils than in rural soils. While lead is no longer a common component of gasoline and paint products, it is clearly still persistent and pervasive in urban soils sampled here. A meta-analysis of soil lead content studies in American cities showed that soil lead content is positively correlated with population size and that it is persistent in the soil over time (Datko-Williams et al. 2013). In the Washington, DC, area, lead was found to be negatively correlated with distance from the city center and there were negative correlations between soil lead concentration and diversity of soil biotic communities, indicating that lead has far reaching effects in urban soils (Santas 1986). Zinc and copper were also higher in urban sites in this study, perhaps reflecting the effects of urban industrial pollution (Pickett and Cadenasso 2009; Calace et al. 2012). Aluminum becomes more soluble in more acidic soils, which may explain its greater concentration in the rural soil samples. Aluminum is not an essential element for plants and inhibits plant growth and function at higher concentrations (Lambers et al. 2008). The lower soil acidity and the greater prevalence of cement and mortar may also explain the greater concentration of calcium in urban soil samples.

There was no evidence of higher soil N or soil nitrification in urban plots versus rural plots. This is in accordance with the findings of previous studies that compared urban forest soils and rural forest soils and suggest that factors such as underlying bedrock, soil type and soil biotic communities may play an overriding role in soil nitrogen dynamics (Groffman et al. 2006; Raciti et al. 2011). Soil N and nitrification rates are also complicated by land-use history, land management and urban habitat type (Scharenbroch et al. 2005). The predominant type of urban habitats sampled was induced edges.

### Table 2. Results from three logistic regression models for a rural (*B. thunbergii*), urban (*S. dulcamara*) and generalist species (*C. orbiculatus*)

| Variable                  | *B. thunbergii* coefficient | *S. dulcamara* coefficient | *C. orbiculatus* coefficient |
|---------------------------|-----------------------------|---------------------------|------------------------------|
| Intercept                 | -3.1901                     | -7.3151                   | -1.3725                      |
| Income                    | —                           | —                         | —                            |
| Urban                     | -1.0564                     | 1.1684                    | -0.9061                      |
| Agricultural              | 0.9359                      | -0.6216                   | -0.6460                      |
| Commercial                | —                           | -1.5798*                  | 1.1300                       |
| Forested                  | —                           | -1.2711                   | -0.8769                      |
| Industrial                | —                           | -1.8461                   | -0.0933                      |
| Residential               | —                           | 0.2596                    | 0.5612                       |
| 26–50%                    | 0.4166                      | -0.9112                   | —                            |
| 51–75%                    | 0.5362                      | -0.7855                   | —                            |
| 76–100%                   | 1.1503                      | -1.3856                   | —                            |
| Richness                  | 0.4107                      | 0.5720                    | 0.8644                       |
| Natural habitat           | 0.7561                      | —                         | —                            |
| Induced edge              | -0.2552                     | —                         | —                            |
| Induced habitat           | -0.0703                     | —                         | —                            |
| AIC                       | 415.84                      | 357.01                    | 469.61                       |
| Pseudo-R²                 | 0.3152                      | 0.3632                    | 0.3692                       |
| Goodness-of-fit           | Deviance = 395.84, df = 451, P = 0.971 | Deviance = 331.01, df = 447, P = 0.999 | Deviance = 451.61, df = 451, P = 0.496 |
| Likelihood ratio test     | (comparison to full model)  | $\chi^2 = 12.251, df = 8, P = 0.140$ | $\chi^2 = 5.757, df = 5, P = 0.331$ | $\chi^2 = 6.973, df = 9, P = 0.640$ |

Coefficients represent log odds of finding the species of interest in a plot. Significant coefficients are in bold. Model fit diagnostics are listed in the last four rows of the table. These diagnostics include the model AIC value, Nagelkerke’s pseudo-$R^2$, $P$ values from the Pearson’s goodness of fit test comparing the model to an empty one, and results from a likelihood ratio test comparing the full model to the model reduced by stepwise regression.

* $P$ between 0.05 and 0.1.
Species distribution

Celastrus orbiculatus was the most commonly encountered species in this study. This species is in part successful due to high population growth potential across different light conditions, high germination rates, high seed set and fast growth rates (Leicht-Young et al. 2007; Merow et al. 2011). Rosa multiflora and B. thunbergii were also common, but were more closely associated with rural environments. Rosa multiflora and B. thunbergii are widely dispersed and are tolerant of many light levels (Lundgren et al. 2004; Ibáñez et al. 2009). The distributions of these two species are tied to historical land use and current level of development (Lundgren et al. 2004; Ibáñez et al. 2009; Mosher et al. 2009). Proximity to roads has also been implicated in their spread (Lundgren et al. 2004; Kuhman et al. 2011).

The spread of B. thunbergii is strongly associated with the wide-scale post-agricultural abandonment that occurred across New England within the last 100 years (Hall et al. 2002; Mosher et al. 2009). In the years following this abandonment, forests regenerated and B. thunbergii tolerated the encroaching shade conditions, surviving well in forest understories (Silander and Klepeis 1999). Historical dense plantings provided the seed sources that made this species prevalent (Brand et al. 2012).

Patterns observed for Lonicera shrub species could be explained by urban growth. Lonicera shrubs are known to be associated with urbanization processes (Borgmann and Rodewald 2005; Shustack et al. 2009; Pennington et al. 2010). Almost half of Lonicera shrub observations were made in suburban plots, and the presence of these species was best explained by intermediate levels of canopy cover in the CCA (Fig. 6). Escape and naturalization of woody ornamentals is thought to be linked to their extensive landscape plantings (Pysek et al. 2009), and many of the species used in this study have historical ties to the horticultural industry (Larkin 2011). Woody ornamental species that escape in urban areas may also be linked to the effect of the urban heat island, which encourages earlier leafing and flowering phenology in urban adapted plants (Kowarik et al. 2013).

It is possible that some species have spread from rural sites into urban sites. The trees Acer platanoides and Catalpa spp., for example, appeared with greater frequency as naturalized elements in urban plots than in rural and suburban plots, where they appeared frequently as planted elements. While it does not seem that the species most common in rural sites spread from urban sites into rural sites, one exception may be the ornamental liana Wisteria spp. This species was planted in half of the six urban and four suburban occurrences but was independently established naturally in all five rural occurrences. Chinese wisteria, W. sinensis, which is currently considered invasive in the south, is also spread by horticultural plantings (Trusty et al. 2007).

The continuous measures of urbanization were not sufficient to fully explain the presence of the representative urban-associated, rural-associated and generalist species. Overall, the logistic regression models explained a relatively small amount (about one-third) of variance (Table 2), suggesting that the variables included in these analyses, while important, are not sufficient to fully explain the variation in species presence. Explanatory power of models may be improved by including historical land-use variables, since this has been shown to be important in predicting the distributions of B. thunbergii and C. orbiculatus (Mosher et al. 2009). For the urban-classified species S. dulcamara, agricultural land use had a marginally significant, but substantial positive effect on the occurrence of this species, while most other land-use categories had a negative effect. In fact, S. dulcamara was present in most plots that were classified as agriculture and avian dispersal of seeds may account for this relationship. Forest and agricultural edges provide roosting habitats for birds, which tend to deposit the seeds consumed where they roost (McCay et al. 2009). Celastrus orbiculatus and B. thunbergii are also dispersed by birds, yet agricultural land use was not retained in the model for B. thunbergii and was not significant for C. orbiculatus, indicating that factors other than agricultural edges were more important in explaining the presences of these two species. Finally, plot-level invasive species richness was a significant predictor for all three species models and was strongest for C. orbiculatus, indicating that in a plot with many invasive species C. orbiculatus is very likely to be one of them, reflective of its ubiquity and the tendency of many invasive plants to co-occur (Kuhman et al. 2011).

Leaf traits

We expected plants affiliated with disturbed habitats to have higher SLA and lower LDMC based on previous findings (Knapp et al. 2008, 2009). High SLA is positively associated with photosynthetic rates while LDMC correlates positively with leaf toughness, drought adaptation and defense from herbivores (Cornellissen et al. 2003; Pérez-Harguindeguy et al. 2013). High SLA and low LDMC are favorable strategies for plants in a resource rich environment where competition is high; the expectation is that plants in these environments will grow quickly and reproduce early and prolifically. Many ruderal species tend to have this strategy (Grime 2001). However, we identified a lower SLA for the urban classified tree, forb and grass species relative to the rural species, and higher LDMC for the urban-classified forb and grass (Supplementary Material S3). These characteristics are consistent with tolerance to drought stress in an environment where light is not limiting (Cornellissen et al. 2003; Pérez-Harguindeguy et al. 2013), i.e. urban areas.

Additional evidence pointing to drought adaptation in urban areas was seen in results for LWR and leaf thickness. LWR is a metric measuring leaf shape. A higher ratio indicating the leaf is long and thin. Narrow leaves have a small boundary area, which helps enhance transpiration (Malhado et al. 2009). A plant with narrow leaves can utilize water efficiently when available, without exposing a large surface area to the sun during warm periods when water is less available (Yates et al. 2008; Malhado et al. 2009). LWR was greater for urban-associated species. Greater leaf thickness is also indicative of leaf adaptation to sunny, dry and low nutrient conditions (Pérez-Harguindeguy et al. 2013). The urban-associated tree, forb and grass species all had thicker leaves than their rural counterparts.

The combination of traits found for trees, forbs and grasses for SLA, LWR and leaf thickness suggests that the urban-classified species of each growth form is more drought adapted. There is evidence that urban floras are more drought tolerant (Williams et al. 2015). For example, Chen et al. (2013) found that over time, drought- and heat stress-tolerant ruderal species in Harbin, China, replaced ruderal species lacking these traits. They suggest that urban plants will tend to be stress-tolerant ruderals, species that employ a strategy allowing them to tolerate stress for the long term (Chen et al. 2013). Bromus tectorum, for example, is an annual species that thrives in arid, open environments of the western USA (Kostivkovsky and Young 2000). Similar results have also been found for woody species in...
urbanized riparian forests and near impervious surfaces and railyards, where drought-tolerant species replaced or were dominant over more mesic species (Pennington et al. 2010; Sung et al. 2011). Drought in urban areas is influenced by well-drained sandy soils, open-canopy habitats and the urban heat island effect, leading to urban drought islands. Additionally, impervious surface and soil compaction prevents rainwater from infiltrating urban soils, further enhancing the urban drought island effect (Pickett and Cadenasso 2009).

The traits of the vines and shrubs did not align with those of trees, forbs and grasses. One possible explanation may be that both the liana C. orbiculatus and the shrub B. thunbergii are habitat generalists that are preadapted to a wide range of environmental conditions. Celastrus orbiculatus was observed frequently in this study across the urban to rural gradient, and is known to colonize many different habitats (Leicht-Young et al. 2007). Berberis thunbergii was primarily observed in shaded forested rural sites. However, B. thunbergii can also germinate and survive in open, dry and sunny habitats (Lubell and Brand 2010). Another explanation may be that multiple environmental stressors are at work in the urban environment, and impact the consistency of a trait signal (Williams et al. 2015). Though some species showed significant differences in trait values in urban versus rural plots, there was insufficient evidence to suggest that traits within a species varied in a consistent and significant way between urban and rural sites.

Conclusions

Urban soils were slightly more alkaline and had higher lead concentrations and were a coarser texture than rural soils. Urban habitats had more open canopies, impervious surface, patch forest types and induced edge habitats than rural habitats, all of which contributed to an ‘urban drought island’ syndrome. Suburban areas form a transition zone between urban and rural areas, occupying intermediate levels between urban and rural sites in per capita income, number of housing units, proportion of patch forest and proportion of core forest. This study found that a priori urban-classified, invasive species were more drought tolerant, which may have allowed them to thrive in an arid urban environmental and outcompete other species. Drought tolerance was reflected in low SLA, high LDMC, high leaf laminar thickness and high LWR values in some species relative to shade-tolerant rural-classified species of the same growth form.

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Supplementary data

Supplementary data are available at JUECOL online.

Conflict of interest statement. None declared.

Statement of data availability

Data from invasive species observations were added to the website of the Early Detection and Distribution Mapping System (EDDMapS), which hosts data from the Invasive Plant Atlas of New England (IPANE).

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