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Plant Invasion Along an Urban-to-Rural Gradient

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Plant Invasion Along an Urban-to-Rural Gradient

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Table of Contents

Abstract

Humans are the most important drivers of invasive species introduction and natural habitat transformation globally. Ecological differences between areas of dense human habitation and minimally managed natural habitats were explored across an urban-to-rural gradient of land use in southern New England. These differences were examined through presence/absence and leaf functional traits for a set of invasive species; and urban and rural environmental conditions. Some species were more restricted to particular sites than others along the urbanization gradient, based on introduction history and habitat preference. *A priori* urban-classified species showed trait values associated with drought tolerance, including higher LWR, greater leaf thickness, higher LDMC and lower SLA. Finally, urban habitats were found to be significantly different from rural habitats. Urban soils were more alkaline, and had higher lead concentrations and sand content than rural soils. Urban habitats had more open canopies, impervious surface, patch forests, and induced edge habitats than rural habitats. Our findings suggest that urban environmental conditions contribute to an "urban drought island" syndrome and will favor species capable of tolerating drought.

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 (Angel et al. 2011, Irwin and Bockstael 2007, Vitousek et al. 1997, Williams et al. 2009). Although cities cover only 0.5% of the Earth's surface (Angel et al. 2011, Schneider et al. 2009) , they contain more than 50% of the world's population (United Nations 2011) and account for a disproportionately large amount of the world's resources consumption (Kareiva et al. 2007). In the US, urban populations have grown every year as cities become increasingly important centers of employment, habitation, transportation, culture, and trade; currently 80.7% of the population of the United States lives in an urban setting (US Census 2011). While these urban services are vital for supporting modern human life, they can have detrimental effects on the persistence of naturally-occurring biota. The relationship between urbanization and biodiversity is especially important to explore because areas of past high human population growth and habitation have been found to coincide with some biodiversity hotspots (Cincotta et al. 2000, Myers et al. 2000, Williams 2013).

Historically, ecological studies have focused on more-remote, undisturbed, or minimally disturbed sites (Martin et al. 2012). In 1997, two urban Long-Term Ecological Research (LTER) centers were established in Baltimore, Maryland and Phoenix, Arizona. These sites have made important contributions to our understanding of urban ecological systems (Cadenasso et al. 2006, Gagné 2013, Pickett and Cadenasso 2006). McDonnell and Pickett (1990) introduced the concept of an urban-to-rural ecological gradient to quantify human impact (Gagné 2013,

McDonnell and Pickett 1990). Urban ecological studies are concerned with the patterns and processes of biotic elements examined within the context of urbanizing or urbanized landscapes (Gagné 2013, Kaye et al. 2006, McDonnell and Pickett 1990, Pickett and Cadenasso 2006, Shochat et al. 2006, Zipperer et al. 2000).

Impervious surface cover is frequently used as a proxy for urban land use (Lu and Weng 2006), but it plays an even larger role in contributing to unique urban biogeochemical conditions in associated soils and streams (Arnold Jr. and Gibbons 1996, Civco et al. 2002). Some studies of urban soils have found them to be more acidic than rural counterparts due to acidic atmospheric deposits (Sukopp 2004), while others have found urban soils to be more alkaline 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, making degraded building materials a component of soils in urbanized landscapes (Jim 1998, Lehmann and Stahr 2007). Heavy metal pollution due to outputs from traffic and industries or erosion of construction materials are notable differences between urban soils and natural soils (Calace et al. 2012, Lehmann and Stahr 2007). Atmospheric N inputs (NO_x gases), and other inputs from fertilization, 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 (Edmondson et al. 2011, Scharenbroch et al. 2005), though urban greenspaces may be potentially less compacted than neighboring agricultural soils (Edmondson et al. 2011). High densities of roads, sidewalks and buildings also contribute to changes in rainwater runoff

2

patterns into urban streams and soils. Urban riparian habitats have lowered water tables, causing "hydrological drought" in soils (Groffman et al. 2003) and urban soils overall tend to be drier than rural soils (Pickett and Cadenasso 2009). These changed hydrological regimes ultimately make water less available for plants, even when rainfall is plentiful (Paul and Meyer 2001, Pickett and Cadenasso 2009). Finally, the urban heat island describes a phenomenon where urban regions have elevated temperatures compared to surrounding rural areas (Pickett et al. 2011), because solar radiation absorbed by impervious surface creates elevated nighttime temperatures (Parlow 2011).

Williams et al. (2009) describe environmental filters specific to cities that act both to add and remove species from the urban species pool: (1) habitat transformation, (2) habitat fragmentation, (3) human species planting preferences and (4) the unique soils and climates associated with cities (Williams et al. 2009). To become established naturally in an urbanizing landscape, species must have some combination of attributes that allow them to pass through these filters. Habitat transformation, frequently in the form of complete destruction and replacement of specific natural habitats, will likely remove species associated with those habitats from the urban species pool. Habitat transformation may lead to landscape fragmentation, creating higher habitat heterogeneity in cities and surrounding areas. Exurban growth at the fringes of cities proliferates into natural areas, fragmenting natural habitats into patches and creating edges (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 selective removal of "undesirable" species (Walker et al. 2009). Planting

preferences are reflected in high species richness in wealthy neighborhoods (Hope et al. 2003, Kinzig et al. 2005) a pattern that carried over to the urban species pool compared to neighboring natural sites in Phoenix (Walker et al. 2009). Removal of undesirable species in wealthy neighborhoods and more abandoned land in poor neighborhoods resulted in a negative relationship between invasive species and income (Gulezian and Nyberg 2010).

In New England, introduced plants comprise about 30% of the region's flora; a small portion of those are considered invasive (Mehrhoff 2000). Invasive species are introduced species that overcome local abiotic and biotic obstacles upon arriving in a new region and spread into surrounding areas (Richardson et al. 2000), sometimes having deleterious impacts on native species survival, native ecosystem processes, and local economies (Pimentel et al. 2005, Stohlgren et al. 2011, Vitousek et al. 1997). Introduced species and invasive introduced species inside and outside of cities contribute to global biotic homogenization (McKinney and Lockwood 1999, McKinney and La Sorte 2007, Trentanovi et al. 2013, Wittig and Becker 2010), where species tolerant to broad ranges of human-caused environmental change thrive and more habitat-specialized species die out (Lizée et al. 2011, McKinney and Lockwood 1999).

Given the serious impacts invasive plants can have on ecosystems, it is important to understand invasive plant distributions and current spread in order to predict future spread (Rejmánek and Richardson 1996, Stohlgren et al. 2011). Evidence suggests that invasive plant distributions are closely tied to anthropogenic landscape change. For example, modern invasive plant distributions have been found to be impacted by housing development, proximity to roads, and

past land-use (including agricultural history) (González-Moreno et al. 2013, Kuhman et al. 2011, Lundgren et al. 2004, Mosher et al. 2009). Socioeconomics at the local and landscape scale have been found to affect the local species pool of invasive plant species and influence their spread (Martin et al. 2004, Kinzig et al. 2005, Hope et al. 2003, Allen et al. 2010, Santos et al. 2011). In New England, housing, road density and mean income are positive correlates of invasive species richness (Gavier-Pizarro et al. 2010). The edges created by forest fragmentation during urban growth and development are known to promote the spread of certain woody invasive species in New England (Allen et al. 2013, Mosher et al. 2009), 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). Similar patterns were discovered in Australia and South Africa, where urban grassland edges contained higher invasive species cover deeper into the edge than rural grassland edges (Cilliers et al. 2008); and in Louisville, KY, where roadside forests contained more invasive species closer to the city center (Trammell and Carreiro 2011). As sites of both disturbed edge habitats and species introductions, urban areas seem primed to promote the spread of invasive species.

Invasive species may spread from urban to undisturbed native ecosystems (Saeumel and Kowarik 2010, von der Lippe and Kowarik 2008); however some studies have indicated that this may not be the case. Invasive species that were considered the largest threat to natural areas around Chicago were not common in cities, suggesting that urban areas were sinks and not sources of these species (Gulezian and Nyberg 2010). Invasive plants introduced after 1500 CE in England were associated with urban habitat and were not invading surrounding natural

5

habitat. Older invasive plants appeared to move from urban to cropland habitats; however this trend was attributed to recovery of formerly declining species due to conservation efforts increasing their preferred habitat (Botham et al. 2009). Movement from urban to rural habitats will also depend on landscape connectivity and plant dispersal effectiveness (Schleicher et al. 2011).

Plants have physiological features that allow them to overcome or tolerate a range of environmental challenges that can be quantified by measuring plant functional traits (PFTs). PFTs are defined as any measurable aspect of a plant with some direct or indirect effect on plant performance and fitness (Violle 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 often 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 (RGR) and photosynthetic capacity (Cornelissen et al. 2003). Given complex environmental demands and limited energy budgets, plants must invest resources in a way that maximizes their success in 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). Traits within a species can also be plastic, or change in response to different environmental conditions (Chapin et al. 1993).

The urban environmental filter should theoretically filter out species intolerant of urban conditions, leaving species with traits adaptive for urbanization (Duncan et al. 2011). 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). Urban areas may have higher proportions of wind-pollinated plants and other long distance dispersers, 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, Knapp et al. 2009). Knapp et al. 2008 described three critical filters in urban environments with respect to traits: the urban heat island favors drought-adaptive traits; intense and irregular disturbance patterns favor high SLA and low LDMC; and urban spatial heterogeneity favors plants with strong dispersal abilities, mostly by animals.

The Invasive Plant Atlas of New England (IPANE) is a database of invasive species in the six New England states (Bois et al. 2011, Mehrhoff et al. 2003). Twenty-five species were selected for surveying 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 IPANE list of invasive species. Using methodology adapted from IPANE protocols, I aimed to answer the following questions: (1) What growing conditions does the urban environment provide to a plant in urban Hartford compared to a plant in rural Storrs? (2) Are there differences in invasive species distribution along an urban-to-rural gradient in southern New England? (3) Is there evidence for relationships between socioeconomic variables and invasive plant distributions? (4) Finally, are there differences in functional traits that could account for differences in species distribution?

Methods

Study area

This study took place in southern New England, primarily in Hartford and Tolland counties in Connecticut (Figure 1). The initial urban-to-rural gradient selected ranged from Hartford and surrounding areas to communities 30-km east, around the University of Connecticut in Storrs-Mansfield. Most sites were located from approximately N 41° 46' to N 41° 47' latitude and W 72° 27' to W 72° 17' longitude, however supplemental sampling extended to limited parts of Windham and New London counties, and a small section of metropolitan Boston, MA. Over this range mean annual temperature and annual precipitation (Hijmans et al. 2005) shows only minor variations of about 1°C and 100 mm respectively, therefore climate variation was not included as a variable in this study.

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

A grid with cell sizes of 1-km^2 covering Connecticut and part of eastern Massachusetts was created using Geospatial Modelling Environment (Beyer 2012) and ArcGIS 10 (ESRI). Block group level 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) and percent impervious cover information, available in a 30-meter resolution raster dataset from 2006, was downloaded from the National Land Cover Database (Fry et al. 2011). The area-weighted sum of the total number of housing units and total population, and the area-weighted mean of estimated per capita household income, were calculated for each grid cell.

Population values in each grid cell were used to *a priori* define rural, suburban, and land-use. An area with less than 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 US Census. Urban was defined as an area with a minimum of 2,500 people mi^{-2} (965 people km^{-2}), based on overall current population densities for the United States and previous definitions of urban areas (U.S. Census). Suburban grid cells had population densities that fell between those of urban and rural grid cells. To express urbanization in a continuous way, a GIS raster layer of square meters of impervious surface per person per block group for Connecticut and the Boston metro area was created using ArcGIS 10 (ESRI). This layer is referred to as the 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. Finally, UCONN's Center for Land Use Education and Research's (CLEAR) Landscape Fragmentation Tool (LFT) v2.0 (http://clear.uconn.edu/tools/lft/lft2/index.htm) was used to create a raster layer of edge, patch, and core forest (Parent and Hurd 2010), with edge distance defined as 30 meters based on prior definitions and studies of edges in this region (Allen et al. 2013). Land use data from CLEAR (http://clear.uconn.edu/index.htm) and from MassGIS (http://www.mass.gov/anf/research-and-tech/it-serv-and-support/application-serv/office-of-geographic-information-massgis/) were used as LFT inputs. Proportion cover of edge, patch and core forest was calculated for each grid cell. See Appendix 2 for information on Census data, and Appendix 3 for GME code and details on the creation of the urbanization metric.

9

Grid cells were haphazardly selected to stratify sampling among the three neighborhood types

and across the urban-to-rural gradient. A total of 110 sites were visited, of which 36 were

urban, 40 were suburban and 34 were rural. Five points were randomly placed for plot sampling

locations at a minimum distance of 100 meters apart in each site. These locations were visited

over the course of the 2012 and 2013 field seasons, for ground-based data collection.

Additional points from Boston were collected by a collaborator.

Sampling Methods

Plots were navigated to using a Trimble Juno ST handheld GPS unit and a GPS position was

taken at the center of every plot. Plots were moved if the point fell in a location that could not

be sampled, such as a building or road. In that case, sampling took place in the nearest available

growing space. Opportunistic plots were also collected. These plots were not part of the

original sampling scheme, but were collected as encountered throughout the study region.

Opportunistic plots were included to supplement data from the original sampling scheme and

to sample as widely as possible. The data collection approach was adapted from the IPANE

surveying methodology. Data collected from each species at a plot included presence/absence

data for a set of 25 nonnative species (Table 1); ordinal measures of species abundance,

percent cover, and distribution; categorical variables of plant reproductive stage, a binary

measure describing if a the individual was planted or "spontaneous"; and categorical measures

of site environment, including habitat types, surrounding land use, plot canopy cover and

neighborhood (Appendix 5).

Species trait sampling

Two species of each of five growth forms, paired by observed differences across the urban-to-rural gradient and habitat preferences (from the IPANE website), were selected from the full set of 25 species. One species in each pair was *a priori* classified as an urban-associated species, while the other was classified as rural based on preference for open canopy edge habitats and closed canopy forested habitats and observed differences in species frequency, respectively.

Leaf samples for trait analysis were collected from populations in two urban sites and two rural sites. Locations were selected for sampling from plots that had been visited in 2012, from recorded IPANE point locations, or from populations found after searching likely areas of occurrence. The standardized procedures for measuring plant traits followed Corneslissen et al. (2003). At each "site", ten individuals were selected along regular intervals. Two fully expanded, representative sun-exposed leaves were selected from five of these individuals. In the shade adapted species *Ailliaria 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. Leaves were taken to the lab to be 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-3000A portable leaf area meter was used to

11

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 specific leaf area (SLA), leaf

water content (LWC), leaf mass per area (LMA), length-width ratio (LWR) and leaf dry matter

content (LDMC) were calculated. See Appendix 9 for a list of all measurements and

measurement units.

Soil Sampling

I collected soil samples from urban and rural sites located at extreme ends of the urban-to-rural

gradient for additional measures of edaphic environmental difference. Sites were selected for

soil sampling based on their accessibility, diversity of habitat types, and proximity to sampling

locations, and were sampled according to guidelines set by the UCONN Soil Analysis Laboratory.

Sampling took place at the end of the 2012 and 2013 field season. Two samples were taken at

11 rural and 11 urban sites. Leaf matter and surface detritus were cleared from the sampling

area, and a soil sample was taken at a depth of 6-8 inches with a spade, stored in sealable

plastic bags, and transported immediately to a refrigerator to halt any soil biological processes.

Half of the samples were taken to the Soil Analysis Lab. 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 (ICP-OES)

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 nitrification rates. These were

bagged and incubated at room temperature 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). Data from the two paired samples were

averaged together for a t-test. Where necessary the log transformation was applied to meet

test assumptions of normality. Categorical measures of soil texture and soil organic content

were tested using Fisher's exact test.

Data analysis

GPS positions were uploaded to Pathfinder Office and differentially-corrected before being

uploaded into shapefiles, merged into one file, and each point was associated with

socioeconomic data from the 1-km grid into which it fell. Analyses were done with R version

3.0.0 (R Core Team 2013). I first determined if there were environmental differences between

plots that fell in urban, suburban or rural areas using t-tests and chi-square tests. I then looked

for differences in species frequencies across plots with chi-square tests, and then differences in

species abundances with Kruskal-Wallis tests. Finally, multivariate methods were employed to

examine relationships between continuous measures of urbanization and species

presence/absence across the urban-to-rural gradient. Canonical correspondence analysis (CCA)

was used to assess the relationships between invasive species presence/absence and

categorical and continuous environmental variables (Palmer 1993, Ter Braak 1986) using the

function "cca" from the R package vegan (Oksanen et al. 2013, R Core Team 2013). Categorical

environmental variables were transformed into dummy variables for use with the cca function.

13

A matrix of plots by species presence/absences was created for entry into the function. The significance of the constraints used in the CCA models was assessed using permutation tests. Three species were selected for entry into logistic regression models to explore influences of a subset of environmental variables on the presences of these species using the R "glm" function. Model residuals were checked for spatial autocorrelation (Appendix 10).

For the plant functional trait analysis principal components analysis and ANOVA models were employed to determine key traits and significant differences between different classification factors. Buffers of 1-km radii were created in ArcGIS around each of the 40 plots. Average values of the urbanization metric, median household income as a measure of socioeconomic status, and the proportion of core and edge forest in each buffer were calculated. Multiple linear regression models were fit for each of the five traits to relate continuous measures of urbanization to trait values, using log transformed income and urbanization metrics and untransformed proportion of core forest and proportion of edge forest as covariates. The ten species were also included in the model as a categorical variable with *A. platanoides* as the reference category.

Results

Environmental differences between urban and rural sites

Soil analysis results showed differences in nutrient content between soils from urban and rural sites, which was tested using two-tailed t-tests. This difference was significant in lead and pH (Figure 2). Lead is a heavy metal that historically was commonly used as an additive component

in gasoline and paint. These practices were phased out in the 1970s due to lead's toxicity to humans, but lead 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. According to U.S. EPA guidelines, soil lead levels above 400 ppm are considered of concern, while soil levels above 1200 are cause for soil remediation (http://www.epa.gov/region1/leadsafe/pdf/chapter3.pdf).

While all the soils sampled in this study were acidic (pH < 7), urban soils were significantly less acidic than rural soils. This difference was the most likely cause of some nutrient differences between urban and rural soils, because 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 acidy for urban soils (Figure 2). This may be one factor in the higher concentration of phosphorus observed in urban soils (t = -2.7245, df = 15.866, p = 0.01509).

There were also significant differences in soil content of calcium, aluminum, iron, and zinc. Aluminum is not an essential element for plants and causes problems for root functioning at higher concentrations (Lambers et al. 2008). Aluminum becomes more soluble in more acidic soils, which may explain its greater concentration in the rural soil samples (t = 4.9749, df = 12.318, p = 0.0002983). Calcium, an essential plant nutrient, was low in rural sites relative to

urban sites, which could also be due to the greater acidity of rural soils (t = -2.938, df = 15.065, p = 0.01014). Iron and zinc are heavy metals, however, unlike lead, they are essential parts of some plant metabolic processes. Both can become toxic to plants at higher levels. Zinc levels were higher in urban sites (t = -3.2619, df = 10.123, p = 0.008414), while iron levels were higher in the acidic rural sites (t = 3.0179, df = 10.384, p = 0.01243). Copper was also significantly higher in urban sites (Wilcox test, p = 0.0014). Nitrogen, a critical element for plants, was not significantly different between urban and rural sites, nor was the nitrification rate, the rate at which microorganisms in soils produce bioavailable nitrates.

Fisher's exact test was performed on a 2 x 4 contingency table with the counts of the four types of soil texture (high organic content, loamy sand, sand, sandy loam; Figure 2) in urban and rural soil samples. There was a significant difference between soil textures of urban versus rural soils (p = 3.42e-05). Most rural soils were sandy loams, while most urban soils were loamy sands or just sands, indicating a greater contribution of sandy texture in urban soils. Soil organic content was also estimated and tested using a 2 x 3 contingency table and Fisher's exact test, but organic content was not significantly different between urban and rural sites (p = 0.4602).

Grid cell level information of socioeconomic and forest cover data is presented in Figure 3. Per capita income and proportion of core forest declined from rural to urban cells. The number of housing units, percent impervious surface and proportion of patch forest in a site increased over the urban-to-rural gradient. The number of housing units and proportion of patch forest in urban sites was more variable than in suburban and rural sites. The proportion edge forest was

16

greatest in suburban sites, though the proportion of edge forest in urban sites was more variable.

The plot level environmental information collected also revealed differing trends across the three urbanization zones (Figure 4), which were tested using Chi-square tests of independence. Land use categories for all plots were significantly different across the three zones ($\chi^2 =$ 199.0988, df = 10, $p < 2.2e\text{-}16$). Rural plots were overwhelmingly located in and surrounded by areas of forested (60%) and residential (26.5%) land use. Agricultural land use was the least frequently encountered out of the six 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 ($\chi^2 = 82.6864$, df = 6, $p = 9.946e\text{-}16$). Half of all rural plots had the highest level of canopy cover, while half of all urban plots had the lowest level of canopy cover. Suburban plots had the highest proportion of intermediate levels of canopy cover. Finally, the frequency of the four habitat types was also significantly different across the three neighborhood types ($\chi^2 = 118.075$, df = 6, $p < 2.2e\text{-}16$). The "natural habitat" type classification, including deciduous, evergreen and mixed forests, and wetlands comprised 57% of rural plots. The "induced edge" classification includes 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 across all sites was the woody vine *Celastrus orbiculatus*, followed by the shrubs *Rosa multiflora* and *Berberis thunbergii* (see Appendix 7). Relative occurrences of these species clearly differed across urban, suburban and rural plots. *Celastrus orbiculatus* was the most observed species overall and was the most frequently observed species in urban and suburban plots, whereas *Rosa multiflora* was more common in rural plots. *R. multiflora* was followed in frequency by plots containing none of the species of interest and *B. thunbergii*. Suburban sites also saw spikes in observations of *Acer platanoides*, shrub *Lonicera* species, and *Solanum dulcamara*. In urban sites *R. multiflora* was observed less frequently than in rural and suburban sites, while *Acer platanoides*, *Solanum dulcamara*, and *Ailanthus altissima* made up a greater proportion of the observations.

To test for significance of the frequencies of the ten most common species across the urban-to-rural gradient, 3 x 2 contingency tables were created of the most encountered species, excluding those which were encountered fewer than five times. The significance of the frequencies of each species across urban, rural and suburban plots was tested using Pearson's chi-square tests. Fisher's exact test was employed where the contingency table contained zeros. For some species, neighborhood class had no effect on their frequency (Appendix 6). *C. orbiculatus*, *Catapla sp.*, *Cynanchum louiseae*, *Alliaria petiolata*, *Artemisia vulgaris*, *Euonymus alatus*, *Lonicera japonica*, *Wisteria sp.*, and *Rhamnus cathartica* were not significantly more or less frequent across the three neighborhood classes. Species that were not generalists include *Acer platanoides*, *Ailanthus altissima*, *B. thunbergii*, *Bromus tectorum*, *Elaeagnus umbellata*,

Frangula alnus, *Ligustrum spp*, *Microstegium vimineum*, *Robinia psuedoacacia*, and *S. dulcamara*. All of these species were most frequently encountered in urban plots. The species that were most encountered in rural plots were the shrubs *B. thunbergii* and *E. umbellata* and the grass species *M. vimineum*, which was never encountered in any urban plots. Only two species, *Lonicera* shrub species and *R. multiflora*, were more frequent in suburban sites. 49% of *Lonicera* observations were in the suburbs, while 70% of *Rosa* observations were evenly split between rural and suburban areas.

Abundance categories of all species together were also assessed (Appendix 6). Plot abundances of all species combined for all sites were tested using a Kruskal-Wallis rank sum test. Species abundances across urban, rural and suburban sites were significantly different (Kruskal-Wallis χ^2 = 13.9465, df = 2, p = 0.0009366). In individual comparisons using the Wilcoxon Rank Sum test, rural and urban sites had significantly different species abundances (W = 116978.5, p = 0.0003195) and so did rural and suburban sites (W = 104798.5, p = 0.003691); however suburban and urban sites did not (W = 186120, p = 0.4501). Species abundances tended to be greater in urban sites for all species. Percent plot cover of a species followed the same pattern.

While using population cutoffs and categorical measures was a convenient and useful way to define different parts of the urban-to-rural gradient, continuous measures of development and urbanization were also available and examined through CCA analysis and linear models. Results of the CCA analysis are shown as biplots, where arrows represent the relative direction and magnitude of each environmental gradient and species are plotted as points with respect to

their relationship to the environmental gradients. The relative length and direction of the arrows represents their influence on sorting species occurrence patterns across plots.

CCA biplots are presented in Figure 5a-f. When dummy variables for urban and rural sites (suburban sites as the reference category) were used as two environmental gradients, the first CCA axis had a species/environment correlation of 0.557 and the second was 0.327 (Figure 5a). The model was significant ($p = 0.005$) given 199 permutations. The rural and urban environmental gradients were separated by the first axis. *B. tectorum*, *R. psuedoacacia, A. altissima* and *P. cuspidatum* are more associated with the urban axis, while *B. thunbergii* and *M. vimineum* were more rural. *C. orbiculatus*, *E. alatus* and *S. dulcamara* appear to be unaffected by neighborhood type, and *F. alnus*, *E. angustifolium*, *R. cathartica* and *Lonicera* shrubs are negatively associated with both urban and rural sites. For habitat types, the first CCA axis had a species/environment correlation of 0.402 and separated induced habitat types from natural habitat types (Figure 5b). The second CCA axis had a species/environment correlation of 0.310 and separated the habitat class of habitat types from edges. *B. thunbergii* and *L. salicaria* were most associated with the natural habitat class, while *Ligustrum* species and *E. angustifolium* were more associated with the induced habitat environmental gradient, which conditions found in yards and gardens. Finally, the induced edge category explained the frequency of species including *C. louiseae*, *B. tectorum* and *Catalpa* better than the other two categories. This model was also significant ($p = 0.005$). The canopy cover CCA model was significant given 199 permutations ($p = 0.005$, Figure 5c). The first axis had a species/environment correlation of 0.389, while the second axis correlation score was 0.279. The first axis separated species

associated with high canopy cover from species associated with low canopy cover, and the second axis separated out median levels of canopy cover from the extremes. The arrows representing all levels of canopy cover are orthogonal, indicating they are uncorrelated. Species including *B. thunbergii* and *E. alatus* appear to be more associated with high levels of canopy cover, while *A. altisima*, *L. salicaria* and *C. louisae* are correlated by low levels of canopy cover. *Microstegium vimineum*, *E. angustifolium F. alnus*, *R. cathartica*, and *L. japonica* were associated with medium levels of canopy cover.

Continuous measures of urbanization were assessed in two CCA models, one containing average percent impervious cover in a grid cell and average per capita income ($p = 0.005$, Figure 5d), and the other containing proportion of different forest types in a grid cell ($p = 0.015$, Figure 5e). The first axis differentiated impervious surface from income with an environment/species correlation of 0.378. The second axis had a correlation of 0.326. Impervious surface and income were not correlated. Species most explained by impervious surface cover include *B. tectorum*, *A. altissima*, *S. dulcamara* and *L. japonica*. Income was most associated with *Lonicera* shrubs, *R. cathartica* and *E. angustifolia*. The first axis of the forest fragmentation model separated edge forest and core forest from patch forest with an environment/species correlation of 0.323, and the second separated edge and patch from core forest with an environment/species correlation of 0.253. Species best explained by increasing proportions of patch forest are *B. tectorum*, *A. altissima*, *Catalpa spp*. and *S. dulcamara*. Species best explained by core forest include *B. thunbergii*, *E. alatus* and *M. vimineum*. The edge forest gradient was not very strong indicating that this gradient is not very important in explaining species presences compared to core forest

21

and patch forest. Finally, a CCA plot with all variables combined is presented in Figure 5f. The first axis separated urban-correlated variables from rural variables and has an environment/species correlation of 0.6560. Five distinct groups of variables emerged in this analysis. The first group represented rural plots with more cover of core forest and in natural habitats, which explained the presence of species like *M. vimineum*, *E. umbellata*, *B. thunbergii*, and *L. salicaria*. The second group represented low canopy cover and induced edge habitats, which explain the species *B. tectorum*, *C. louisae*, *A. altissima*, *A. vulgaris*, and *P. cuspidatum*. Another group contains the most urban plots, consisting of urban grid cells, impervious surface, and proportion cover of edge and patch forest. The species *R. pseudoacacia*, *Ligustrum spp*. and *A. platanoides* were more associated with these variables. Finally, a group of intermediate and high levels of canopy cover and income best explained *E. alatus*, and *Lonicera spp*. Induced habitats were not correlated with any other variable and explained the presence of *E. angustifolium*.

Modeling

Generalized linear regression was employed to further explore and explain the influences of various land use characteristics on presence and absence of invasive species across the urban-to-rural gradient. Logistic regression models were built, using the glm function in R (R Core Team 2013) for the woody invasives *B. thunbergii*, *A. altissima* and *C. orbiculatus*. These species were selected for modeling as *a priori* representatives of rural-associated, urban-associated and neighborhood-indifferent species. Site-level per capita income, average impervious cover per person, and proportion of core forest were chosen for continuous explanatory values of the full

model, representing socio-economic status, degree of development intensity and population and forest cover, respectively. 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. Site neighborhood classification was also included. Finally, plot-level information on land use, canopy cover, number of invasive species in a plot (excluding the response species) and habitat type were also considered. The reference category for grid cell classification was "suburban"; for landuse, "mixed-use"; for canopy cover, "51-75%"; and for habitat type "natural edge". Income and the urbanization metric were log transformed for entry into the model. Stepwise regression based on Aikaike's Information Criterion was used to select the optimal combination of explanatory variables.

Regression results are presented in Table 2. Different variables were significant for the three modeled species. The presence of *B. thunbergii*, the *a priori* identified rural-associated species, was significantly positively influenced by rural sites and natural habitats. It was also significantly negatively influenced by urban sites and the urbanization metric. The urbanization metric was a significant predictor of the *a priori* urban species, *S. dulcamara*. Distribution of this species was significantly positively influenced by urban grid cells and negatively influenced by rural grid cells compared to surburban cells, though the negative relationship with rural cells was not significant. *Solanum dulcamara* was influenced differently by all the different categories of land use compared to mixed-use, the base level. The strongest significant relationship was with agricultural land use. For the model explaining the presence of *C. orbiculatus* in a plot, only plot invasive species richness and urban sites were significant. Income was included in the model

and had a slight negative impact on the presence of *C. orbiculatus*. The number of other

invasive species in a plot had a significant positive impact on all species, however this

relationship was the strongest for *C. orbiculatus*.

Trait selection and ANOVA models

A total of 12 measurements were obtained for all leaves. For all analyses, the two leaf trait

values from the same individual were averaged together, as suggested by Cornelisson et al.

(2003). Measurements, units and explanations of each functional trait are presented in

Appendix 9. Principal components analysis was applied to the trait database to explore visually

all variables in multivariate space using the function prcomp (R Core Team 2013). Height and

dbh were omitted because they were only collected for two of the ten species. Variables were

scaled to unit variance for entry into the analysis. The first two components of the analysis

explained 75% of the total variance present in the dataset (Appendix 9). The first component

has negative loadings for area, width, length, mass, LMA and LDMC and positive loadings for

LWR, SLA, and LWC. This axis represents investment in size versus investment in traits that help

with regulating heat loss, resource capture, and water storage; indicating tradeoffs between

leaf size and traits that help tolerate stressful environments. The second component separates

area, length, width, water content and SLA from LMA, LDMC, LWR and thickness. A biplot of all

variables was plotted for data visualization (Figure 6). Measurements from the same species are

clearly clustered together. Some clustering in the biplot is present among growth forms,

especially for the vine species. The species with the smallest and narrowest leaves (the two

grasses and *B. thunbergii*) are clustered on the other side of the first axis. Along the second axis,

urban species tend to have negative scores while the corresponding rural species tends to have a more positive score. The vines do not show this trend.

SLA, LDMC, LWR, leaf thickness and leaf area were selected from this analysis for consideration in analysis of variance (ANOVA) models. Trait values were subjected to two-factor ANOVA models to determine if the mean of an urban-classified species trait value differed significantly from the mean trait value of the corresponding rural species. One model was fit for each of the five traits. The log transformation was applied to all variables to meet assumptions of normality and homoscedasticity. Tukey's honestly significant difference (HSD) was used to determine significance of specific comparisons while penalizing p-values for multiple comparisons. All means and standard deviations are presented in Appendix 9.

Main effects for the first set of ANOVA analyses were the species growth form (trait, shrub, vine, forb and grass), and species classification (urban, rural). For the SLA model the interaction effect was significant ($F(4, 190) = 43.23$, $MSE = 2.577$, $p = $ <2e-16), as was the effect of urban/rural species classification ($F(1, 190) = 250.23$, $MSE = 14.914$, $p = $ <2e-16) and growth form ($F(4, 190) = 103.97$, $MSE = 6.375$, $p = $ <2e-16). Post-hoc Tukey's HSD showed significant differences between SLA of urban and rural-associated trees (p <0.001), shrubs (p <0.001), forbs (p <0.001) and grasses (p <0.001). For these growth forms the urban associated-species had a smaller SLA than the rural-associated species. For vines, the difference between the urban and rural species was slight though still significant ($p = 0.047$), and the urban species was the greater of the two.

25

The effect of urban/rural classification (F(1, 190) = 49.89, *MSE* = 0.2766, *p* = <2.99e-11), growth

form (F(4, 190) = 100.79, *MSE* = 0.5588, *p* = <2e-16), and the interaction of the two factors (F(4,

190) = 40.29, *MSE* = 0.2234, *p* = <2e-16) on LDMC was significant. However, only urban/rural

shrubs and urban/rural forbs were significantly different according to the post-hoc test (*p* =

0.00 in all cases). In both these growth forms the urban associated species had higher trait

values. The results from the ANOVA for LWR for the classification, growth form and interaction

were as follows: F(1, 190) = 600.96, *MSE* = 16.463, *p* = <2e-16; F(4, 190) = 1018.41, *MSE*

=27.899, *p* = <2e-16; and F(4, 190) = 96.94, *MSE* = 2.656, *p* = <2e-16). Trees, forbs and grasses

showed significant differences in LWR in post-hoc comparisons. The urban species had the

higher trait values for all three pairs. There was no strong difference or pattern between shrub

species or vine species.

Leaf thickness varied significantly with species association, (F(1, 190) = 124.24, *MSE* = 0.07338,

p = <2e-16), growth form (F(4, 190) = 136.08, *MSE* = 0.08038, *p* = <2e-16) and their interaction

(F(4, 190) = 49.55, *MSE* = 0.02927, *p* = <2e-16). Trees, forbs, vines and grasses show significant

differences in thickness in the post-hoc test, with the urban species showing greater leaf

thickness than the rural species in the trees, forbs and grasses. Shrubs were not significantly

different in leaf thickness. For the leaf area model, species association (F(1, 190) = 30.14, *MSE* =

3.84, *p* = 1.27e-07), growth form (F(4, 190) = 481.62, *MSE* = 61.29, *p* = <2e-16) and the

interaction term (F(4, 190) = 145.46, *MSE* = 18.51, *p* = <2e-16) were significant. Tukey's HSD

showed that all urban and rural species were different. For all growth forms except the shrubs, leaf area was smaller in the urban associated species.

Trees, forbs and grasses emerge as regularly having consistent patterns between the urban and rural species. The urban classified species had a lower SLA, higher leaf thickness, higher LWR and lower leaf area. In 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. Another set of two-way ANOVA models was created to determine if there were any differences between leaf trait samples from urban sites and from rural sites, using growth form and site as main effects. Model results are presented in Appendix 9. Site was not a significant effect for any model, and post-hoc test for individual comparisons showed that the relevant comparisons of rural sites versus urban sites for each growth form were not significant. Additional two-way models were created for every trait for each individual growth form (Appendix 9). The species association term was always significant, and the site term was significant for SLA in grasses and vines, and LWR and LDMC in trees. Post-hoc testing showed that some species had significantly different trait measurements in urban versus rural sites. For example, *A. platanoides* in urban sites had lower LWR than in rural sites, B. *thunbergii* had lower leaf thickness in urban sites than in rural sites, and *C. orbiculatus* had a higher leaf area in rural sites.

While there were significant differences between many mean trait values for paired urban and rural species, these differences do not appear to carry over to consistent differences between species trait values for samples from species that occurred in both urban sites and rural sites within the five growth forms most cases. Potential exceptions were for SLA in vines and grasses, LDMC in trees, LWR in vines, leaf thickness in shrubs and leaf area in vines. These differences were usually not significant in post hoc tests. Overall, these results indicate that differences between species and growth forms were more important than differences within species between sites in explaining trait values.

MLR models

Multiple linear regression (MLR) models were created to examine the effect of continuous measures of urbanization on trait values of the ten species. These models were intended to determine if the degree of development surrounding a site influenced trait values. Including species as a predictor in these regression models improved the overall model fit and increased the amount of variance in the data captured by the models from <10% in a model without a species term to over 80% in models with the species term. Results for models without the species term are presented in Appendix 9.

Regression results for models including species are presented in Appendix 9. Between 83 and 96% of the variation in leaf traits was explained by these models. Analysis revealed some patterns between continuous measures and trait values. The urbanization metric, square meters of impervious surface per person, had a very slight negative effect on leaf area and SLA

and a positive effect on LWR, LDMC and leaf thickness, though the effect was only significant

for SLA and LDMC. Smaller SLA and larger LDMC in urban sites corroborates with the ANOVA

results for urban and rural classified species. Income had small and insignificant effects on trait

levels. Neighborhood socioeconomics may play a role in shaping local biodiversity, but any

connection between income and leaf trait measurements would more likely be indicative of

local wealth influencing neighborhood planting preferences.

Proportion of edge forest and proportion of core forest in the 1-km radius buffer area were

both significant and strong predictors of leaf area. Edge forest had a strong positive affect on

leaf area, while core forest had a weaker positive impact. Core forest may have also

encouraged larger leaves in some species due to light competition under a closed canopy. The

proportion of edge forest had a significant negative affect on LDMC and a significant positive

affect on SLA. Core forest did not significantly affect either of these traits. Leaf thickness was

not impacted by either forest type.

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 or

unnaturally created habitats, patch forests and open canopies reflect the forest fragmentation

and extreme habitat conversion that native forests underwent to support higher densities of

human population, which is also reflected in the increasing average percent impervious surface cover and number of housing units from rural to urban sites (Figure 3).

Lead content was significantly higher in urban soils than 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 recent 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 D.C. 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). The heavy metals zinc and copper were also higher in urban sites in this study, reflecting the effects of urban industrial pollution (Calace et al. 2012, Pickett and Cadenasso 2009).

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 nutrient 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, or edges created by unnatural means. This included

roadsides, sidewalks, parking lots and railway edges, along which there could be horticultural

plantings or small patches of spontaneous growth in small strips of growing area.

Species distribution

Many of the 25 species observed showed the greatest frequency in the urban neighborhood

type, which was defined by population densities above 965 people per km^2, and all species

combined were more abundant in urban plots (Appendix 6). *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 (Ibáñez et

al. 2009, Lundgren et al. 2004); so why were they more common in rural sites? The distributions

of these two species have been shown to be strongly tied to past land use and current level of

development (Ibáñez et al. 2009, Lundgren et al. 2004, Mosher et al. 2009). Proximity to roads

has also been implicated in their spread (Kuhman et al. 2011, Lundgren et al. 2004). *Berberis*

thunbergii's spread 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 subsequent years forests regenerated over this species and barberry tolerated the

encroaching shade conditions and now survives in forest understories (Silander Jr. and Klepeis

1999). Historical dense plantings provided the seed sources that made this species prevalent

(Brand et al. 2012). *Rosa multiflora* is also tied to historical land use (Lundgren et al. 2004).

The trees *Acer platanoides*, *Ailanthus altissima*, *Robinia pseudoacacia* were more frequent in urban sites than rural sites, while the tree *Catalpa* was indifferent to site neighborhood in the frequency analysis (Appendix 6). However, 40% of all suburban and rural observations of *Catalpa* were likely planted individuals, compared to a quarter of urban observations, so its current distribution is primarily determined by human planting preferences. Other urban species include *Bromus tectorum*, *Cynanchum louisae*, and *Ligustrum* shrubs. *Ligustrum* was also mostly found as planted, which is reflected in its position along the induced habitat axis in the habitat type biplot (Figure 5b).

While not a major predictor for most distributions, income had an important affect on some of the plants studied. *Rhamnus cathartica*'s frequencies across urban, suburban and rural plots were not significantly different according to frequency analysis (Appendix 6). In the CCA plots, its presence was best explained by income and low-intermediate levels of canopy cover; this species was not well explained by either urban or rural site categories (Figures 5a-e). *Lonicera* shrubs are known to be associated with urbanization processes (Borgmann and Rodewald 2005, Pennington et al. 2010, Shustack et al. 2009). Almost half of *Lonicera* shrub observations were made in suburban plots, and also seem to be partially explained by income in CCA plots (Figure 5). *R. cathartica* and *Lonicera*'s association with income and intermediate levels of population seems indicative of escape from cultivation in wealthier neighborhoods at the fringes of urban growth. Escape and naturalization of woody ornamentals is thought to be linked to their extensive planting (Pysek et al. 2009). Woody ornamental species 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 plants and allows plants from different functional groups to become established (Kowarik et al. 2013). *E. angustifolia* also showed strong relationships between income and intermediate levels of canopy cover, however this species was observed very infrequently.

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

The continuous measures of urbanization were not adequate by themselves to explain fully the presence of the representative urban, rural and generalist species and they were frequently excluded from the best fit logistic regression model. Pseudo R^2 values for the three distribution models ranged between 0.29 and 0.45 (Table 2). The models may be improved by including historical land use variables, since historic land use 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 strong positive effect on the

appearance of this species, while other land use categories had negative effects. When an agricultural plot was visited *S. dulcamara* was usually present. *Solanum* dispersal via birds could account for this relationship. Forest and agricultural edges provide roosting habitats for birds, who deposit the seeds they consumed where they roost (McCay et al. 2009). *Celastrus orbiculatus* and *Berberis thunbergii* are also bird dispersed species, however agricultural land use was excluded from the model in the case of *B. thunbergii* and not significant in the case of *C. orbiculatus*, indicating that factors other than agricultural edges were more important in explaining the presences of these two species. The *C. orbiculatus* model was the only model where income was maintained in the model of best fit. While non-significant, income negatively affected the presence of this species. A negative association with income may reflect the fact that *Celastrus* occurred in unmanaged roadsides and wastelands to a greater extent than the other two species, which were more common in poorer areas in Chicago (Gulezian and Nyberg 2010). Finally, plot invasive species richness was a significant predictor for all three species models, and the 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 reflective of the tendency of many invasive plants to co-occur (Kuhman et al. 2011).

Leaf traits

I expected plants affiliated with disturbed habitats to have higher SLA and lower LDMC based on previous findings. High SLA is positively associated with photosynthetic rates while LDMC correlates positively with leaf toughness, drought adaptation and defense from herbivores (Cornelissen 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, ANOVA results showed a lower SLA for the urban classified tree, forb and grass species relative to the rural classified species, and higher LDMC for the urban classified forb and grass, suggesting tolerance to drought stress in an environment where light is not limiting. These results were echoed in the MLR models, where urbanization and impervious surface had negative effects on SLA and positive effects on LDMC. Shrubs and vines did not adhere to regular trends, and frequently had non-significant differences between the urban and rural classified species.

Additional evidence pointing to drought adaptation was seen in results for LWR and leaf thickness. LWR is a metric measuring leaf shape. A higher ratio means the leaf is long and thin. Narrow leaves have a small boundary area, which helps enhance transpiration (Malhado et al. 2009). This means that when water is available the plant is able to uptake it efficiently, without exposing a large surface area to the sun during warm periods when water is not available (Malhado et al. 2009, Yates et al. 2008). Narrow leaves may also have added benefits in low nutrient conditions (Malhado et al. 2009). LWR was greater for urban associated species. Leaf thickness is also indicative of leaf adaptation to sunny, dry and low nutrient conditions (Pérez-Harguindeguy et al. 2013), and was greater for the urban associated tree, forb and grass species.

The regular combination of traits found for trees, forbs and grasses for SLA, LWR, and leaf thickness suggests that the urban-classified species of each of these growth forms is more drought-adapted. These results align with those of Chen et al. (2013), who found that over time drought- and heat-stress tolerant ruderal species in a city in China replaced ruderal species lacking these traits. They suggest that urban plants will tend to be stress-tolerant ruderals, species which employ a strategy that allows them to tolerate stress for the long term and reproduce quickly and prolifically (Chen et al. 2013). *Bromus tectorum*, for example, is an annual species that thrives in arid, open environments (Kostivkovsky and Young 2000). Similar results have also been found for woody species in urbanized riparian forests and in close proximity to impervious surfaces and railyards, where drought tolerant species replaced or were dominant to more mesic species (Pennington et al. 2010, Sung et al. 2011). Drought in urban areas is influenced by the well-drained sandy soils, the open-canopy habitats and the urban heat island effect that characterize urbanization, inducing urban drought islands. Additionally, impervious surface and soil compaction prevents rainwater from infiltrating urban soils, so that urban soils are generally less moist (Pickett and Cadenasso 2009).

The traits of the shrubs and vines did not align with those of the trees, forbs and grasses. One possible explanation may be that both the liana *Celastrus orbiculatus* and the shrub *Berberis thunbergii* are both habitat generalists that are preadapted to a wide range of environmental conditions. *Celastrus orbiculatus* was observed frequently in this study across the three sites, and is known to be capable of colonizing many different habitats (Leicht-Young et al. 2007). *B. thunbergii* was primarily observed in shaded forested rural sites. However, barberry can also

germinate and survive in open, dry and sunny habitats (Lubell and Brand 2010). 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 plots. Finally, results from the MLR models did not show regular

trends for the effects of income and proportion of core and edge forest cover on the values of

the five traits.

Future suggestions

The degree of "urbanness" was characterized by population thresholds, and in a combined

urbanization metric that also depended to some extent on thresholds by using the NLCD

percent impervious surface cover data. It is possible to gain even finer understanding of

urbanization land cover by using spectral reflectance available from satellite data or other

landscape measures. Spectral reflectance is used to characterize urbanization (Xian and Crane

2005), and similar data (for example, NDVI, a vegetation index derived from satellite data) have

also been used in urban ecological studies; as have shape metrics describing landscape

character (Aguilera et al. 2011, Gavier-Pizarro et al. 2010, Uuemaa et al. 2009, Zhang et al.

2013).

Finally, while native species were not included in this study, they too made up some

component of the urban flora, and they may also display drought tolerant traits compared to

rural native species. All species surviving in urban environments should be part of a broader

census of urban flora to determine a true urban trait syndrome. Drought tolerance of urban

plants can then be assessed directly in these species.

Conclusions

Urban soils were slightly more alkaline, and had higher lead concentrations and sand content

than rural soils. Urban habitats had more open canopies, impervious surface, patch forests, and

induced edge habitats than rural habitats, which contributed to an "urban drought island"

syndrome. Suburban areas were 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 allowed them to survive in

an arid urban environmental. 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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Figures

Figure 1. Extent of sampling region. Clockwise from left panel: Sampling points in the region from Hartford to Storrs in northeastern Connecticut and in Boston, MA; population in census block groups in the Hartford/Storrs region; impervious surface cover from the 2006 NLCD; and land use cover from CLEAR.
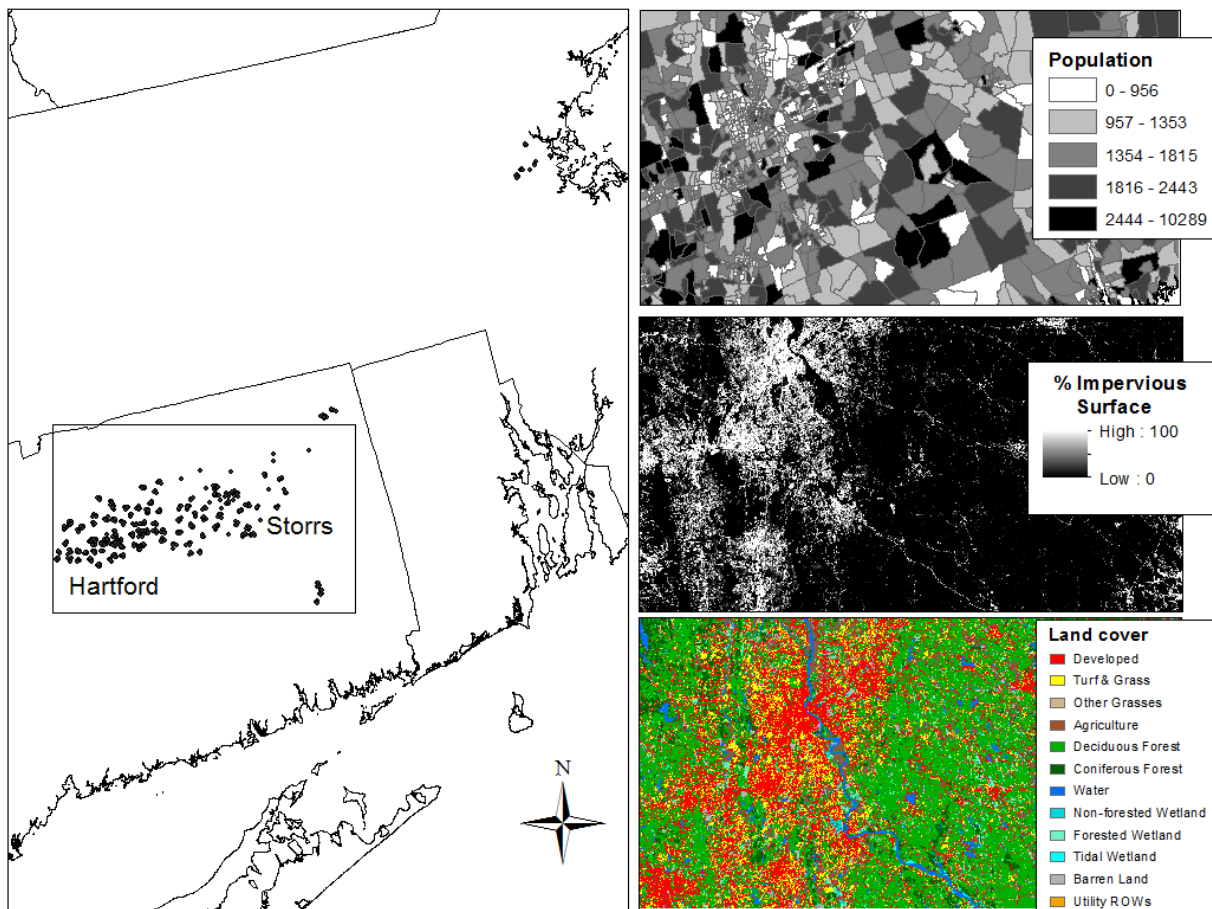
Figure 2. Content, composition and texture of urban and rural soils (N = 44). Soils were only sampled from rural and urban sites. Lead and pH content of soil samples from rural and urban sites was significantly different according to the results of two tailed t-tests (lead: t = -4.033, df = 10.714, p = 0.002078; pH: t = -6.5837, df = 19.606, p = 2.271e-06). The outlying point for lead has a value of 1388 ppm. The association between soil texture and organic content and rural/urban grid cells were tested with the Fisher's exact test. Significant associations were found for soil texture (p = 3.42e-05) but not for soil organic content (p = 0.4602).
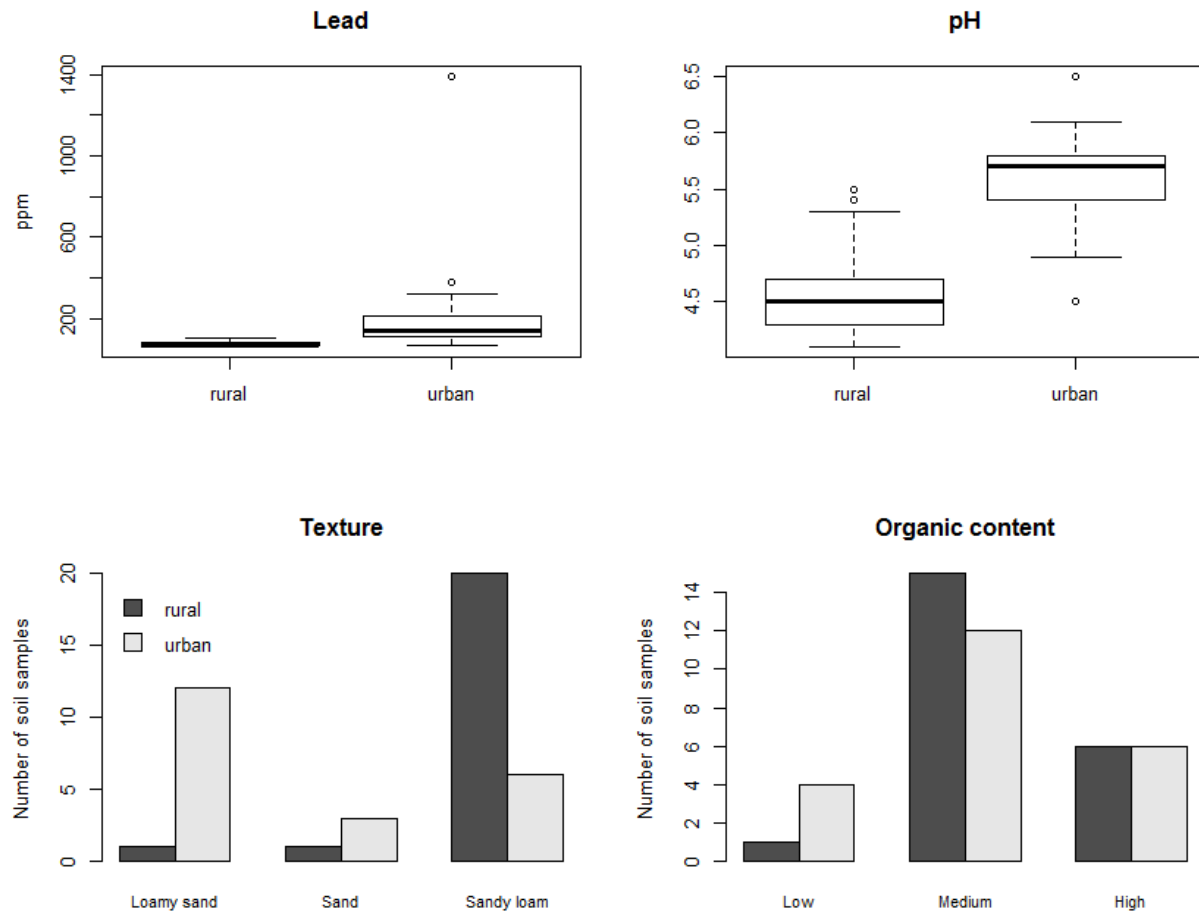
Figure 3. Distribution of continuous variables across grid cells. N = 110, with 36 urban, 40 suburban and 34 rural sites, respectively.
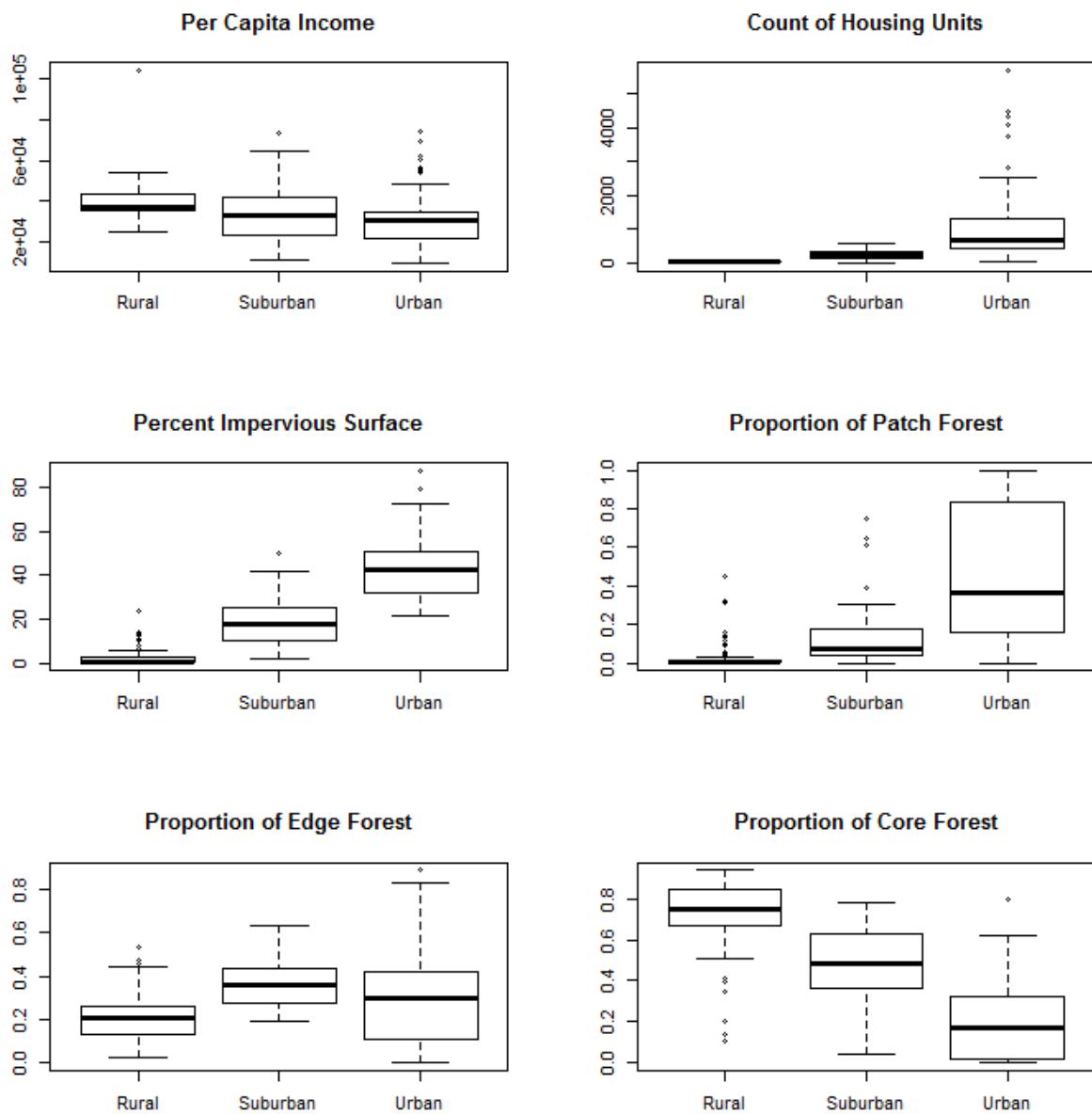
Figure 4. The proportion of urban, rural and suburban plots (n = 228, 203 and 200, respectively) for the six categories of land use and four categories of canopy cover and habitat type.
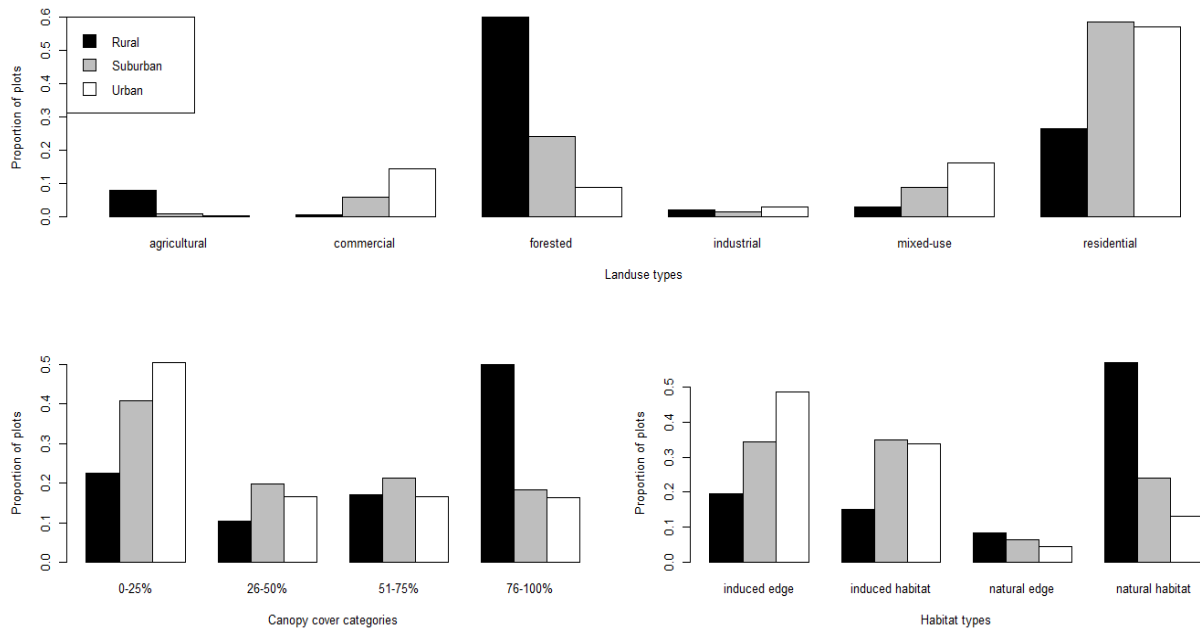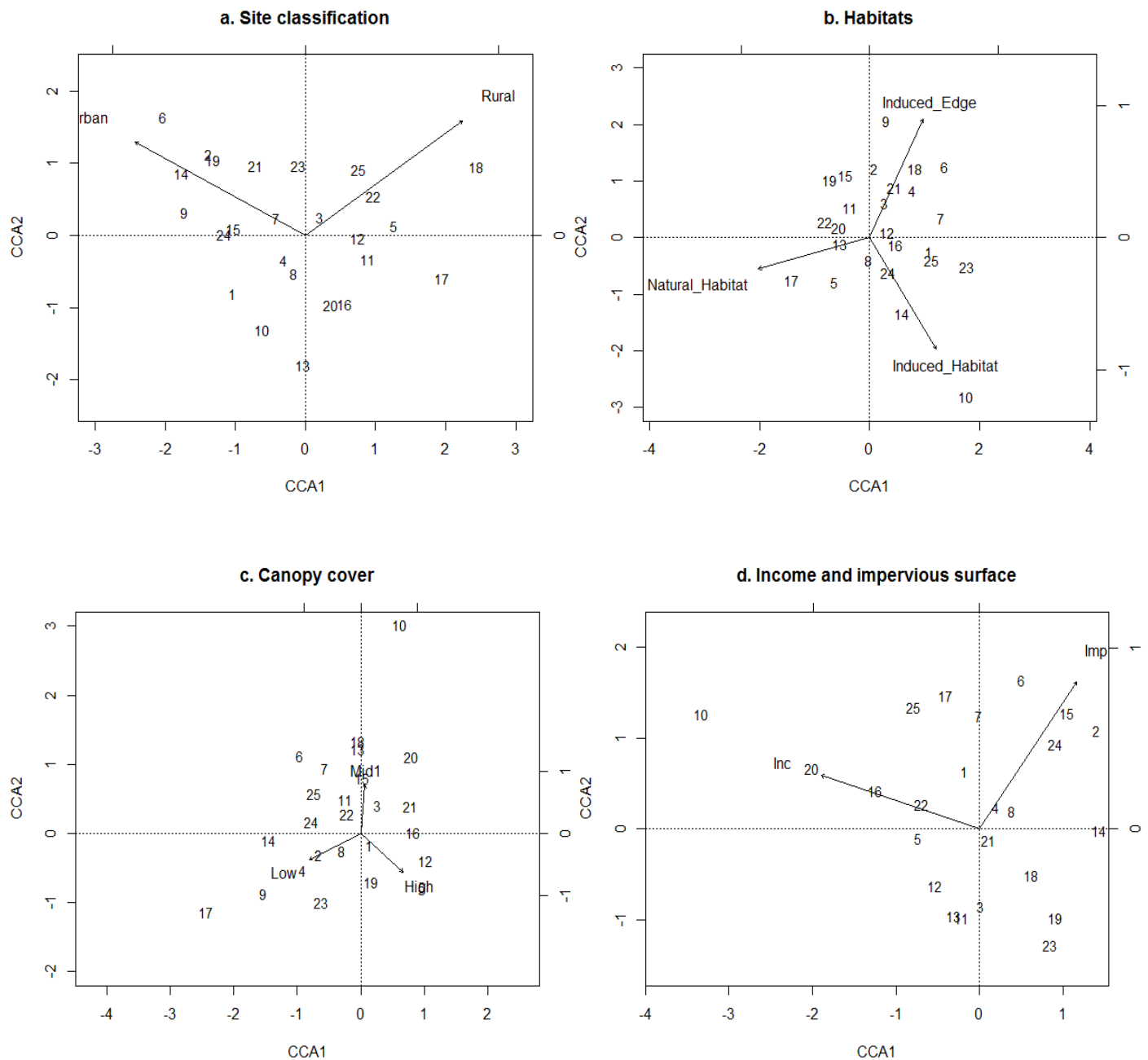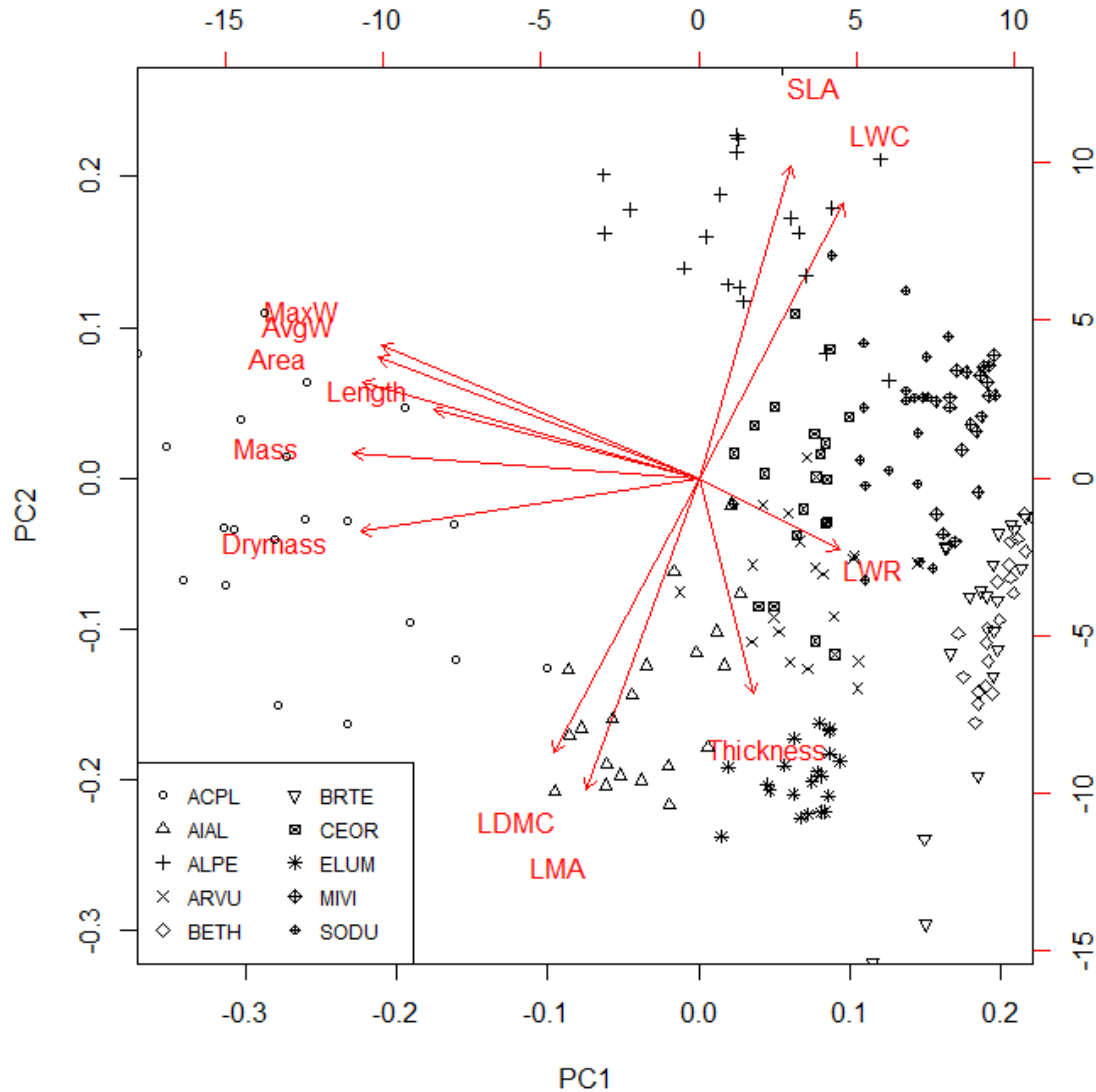
Figure 5. Biplots of canonical correspondence analysis. Arrows represent environmental gradients and numbers represent species. Neighborhood, habitat type and canopy cover classes were entered as dummy variables, with the missing variable acting as a baseline (suburban, natural edge and 51-75% canopy cover). Species codes are listed below.

e. Forest fragmentation

f. All variables
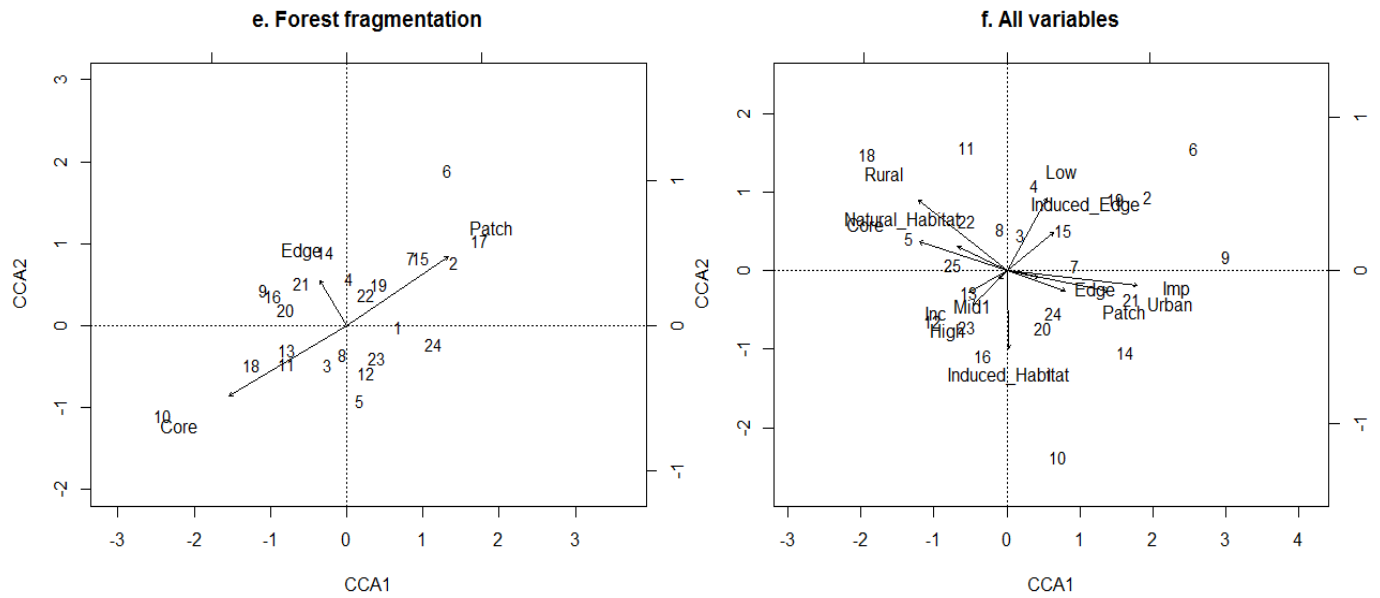
1 = *Acer platanoides*, 2 = *Ailanthus altissima*, 3 = *Allialaria petiolata*, 4 = *Artemisia vulgaris*, 5 = *Berberis thunbergii*, 6 = *Bromus tectorum*, 7 = *Catalpa spp.*, 8 = *Celastrus orbiculatus*, 9 = *Cynanchum louisae*, 10 = *Elaeagnus angustifolium*, 11 = *Elaeagnus umbellata*, 12 = *Euonymus alatus*, 13 = *Frangula alnus*, 14 = *Ligustrum spp.*, 15 = *Lonicera japonica*, 16 = *Lonicera spp.*, 17 = *Lythrum salicaria*, 18 = *Microstigeum vimineum*, 19 = *Polygonum cuspidatum*, 20 = *Rhamnus cathartica*, 21 = *Robinia pseudoacacia*, 22 = *Rosa multiflora*, 23 = *Rumex acetosella*, 24 = *Solanum dulcamara*, 25 = *Wisteria spp.*

Figure 6. Biplot of trait measurements. The horizontal axis represents the first principal component and the vertical axis represents the second. Species codes are plotted against the arrows representing different variables. The codes are as follows, listed by growth form and rural/urban pairing: trees: ACPL = A. platanoides, AIAL = A. altissima; shrubs: BETH = B. thunbergii, ELUM = E. umbellata; vines: CEOR = C. orbiculatus, SODU = S. dulcamara; forbs: A. petiolata, ARVU = A. vulgaris; grasses: MIVI = M. vimineum, BRTE = B. tectorum.

57

Tables

Table 1. List of information on the 25 invasive plant species selected for inclusion in the study. Those marked with a star (*) are not currently IPANE listed species. Information on these species was taken primarily from the IPANE website, the USDA Plants Database and *The Reference Manual of Woody Plant Propogation: From Seed to Tissue Culture* by M.A. Dirr and C.W. Heusser Jr.

Scientific name	Common name	Growth form	Life cycle	Intro date	Intro purpose	Dispersal syndrome	Native range
Acer platanoides L.	Norway maple	Tree	perennial	1868	horticulture	wind	Europe
Ailanthus altissima (Mill.) Swingle	Tree-of-heaven	Tree	perennial	1784	horticulture	wind	central China
Alliaria petiolata (Bieb.) Cavara & Grande)	Garlic mustard	Herb	biennial	first recorded in 1868	food/medicine	mechanical	Europe
Artemisia vulgaris L.*	Mugwort	Herb	perennial	mid-1800s	thought to have many medicinal and culinary uses	Wind, mostly vegetative growth	Europe, Asia
Berberis thunbergii DC.	Japanese barberry	Shrub	perennial	1875	ornamental	birds, small mammals	Japan
Bromus tectorum L.	Drooping cheatgrass	Graminoid	annual	1860	seed lot contaminant, packing material	gravity, wind, mechanical	Mediterranean Europe
Catalpa spp. Includes *C. speciosa* and *C. bignonoides*	Catalpa	Tree	perennial	1800s	ornamental	wind	North America, East Asia
Celastrus orbiculatus Thunb.	Oriental bittersweet	Liana	perennial	1860	ornamental	birds	China
Cynanchum louiseae Kartesz & Gandhi	Black swallow-wort	Herb	perennial	first recorded in 1878	may have come from the Harvard Botanic Garden	wind	Europe
Elaeagnus angustifolia L.	Russian olive	Shrub	Perennial	1800s	horticulture	Birds, mammals	Asia
Elaeagnus umbellata Thunb.	Autumn olive	Shrub	perennial	1830	horticulture, wildlife	birds, mammals	China, Korea, Japan
Euonymus alatus (Thunb.) Sieb.	Winged euonymus	Shrub	perennial	1860	horticulture	birds	NE Asia
Frangula alnus Mill.	Glossy buckthorn	Shrub	perennial	before 1800	ornamental, rehabilitation plantings	birds	Europe, N Africa, Central Asia
Ligustrum spp includes *L. vulgare* and *obtusifolium*	Privet	Shrub	perennial	1700s; 1860; 1945; 1952	gardening purposes	birds	Asia, Europe
Lonicera spp Includes species *morrowii,*	Honeysuckle	Shrub	perennial	1898	ornamental	birds	central and northeastern

							China, Manchuria, Korea
maackii, tartarica							
Lonicera japonica Thunb.	Japanese honeysuckle	Liana	perennial	1806	horticulture	birds	China, Japan, Korea
Lythrum salicaria L.	Purple loosestrife	Herb	perennial	1814	ornamental, medicinal	water	central and southern Europe
Microstegium vimineum (Trin.) A. Camus	Stiltgrass	Graminoid	annual	1919	packing material	mechanical	tropical Asia
Polygonum cuspidatum Sieb. & Zucc.	Japanese knotweed	Herb	perennial	1855	horticulture	wind	China, Japan, Korea
Rhamnus cathartica L.	Common buckthorn	Shrub	perennial	<1880	horticulture, wildlife	birds	Europe, N and W Asia
Robinia pseudoacacia L.	Black locust	Tree	perennial	early 1900s	utilitarian purposes	wind	United States
Rosa multiflora Thunb. ex Murr.	Multiflora rose	Shrub	perennial	1886	horticulture	birds	Japan
Rumex acetosella L.	Sheep sorrel	Herb	perennial	unknown: listed at worst weed in 1889	accidental means	wind, insects	Europe, Russia, the Middle East, North Africa
Solanum dulcamara L.	Bittersweet nightshade	Liana	perennial	Became widespread in the late 1800s	ornamental, medicinal	birds	Europe, North Africa, eastern Asia
Wisteria spp* Including *sinensis* and *fructescens (native to south)*	Wisteria	Liana	perennial	1816 and 1830	ornamental, horticultural purposes	water	China, Japan, southern N. America

Table 2. Results from three logistic regression models for a rural, urban and generalist species. 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 Naglekerke'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.

Variable	B. thunbergii coefficient	S. dulcamara coefficient	C. orbiculatus coefficient
Intercept	-0.6589	**-9.9109**	3.635332
Income	---	---	-0.523526
Urbanization metric	**-0.49478**	**0.9237**	---
Proportion core forest	---	---	---
Urban	**-0.92667**	**1.2604**	**-1.080991**
Rural	**0.93732**	-0.8790	-0.472178
Agricultural	---	**2.0142**	1.011030
Commercial	---	**-1.5694**	**-1.170387**
Forested	---	**-1.8104**	0.008802
Industrial	---	**-1.4030**	1.718068 †
Residential	---	0.2858	0.428059
26-50%	---	-0.4222	---
0-25%	---	0.7042 †	---
76-100%	---	-0.7712	---
Richness	**0.41612**	**0.7385**	**1.002408**
Natural habitat	**1.08564**	---	---
Induced edge	-0.18527	---	---
Induced habitat	-0.23418	---	---
AIC	451.9	338.48	464.54
Pseudo-R^2	0.2855600	0.4187268	0.4505057
Goodness-of-fit	Deviance = 435.90, df = 474, p-value = 0.894407	Deviance = 312.48, df = 468, p-value = 1	Deviance = 444.54, df = 472, p-value = 0.81323
Likelihood ratio test	χ^2 = 8.6368, p-value = 0.1245	χ^2 = 3.9449, p-value = 0.5574	χ^2 = 6.25882, p-value = 0.6183

† p-values between 0.05 and 0.1.

Appendix

Appendix 1. *Invasive species controversy and the role of citizen science in urban ecology.*

Some debate surrounds the role of invasive species in urban areas. Conservation and restoration efforts tend to focus on returning degraded or invaded habitats to historical reference states. Invasive species are regarded as agents of negative change due to the damage they do to natural systems. However, urban areas are far from natural systems, and invasive species comprise a large part of the urban flora. It has been argued that invasive plants that occur spontaneously in the neglected urban periphery provide the ecosystem services that extirpated native species no longer can, and therefore play an important role in urban systems; and that a rapidly changing world means accepting a correspondingly changed flora (Davis et al. 2011, del Tredici 2010). Other arguments state that unique mixes of native and invasive vegetation that assemble without human assistance in degraded and heavily human-influenced environments actually comprise novel ecosystems (Hobbs et al. 2009) that deserve study and recognition in their own right. Other human-influenced environments can act not as novel habitats but as analogs of natural habitats (Francis 2011, Lundholm and Richardson 2010). All of these ideas run counter to traditional conservation attitudes, which assume invasive species are bad and degraded urban habitats are valueless and prize native species and historical habitat states, and have not been met without resistance from the wider scientific community (Simberloff 2011).

Many urban ecology projects make use of citizen generated data (Gagné 2013). Citizen science is especially valuable in urban settings because most people live in or near urban areas. Science outreach efforts can therefore be maximized by focusing on places where most people live and work. Outreach efforts in the natural sciences are incredibly important in urban areas because there is an increasing lack of connection between urban people and nature (Turner et al. 2004). As populations become increasingly urban most people's interactions with nature will necessarily be in urban areas (Fuller and Irvine 2010). Their interactions will be with a nature that is vastly different from the remote places ecologists used exclusively study (Collins et al. 2000), and in areas where biodiversity and conservation efforts have been largely ignored in the past (Collins et al. 2000, Miller and Hobbs 2002). It is critical that ecologists and conservations work on understanding these changed places because of the important health benefits people receive from interacting with nature (Fuller et al. 2007, Kaplan 2001, Keniger et al. 2013, Ulrich 1984), and because involving people in nature in familiar surroundings may be a way to interest and involve non-scientist stakeholders in conservation issues outside of cities.

Using citizen science in urban ecology studies is a way to integrate urban stakeholders with science (Cooper et al. 2007, Goddard et al. 2010, McKinney 2002). Ideally, involving urban dwellers with the ecology of the urban environment around them will raise an understanding and interest in science and ultimately result in a populace that is more aware and involved in conservation issues. By adding to the IPANE dataset, modifying the IPANE methods specifically for urban environments, and sharing these methods with an instructor at the Urban Ecology Institute in Boston, I hope to add to the growing body of knowledge on the relationship between invasive species and urbanization and also to further the goals of IPANE.

Appendix 2. *Information on census data, and using Census 2010 versus ACS 2010 for income.*

There is no global and uniform standard for defining an urban area. Definitions may vary according the variables important to the organization making the definition and across disciplines (McIntyre et al. 2000), though common measures revolve around population and impervious surface cover (Seto et al. 2011).

The US Census Bureau uses a combination of location and population to define urban geographies. The 2010 census used population to classify urban blocks and tracts into Urbanized Areas (UA) or Urban Clusters (UC), which are both called urban areas. UAs have 50,000 or more people over a core of a few census tracts, while UCs contain between 2,500 and 50,000 people. Tracts and blocks can have a minimum of 500 people per square mile and still be considered part of an UA or UC, as long as they are contiguous with an urban core tract or block. The overall urbanized area population density for the United States is 2,534.4 people per square mile. All blocks outside of these urban clusters and urban areas are considered rural. Prior to this definition, any area with at least 2,500 people was considered urban. For the purposes of this study a more explicit definition of urban, rural and suburban based on population density was more useful than the urban area and urban cluster concept.

Per capita income was phased out of the decennial census data collection and is now reported by the 1-, 2-, and 5-year American Community Survey (ACS). The two programs collect data very differently. The decennial census is a complete (100%) count of the total population, while the ACS takes population based samples over three different time periods. About 3 million addresses are selected to complete the survey every year. The annual (1-year) ACS provides data for geographic areas with a population of 65,000 or more individuals. These geographies include the entire nation, all states and the District of Columbia, 800 counties, and other areas.

The 3-year ACS includes data for geographies with a population of 20,000 or greater (including the country, all states and DC, more counties and metropolitan areas, etc.). The 5-year ACS includes data for all geographic areas, including smaller ones not covered in the other two surveys. The 5-year data is collected by combining the 1-year estimates and taking into account the population for each year and then calculating the margin of error values for each variable.

In consultation with Michael Howser of Uconn's MAGIC, it was determined that working at the 5-year block group level was best because there was less error associated with the income estimate, but still at a smaller geographic area.

Table A1-1. Various options for Census data combinations.

Geography	Housing source/date	Population source/date	Income source/date	Pros and cons
Block	Census 2000	Census 2000	Census 2000	pro: all from same source; block is smallest possible unit for which all info is available con: outdated

Block group	Census 2010	Census 2010	ACS, 5-year 2010	Pro: all 2010 data, block group smaller than tract Con: different sources, ACS blck group is not as reliable as tract level
Tract	Census 2010	Census 2010	ACS, 5-year 2010	Pro: 2010, ACS Con: tract is larger
Block group	ACS, 5-year 2010	ACS, 5-year 2010	ACS, 5-year 2010	Pro: all from same source Con: ACS blck group is not as reliable as tract level

Appendix 3. *GME code for summarizing layers into 1-km grid, and creation of urbanization metric.*

```
isectpolypoly(in="C:\Users\Lara\Desktop\Land_Use_Data\data_layers\active_layers\CTblckgrp_pophouinc_FinalGrid_Albers.sh
p", poly="C:\Users\Lara\Desktop\Land_Use_Data\data_layers\active_layers\MACT_blckgrp_Area_Albers.shp",
field="MRUE001", prefix="Inc", thematic=FALSE, proportion=FALSE, awm=TRUE, min=FALSE, max=FALSE, aws=FALSE);

isectpolypoly(in="C:\Users\Lara\Desktop\Land_Use_Data\data_layers\active_layers\CTblckgrp_pophouinc_FinalGrid_Albers.sh
p", poly="C:\Users\Lara\Desktop\Land_Use_Data\data_layers\active_layers\MACT_blckgrp_Area_Albers.shp", field="H7V001",
prefix="Pop", thematic=FALSE, proportion=FALSE, awm=FALSE, min=FALSE, max=FALSE, aws=TRUE);

isectpolypoly(in="C:\Users\Lara\Desktop\Land_Use_Data\data_layers\active_layers\CTblckgrp_pophouinc_FinalGrid_Albers.sh
p", poly="C:\Users\Lara\Desktop\Land_Use_Data\data_layers\active_layers\MACT_blckgrp_Area_Albers.shp", field="IFC001",
prefix="Hou", thematic=FALSE, proportion=FALSE, awm=FALSE, min=FALSE, max=FALSE, aws=TRUE);

isectpolyrst(in="C:\Users\Lara\Desktop\Land_Use_Data\data_layers\active_layers\CTblckgrp_pophouinc_FinalGrid_Albers.shp
", raster="C:\Users\Lara\Desktop\Land_Use_Data\data_layers\active_layers\MACT_Edges_30m1_Albers.tif", prefix="Edge",
thematic=TRUE, proportion=TRUE, allowpartialoverlap=FALSE, medquant=FALSE);

isectpolyrst(in="C:\Users\Lara\Desktop\Land_Use_Data\data_layers\active_layers\CTblckgrp_pophouinc_FinalGrid_Albers.shp
", raster="C:\Users\Lara\Desktop\Land_Use_Data\data_layers\active_layers\nlcd2006_CTMA.tif", prefix="Imp",
thematic=FALSE, proportion=FALSE, metrics="MEAN", allowpartialoverlap=FALSE, medquant=FALSE);

isectpolyrst(in="C:\Users\Lara\Desktop\Land_Use_Data\data_layers\active_layers\CTblckgrp_pophouinc_FinalGrid_Albers.shp
", raster="C:\Users\Lara\Desktop\Land_Use_Data\data_layers\active_layers\SumImpSurfMSqDivbyPop_blckgrp3.tif",
prefix="ImpCap", thematic=FALSE, proportion=FALSE, metrics="MEAN", allowpartialoverlap=FALSE, medquant=FALSE);

isectpntpoly(in="C:\Users\Lara\Desktop\Land_Use_Data\data_layers\active_layers\AllPoints_2012_2013_Final_102313_Albers
.shp", poly="C:\Users\Lara\Desktop\Land_Use_Data\data_layers\active_layers\MACT_1kmgrid_Final_Albers.shp",
field=c("IncAWM", "PopAWS", "HouAWS", "ImpMN", "ImpCapMN", "EdgeV1", "EdgeV2", "EdgeV3", "EdgeV4", "EdgeV5",
"EdgeV6", "EdgeVSUM"));
```

Steps in continuous urban cover layer creation in ArcGIS 10
First, the raster calculator was used to convert each grid cell of the NLCD impervious surface layer in meters squared, by multiplying the value of each cell by 9. Zonal statistics was used to obtain the average impervious surface in meters squared in each block group, and the Polygon to Raster tool was to create raster files of population and median household income in each block group. Input original clipped impervious surface layer to the cell size so the two layers overlap correctly and have the same 30 m cell size. The final impervious surface area layer was created by dividing the meters squared impervious surface per block group layer by the population per block group layer.

Appendix 4. *Comparison between using GME and ArcGIS functions for grid creation and summarizing variables into grid cells*.

In exploring differences between creating the 1-km by 1-km sampling grid via the programs ArcGIS and GME I generated two grid layers from each method and compared population, housing and impervious surface estimates. The comparison was carried out for two spatial scales, first all grid squares created for Connecticut and Massachusetts and second in only the sites sampled in this study (about 110). Both programs calculated an area-weighted sum for housing and population and an area-weighted mean for each grid cell. The functions "isectpolypoly" and "isectpolyrast" were used to accomplish this task in GME, and a series of functions were used to accomplish this in ArcGIS.

The methods used for the two sampling ranges were compared using a Wilcoxon Rank Sum test. Results show that for housing and population the two programs produced different results for all sites, while the results of impervious surface were not significantly different across methods. Estimates of all three variables were not significantly different in the smaller sampling range. Observed differences are most likely due to how the programs handled grid cells on edges, where the grid cell polygon only partially overlaps the block group polygon. The methods used by both programs to summarize a raster into a polygon were similar enough at the smaller spatial scale, which did not include any edge polygons. Ultimately GME was used for other layer summarizing needs for this project due to its simple function building capacity.

Table 4A-1. Results from Wilcoxon Rank Sum test.

	All sites	Sampled sites only
Population	W = 91450723, p-value = 5.656e-06	W = 12114, p-value = 0.5971
Housing units	W = 93920171, p-value < 2.2e-16	W = 12090, p-value = 0.6188
Impervious surface	W = 89682947, p-value = 0.06151	W = 11864, p-value = 0.8372

Appendix 5. *Variables collected at plots and sites.*

Categorical variables were collected at each plot, and continuous variables summarized at each 1-km by 1-km site using ArcGIS and GME. Some variables were used as input to regression models.

Table 5A-1. Plot level categorical variables.

Name	Type	Description
Species	Binary/categorical	The first few letters of the species name and genus name (ex. "acerplata" for *Acer platanoides*) of the 25 species of interest, marked with a 0 if absent and 1 if present in each plot for frequency analysis.
Neighborhood	Categorical	Three categories; classifying the plot as urban, suburban or rural, determined by population size cutoffs from the 2010 Census.
Aspect	Categorical	Nine categories; describing plot aspect. Determined with a compass in the field. 1 – North, 2 – NE, 3 – East, 4 – SE, 5 – South, 6 – SW, 7 – W, 8 – NW, 9 – Flat
Canopy	Ordinal	Four categories; describing canopy closure at the site. Visually estimated in the field. 1 – 0 to 25%, 2 – 26 to 50%, 3 – 51 to 75%, 4 – 76 to 100%
Elevation	Continuous	Plot elevation. Data taken from Trimble Juno ST and geocorrected.
Trailside	Binary	1 if the plot was located next to or near a trail and 0 if it was not
Moisture	Categorical	Four categories; describing soil moisture at the site. Visually estimated in the field. 1 – Xeric (dry), 2 – Mesic (moist), 3 – Saturated, 4 – Inundated
Habitat	Categorical	19 categories; describing habitat at that plot. Adapted from IPANE habitat categories and aggregated into four habitat types (below).
Habitat types	Categorical	4 categories; Natural Edges, Natural Habitats, Induced Edges and Induced Habitats. These categories encompass the 19 habitats described in the Habitat1 variable
Landuse	Categorical	Six categories; describing visually determined land use at the plot. These categories are industrial, commercial, residential, agricultural, forested, and mixed-use.
Latitude	Continuous (coordinate)	Latitude, recorded in decimal degrees in the center of the plot with the Trimble Juno ST GPS unit and geocorrected. Measured in geographic coordinate system WGS84.
Longitude	Continuous (coordinate)	Longitude, recorded in decimal degrees in the center of the plot with the Trimble Juno ST GPS unit and geocorrected. Measured in geographic coordinate system WGS84.
Abundance	Ordinal	Five categories; describing abundance (number of individuals) of a species in a plot. 1 – Single plant, 2 – Less than 20, 3 – 20 to 99, 4 – 100 to 999, 5 – More than 1000
Distribution	Categorical	Five categories; describing distribution of a species in a plot. 1 – Single plant, 2 – Evenly sparse, 3 – Single patch, 4 – Multiple patches, 5 – Dense throughout
Percent Cover	Ordinal	Six categories; 1 – Less than 1%, 2 – 1 to 5%, 3 – 6 to 25 %, 4 – 26 to 50%, 5 – 51 to 75%, 6 – 76 to 100%
Reproduction	Binary	Five options describing the reproductive state of a species in each plot. Each state was marked with a 1 if it was true, and a 0 if it was false. The options were: vegetative, flowers, pollinators, fruit, seedlings present
Spontaneous	Categorical	Three options describing if a species was obviously planted and maintained or if it existed as a wild element, establishing independently of human assistance. 0 – no, indicated the individual or population was planted/maintained; 1 – yes, indicated the individual or population was independently established

Table 5A-2. Site level continuous variables.

Name	Type	Description
Housing Units	Continuous	Average number of housing units. Data from 2010 US Census report, shapefiles and data obtained from NHGIS
Population	Continuous	Number of people, in people per square kilometer. Data from 2010 US Census report, shapefiles and data obtained from NHGIS
% Impervious Surface	Continuous	Percent impervious surface occurring in a 30m grid cell into which plot fell. Data from 2006 USGS NLCD
Per capita household income	Continuous	Average per capita income in 2011 for the census block groups containing the plot. Data from the American Community Survey. Obtained from National Historical Geographic Information System (NHGIS)
Derived metric	Continuous	Average meter squared of impervious surface per person per block group. Calculated using US Census data and impervious surface data from the NLCD
Patch	Continuous	Proportion of patch forest in a site, determined from CLEAR's Forest Fragmentation tool
Edge	Continuous	Proportion of edge forest in a site, determined from CLEAR's Forest Fragmentation tool
Perforated	Continuous	Proportion of perforated forest in a site, determined from CLEAR's Forest Fragmentation tool
Core	Continuous	Proportion of core forest in a site, determined from CLEAR's Forest Fragmentation tool

Appendix 6. *Species sampling information and presence/absence data.*

A total of 631 plots were sampled, capturing 1659 individual species observations in 110 sites. 146 of those plots were null plots, or plots where no invasive species relevant to this study were present. Half of all the null plots were in rural sites. 119 plots were opportunistic, meaning they were plots sampled that were not part of the original sampling schemes. Most opportunistic and non-opportunistic sampling sites were from the 2012 and 2013 field season and located along an urban-to-rural gradient from Hartford, CT to Storrs. A second set of data consisted of 31 plots from the Boston metropolitan area collected by volunteers from a class project. Finally, of the 631 plots, 228 plots were urban, 203 were suburban and 200 were rural; and of the 110 sites, 36 were urban, 40 were suburban and 34 were rural.

Table 6A-1. Results of two-tailed Pearson's chi-square tests and Fisher's exact tests for a subset of species frequencies across the three neighborhood categories. Where the Fisher's test was performed only a p-value is reported. Species frequencies are also listed by rural, suburban and urban sites. Tests were run on 2 x 3 tables where the first row was the number of observations where the species was present and the second row was the number of observations where the species was absent. Null plots were excluded, as were species with less than 5 observations. Of a total 1494 individual observations, 327 were rural, 542 were suburban and 625 were urban.

Species	Species frequencies	Test results for species frequencies
Acer platanoides	3; 47; 64	X2 = 27.7795, df = 2, p-value = 9.285e-07
Ailanthus altissima	0; 7; 43	p-value = 6.334e-11
Alliaria petiolata	15; 22; 36	X2 = 1.8877, df = 2, p-value = 0.3891
Artemiesia vulgaris	7; 14; 22	X2 = 1.7262, df = 2, p-value = 0.4218
Berberis thunbergii	56; 39; 27	X2 = 48.0103, df = 2, p-value = 3.756e-11
Bromus tectorum	0; 0; 6	p-value = 0.01518
Catalpa spp	5; 17; 23	X2 = 3.4451, df = 2, p-value = 0.1786
Celastrus orbiculatus	76; 125; 114	X2 = 5.2285, df = 2, p-value = 0.07322
Cynanchum louiseae	0; 1; 6	p-value = 0.101
Elaeagnus umbellata	22; 21; 10	X2 = 16.7634, df = 2, p-value = 0.000229
Euonymus alatus	27; 40; 37	X2 = 2.0406, df = 2, p-value = 0.3605
Frangula alnus	3; 26; 12	X2 = 14.2371, df = 2, p-value = 0.0008099
Ligustrum spp	0; 2; 9	p-value = 0.02244
Lonicera spp	15; 42; 29	X2 = 6.227, df = 2, p-value = 0.04444
Lonicera japonica	2; 5; 9	X2 = 1.5674, df = 2, p-value = 0.4567
Microstegium vimineum	5; 2; 0	p-value = 0.002775
Polygonum cuspidatum	4; 6; 25	X2 = 12.912, df = 2, p-value = 0.001571
Rhamnus cathartica	3; 11; 9	X2 = 1.7342, df = 2, p-value = 0.4202
Robinia pseudoacacia	1; 5; 24	X2 = 18.7209, df = 2, p-value = 8.606e-05
Rosa multiflora	75; 75; 65	X2 = 23.8857, df = 2, p-value = 6.506e-06
Solanum dulcamara	8; 29; 53	X2 = 14.4862, df = 2, p-value = 0.0007151
Wisteria spp	5; 4; 6	p-value = 0.5288

Table 6A-2. Percentages of obviously planted individuals for rural, suburban and urban observations for twelve species. A dashed line means no observations for that species were planted, and an NA means the species was not observed at all in the given neighborhood category.

	A.platanoides	A. altissima	B. thunbergii	Catalpa sp.	E. umbellata	E. alatus
Rural	100%	NA	4	40	9	14.81
Suburban	25.53%	14.29	15.38	41.18	23.81	22.5
Urban	25%	11.63	48.15	26	40	59.46

	F. alnus	Ligustrum sp	Lonicera sp	R.pseudoacacia	R. multiflora	Wisteria
Rural	--	NA	--	--	1.33	--
Suburban	--	50	7.14	60	1.33	50
Urban	8.33	77.77	--	12.5	7.69	50

Appendix 7. *Species composition of sites.*

Figure 7A-1. Total number of species observations (n = 1744) captured in all plots (n = 674), including opportunistic and null plots. The grey bar labeled "NoInv" represents null plots, plots that were visited as part of the original sampling scheme but contained no invasive species of interest.
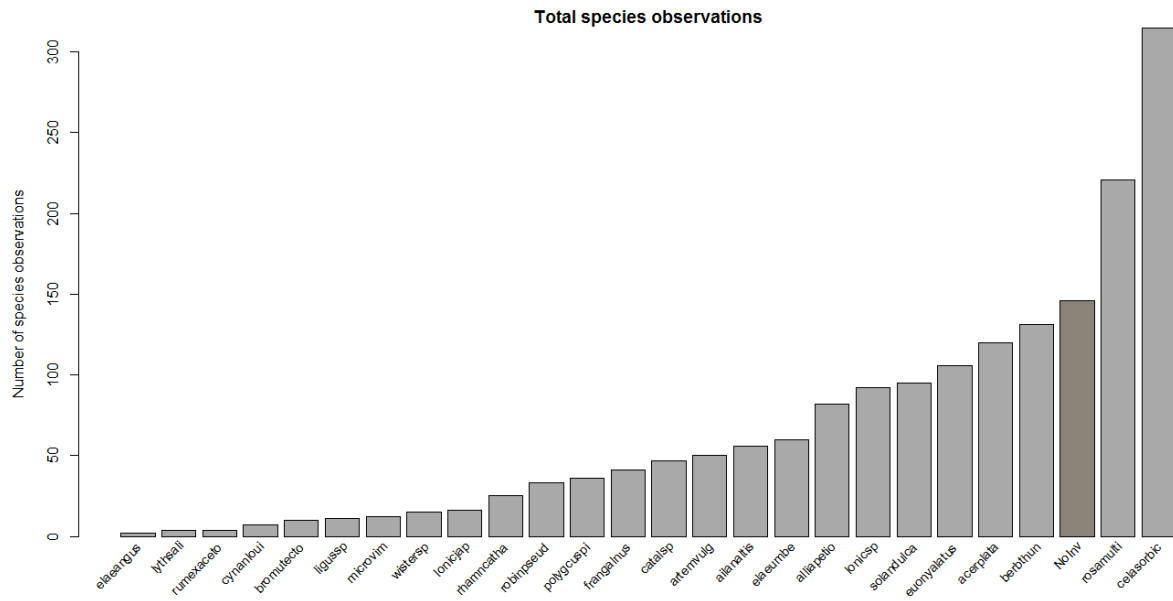
Figure 7A-2. The proportion of each species observed in rural, suburban, and urban sites, sorted by rural species' frequencies.
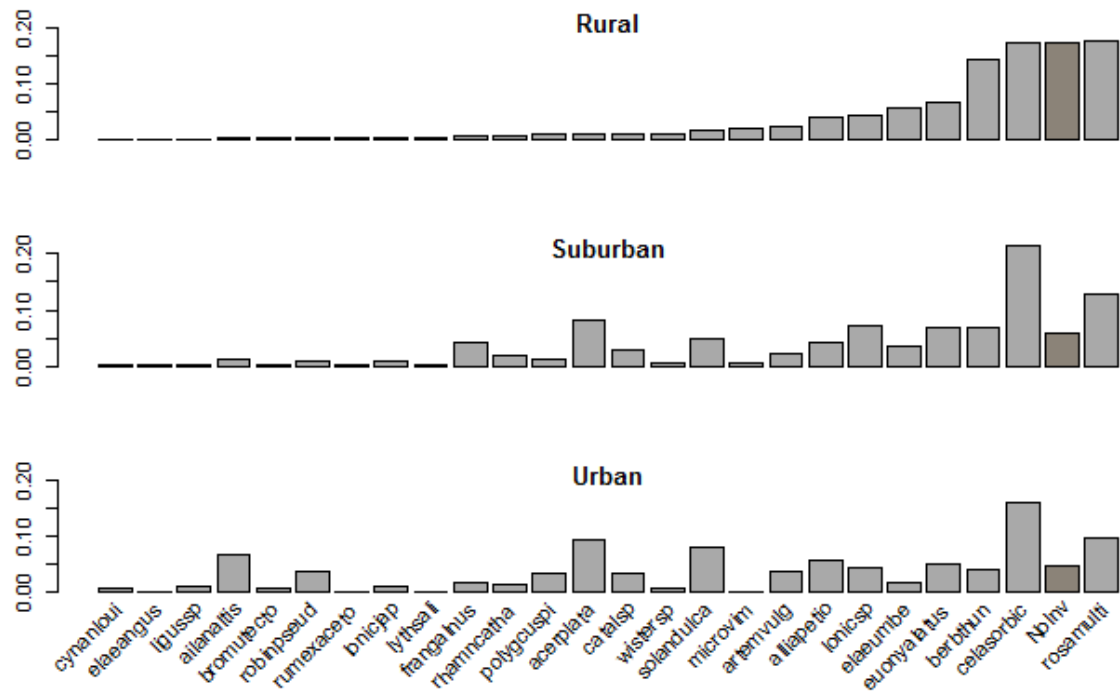
Appendix 8. *Species pairs*.

A. altissima is a classic urban tree species, introduced for use as a street planting, and is shade-intolerant. *A. platanoides* is an extremely common street and lawn planting which has a strong presence in urban woodlands. Norway maple is less tolerant of dry soils, but is more shade tolerant than *A. altissima* and therefore has a greater capacity to invade native mesic woods (Bertin et al. 2005). It appeared here in a wider variety of habitats than *A. altissima*. *Berberis thunbergii* is a shade-tolerant shrub which was primarily located in forested rural plots. *Elaeagnus umbellata* was also introduced as a horticultural planting, intended as erosion control and food for wildlife. *E. umbellata* tends to spread in open canopy habitats and roadsides. *Celastrus orbiculatus* is a woody vine prevalent across all sites that is tolerant of a wide variety of environmental conditions. The woody vine *Solanum dulcamara*, found largely in this study in urban edges, is shade intolerant. The biennial forb *Alliaria petiolata* was paired with the perennial forb *Artemisia vulgaris*. *A. vulgaris* grows in open, dry habitats; while *A. petiolata* prefers closed canopy rich woods. *A. vulgaris* was more strongly explained by impervious surface than *A. petiolata* in CCA plots. Only two grasses were surveyed in this project. *Bromus tectorum* was exclusively located in open urban habitats, while *M. vimineum* was exclusively located in more closed-canopy shaded habitats.

Appendix 9. *Trait data analysis.*

Table 9A-1. List of leaf and plant measurements and corresponding units. Interpretation of derived trait meaning is also included according to Cornelissen et al. 2003 and Pérez-Harguindeguy et al. 2013.

Measurement	Units	Meaning
Area	cm^2	One sided area of a leaf
Length	cm	Leaf length
Width	cm	Average and max leaf width
Mass	g	Leaf wet mass
Dry mass	g	Leaf dry mass
DBH	m	Diameter at breast height; tree diameter measured at a standardized height from the base of the tree.
Plant height	m	Height of highest foliage of an individual plant. Associated with competitive strength and overall size.
Thickness	mm	Leaf laminar thickness; high values may indicate leaf toughness, succulence, adaptation to a hot and dry environment.
LDMC	$mg\ g^{-1}$	Leaf dry matter content; ratio of leaf dry mass to wet mass. Measures leaf density. High values relative to low values indicate leaf investment in "toughness" and longevity.
SLA	$mm^2\ mg^{-1}$	Specific leaf area; leaf area divided by dry mass; correlates positively with relative growth rate, photosynthetic rate and leaf nitrogen concentration. High values indicate investment in resource capture; low values indicate investment in longevity.
LMA		1/SLA, inverse of SLA.
LWC	%	Leaf water content; (Wet mass – dry mass)/wet mass; measure of leaf succulence
LWR	Unitless	Length width ratio; maximum leaf width divided by leaf length. Measure of leaf shape. Larger values indicate a narrower leaf.

		May be adaptive for dry and/or low nutrient conditions.

Table 9A-2. Loadings and variance explained from the first two components of PCA analysis.

	Component 1	Component 2
Mass	-0.411	0.037
Dry mass	-0.403	-0.080
Area	-0.400	0.143
Length	-0.314	0.103
Average width	-0.381	0.180
Max width	-0.378	0.200
LMA	-0.133	-0.466
LWC	0.173	0.410
SLA	0.111	0.468
LDMC	-0.173	-0.410
LWR	0.167	-0.108
Thickness	0.064	-0.323
St. deviation	2.358	1.876
Proportion of variance	0.46	0.29

Table 9A-3. Mean of 5 untransformed trait values for 10 species, ± standard deviation. Species codes are as follows, listed by growth form and rural/urban pairing: trees: ACPL = A. platanoides, AIAL = A. altissima; shrubs: BETH = B. thunbergii, ELUM = E. umbellata; vines: CEOR = C. orbiculatus, SODU = S. dulcamara; forbs: A. petiolata, ARVU = A. vulgaris; grasses: MIVI = M. vimineum, BRTE = B. tectorum.

Species	SLA ($mm^2 mg^{-1}$)	LDMC ($mg\ g^{-1}$)	Thickness (mm)	LWR	Area (cm^2)
ACPL	2.124 ± 0.651	441.864 ± 48.594	0.112 ± 0.014	0.914 ± 0.225	129.892 ± 38.713
AIAL	1.354 ± 0.386	390.811 ± 43.973	0.198 ± 0.040	2.568 ± 0.318	41.105 ± 7.880
BETH	2.451 ± 0.697	276.718 ± 37.611	0.237 ± 0.036	2.140 ± 0.380	2.058 ± 0.664
ELUM	1.214 ± 0.148	397.971 ± 29.034	0.239 ± 0.022	2.299 ± 0.321	16.987 ± 4.117
CEOR	2.856 ± 0.908	250.419 ± 45.102	0.190 ± 0.028	1.450 ± 0.258	32.810 ± 10.302
SODU	3.676 ± 1.226	217.069 ± 33.642	0.153 ± 0.035	1.553 ± 0.344	19.008 ± 8.484
ALPE	6.062 ± 1.584	156.532 ± 35.695	0.137 ± 0.013	1.120 ± 0.111	59.509 ± 21.223
ARVU	1.961 ± 0.341	301.296 ± 45.471	0.189 ± 0.019	1.968 ± 0.509	23.500 ± 8.242
MIVI	5.564 ± 1.132	314.817 ± 47.825	0.070 ± 0.007	5.846 ± 0.495	6.578 ± 2.425
BRTE	2.646 ± 0.570	355.343 ± 144.446	0.158 ± 0.023	18.479 ± 5.068	2.974 ± 1.947

Table 9A-4. Mean of 5 untransformed trait values for the 10 species, ± standard deviation, broken down into samples from urban and rural sites. Species codes are as follows, listed by growth form and rural/urban pairing: trees: ACPL = A. platanoides, AIAL = A. altissima; shrubs: BETH = B. thunbergii, ELUM = E. umbellata; vines: CEOR = C. orbiculatus, SODU = S. dulcamara; forbs: A. petiolata, ARVU = A. vulgaris; grasses: MIVI = M. vimineum, BRTE = B. tectorum.

Species	Site	SLA (mm^2 mg^{-1})	LDMC (mg g^{-1})	Thickness(mm)	LWR	Area (cm^2)
ACPL	R	2.130 ± 0.833	420.573 ± 55.083	0.114 ± 0.016	1.047 ± 0.239	123.982 ± 44.195
	U	2.118 ± 0.421	463.154 ± 29.303	0.111 ± 0.012	0.781 ± 0.100	135.803 ± 32.397
AIAL	R	1.500 ± 0.441	375.465 ± 45.957	0.181 ± 0.046	2.692 ± 0.343	44.278 ± 6.671
	U	1.208 ± 0.258	406.156 ± 36.895	0.215 ± 0.025	2.444 ± 0.240	37.933 ± 7.858
BETH	R	2.345 ± 0.742	272.786 ± 29.008	0.253 ± 0.039	2.250 ± 0.350	2.094 ± 0.609
	U	2.557 ± 0.651	280.651 ± 45.051	0.220 ± 0.023	2.030 ± 0.385	2.022 ± 0.730
ELUM	R	1.170 ± 0.130	402.708 ± 27.950	0.244 ± 0.021	2.189 ± 0.259	19.070 ± 4.648
	U	1.257 ± 0.155	393.235 ± 30.032	0.234 ± 0.022	2.409 ± 0.344	14.904 ± 2.014
CEOR	R	3.268 ± 0.872	231.539 ± 44.678	0.189 ± 0.024	1.557 ± 0.305	38.705 ± 10.879
	U	2.443 ± 0.758	269.298 ± 37.800	0.190 ± 0.033	1.343 ± 0.140	26.916 ± 5.131
SODU	R	3.768 ± 0.887	213.109 ± 22.502	0.150 ± 0.033	1.669 ± 0.379	14.824 ± 2.873
	U	3.583 ± 1.510	221.028 ± 42.235	0.157 ± 0.037	1.437 ± 0.265	23.193 ± 10.131
ALPE	R	6.564 ± 1.128	143.292 ± 27.630	0.137 ± 0.012	1.048 ± 0.055	60.240 ± 19.757
	U	5.561 ± 1.829	169.771 ± 38.509	0.137 ± 0.015	1.192 ± 0.105	58.777 ± 23.089
ARVU	R	1.940 ± 0.329	307.282 ± 54.649	0.186 ± 0.016	2.068 ± 0.586	23.332 ± 9.258
	U	1.981 ± 0.360	295.311 ± 34.381	0.192 ± 0.023	1.869 ± 0.408	23.669 ± 7.326
MIVI	R	5.812 ± 1.121	313.644 ± 48.096	0.068 ± 0.006	5.761 ± 0.477	5.444 ± 2.402
	U	5.066 ± 1.004	317.165 ± 48.431	0.074 ± 0.006	6.016 ± 0.498	6.948 ± 2.490
BRTE	R	2.732 ± 0.612	371.926 ± 167.918	0.152 ± 0.023	19.893 ± 5.430	3.082 ± 1.893
	U	2.560 ± 0.525	338.761 ± 118.540	0.163 ± 0.022	17.065 ± 4.361	2.866 ± 2.042

Table 9A-4. Results of two-way ANOVA for species association (a priori classification of rural or urban) and site.

SLA

	df	SSE	MSE	F value	*P*
Association	4	25.5	6.375	33.878	<2e-16
Site	1	0.32	0.323	1.716	0.192
Interaction	4	0.47	0.117	0.621	0.648
Residuals	190	35.75	0.188		

LDMC

	df	SSE	MSE	F value	*P*
Association	4	11.852	2.9629	48.625	<2e-16
Site	1	0.115	0.1155	1.895	0.17
Interaction	4	0.097	0.0241	0.396	0.811
Residuals	190	11.578	0.0609		

LWR

	df	SSE	MSE	F value	*P*
Association	4	111.6	27.899	167.084	<2e-16
Site	1	0.25	0.252	1.506	0.221
Interaction	4	0.31	0.079	0.471	0.757
Residuals	190	31.73	0.167		

THICKNESS

	df	SSE	MSE	F value	*P*
Association	4	13.713	3.428	44.704	<2e-16
Site	1	0.036	0.036	0.463	0.497
Interaction	4	0.219	0.055	0.715	0.582
Residuals	190	14.571	0.077		

AREA

	df	SSE	MSE	F value	*P*
Association	4	245.16	61.29	114.324	<2e-16
Site	1	0.05	0.05	0.093	0.761
Interaction	4	0.15	0.04	0.069	0.991
Residuals	190	101.86	0.54		

Table 9A-4. Results of two-way ANOVA for species association (a priori classification of rural or urban) and site, for each growth form pair.

TREES

SLA

	df	SSE	MSE	F value	P
Association	1	1.8708	1.8708	24.268	1.88E-05
Site	1	0.0444	0.0444	0.576	0.453
Interaction	1	0.1474	0.1474	1.912	0.175
Residuals	36	2.7752	0.0771		

LDMC

	df	SSE	MSE	F value	P
Association	1	0.1618	0.16183	*14.601*	0.000506
Site	1	0.077	0.07697	6.945	0.012323
Interaction	1	0.0023	0.00227	0.205	0.65363
Residuals	36	0.399	0.01108		

LWR

	df	SSE	MSE	F value	P
Association	1	10.999	10.999	617.952	< 2e-16
Site	1	0.351	0.351	19.73	8.15E-05
Interaction	1	0.088	0.088	4.944	0.0325
Residuals	36	0.641	0.018		

THICKNESS

	df	SSE	MSE	F value	P
Association	1	3.0182	3.0182	109.585	1.80E-12
Site	1	0.0856	0.0856	3.107	0.0864
Interaction	1	0.1167	0.1167	4.236	0.0469
Residuals	36	0.9915	0.0275		

SHRUBS

SLA

	df	SSE	MSE	F value	P
Association	1	4.527	4.527	113.908	1.06E-12
Site	1	0.076	0.076	1.924	0.174
Interaction	1	0.003	0.003	0.064	0.802
Residuals	36	1.431	0.04		

LDMC

	df	SSE	MSE	F value	P
Association	1	1.3566	1.3566	162.968	6.27E-15
Site	1	0	0	0.003	0.96
Interaction	1	0.0052	0.0052	0.621	0.436
Residuals	36	0.2997	0.0083		

LWR

	df	SSE	MSE	F value	P
Association	1	0.0585	0.05847	3.322	0.0767
Site	1	0.0004	0.00043	0.024	0.8773
Interaction	1	0.0979	0.09793	5.564	0.0239
Residuals	36	0.6337	0.0176		

THICKNESS

	df	SSE	MSE	F value	P
Association	1	45.44	45.44	678.197	<2e-16
Site	1	0.19	0.19	2.857	0.0996
Interaction	1	0.07	0.07	1.113	0.2984
Residuals	36	2.41	0.07		

AREA

	df	SSE	MSE	F value	P	
Association	1	12.701	12.701	233.475	<2e-16	
Site	1	0.001	0.001	0.024	0.8785	
Interaction	1	0.212	0.212	3.902	0.0559	.
Residuals	36	1.958	0.054			

AREA

	df	SSE	MSE	F value	P
Association	1	45.44	45.44	678.197	<2e-16
Site	1	0.19	0.19	2.857	0.0996
Interaction	1	0.07	0.07	1.113	0.2984
Residuals	36	2.41	0.07		

VINES

SLA

	df	SSE	MSE	F value	P
Association	1	0.618	0.6182	6.52	0.0151
Site	1	0.415	0.4153	4.379	0.0435
Interaction	1	0.109	0.1087	1.146	0.2915
Residuals	36	3.414	0.0948		

FORBS

SLA

	df	SSE	MSE	F value	P
Association	1	12.467	12.467	344.235	<2e-16
Site	1	0.068	0.068	1.876	0.179
Interaction	1	0.102	0.102	2.824	0.102
Residuals	36	1.304	0.036		

LDMC

	df	SSE	MSE	F value	P
Association	1	0.1881	0.18812	7.309	0.0104
Site	1	0.0857	0.08573	3.331	0.0763
Interaction	1	0.0441	0.04407	1.712	0.199
Residuals	36	0.9266	0.02574		

LDMC

	df	SSE	MSE	F value	P
Association	1	4.421	4.421	141.371	5.02E-14
Site	1	0.049	0.049	1.554	0.2205
Interaction	1	0.097	0.097	3.102	0.0867
Residuals	36	1.126	0.031		

LWR

	Df	df	SSE	MSE	F value
Association		1	0.0372	0.03716	1.576	0.21737
Site		1	0.1961	0.19612	8.319	0.00658
Interaction		1	0	0.00004	0.002	0.9667
Residuals		36	0.8487	0.02357		

LWR

	df	SSE	MSE	F value	P
Association	1	2.9037	2.9037	90.596	2.28E-11
Site	1	0.0032	0.0032	0.1	0.7531
Interaction	1	0.1223	0.1223	3.817	0.0585
Residuals	36	1.1538	0.0321		

THICKNESS

	df	SSE	MSE	F value	*P*
Association	1	3.39	3.39	46.613	5.54E-08
Site	1	0.002	0.002	0.024	0.878924
Interaction	1	1.377	1.377	18.94	0.000107
Residuals	36	2.618	0.073		

THICKNESS

	df	SSE	MSE	F value	*P*
Association	1	8.628	8.628	62.218	2.33E-09
Site	1	0.003	0.003	0.02	0.887
Interaction	1	0.02	0.02	0.143	0.708
Residuals	36	4.992	0.139		

AREA

	df	SSE	MSE	F value	*P*
Association	1	3.39	3.39	46.613	5.54E-08
Site	1	0.002	0.002	0.024	0.878924
Interaction	1	1.377	1.377	18.94	0.000107
Residuals	36	2.618	0.073		

AREA

	df	SSE	MSE	F value	*P*
Association	1	8.628	8.628	62.218	2.33E-09
Site	1	0.003	0.003	0.02	0.887
Interaction	1	0.02	0.02	0.143	0.708
Residuals	36	4.992	0.139		

GRASS

SLA

	df	SSE	MSE	F value	*P*
Association	1	5.737	5.737	173.63	2.44E-15
Site	1	0.186	0.186	5.628	0.0231
Interaction	1	0.06	0.06	1.807	0.1873
Residuals	36	1.19	0.033		

LDMC

	df	SSE	MSE	F value	*P*
Association	1	0.0765	0.07653	1.13	0.295
Site	1	0.0007	0.00069	0.01	0.92

	1	0.0367	0.03672	0.542	0.466
Interaction	1	0.0367	0.03672	0.542	0.466
Residuals	36	2.4372	0.0677		

LWR

	df	SSE	MSE	F value	*P*
Association	1	13.088	13.088	525.098	<2e-16
Site	1	0.015	0.015	0.598	0.4445
Interaction	1	0.157	0.157	6.284	0.0168
Residuals	36	0.897	0.025		

THICKNESS

	df	SSE	MSE	F value	*P*
Association	1	7.718	7.718	28.031	6.09E-06
Site	1	0	0	0.001	0.98
Interaction	1	0.405	0.405	1.47	0.233
Residuals	36	9.912	0.275		

AREA

	df	SSE	MSE	F value	*P*
Association	1	7.718	7.718	28.031	6.09E-06
Site	1	0	0	0.001	0.98
Interaction	1	0.405	0.405	1.47	0.233
Residuals	36	9.912	0.275		

Table 9A-7. Regression model results for trait values without including species as a predictor. Residual plots of these models showed some irregular patterns that were removed by including species as a term.

SLA

	Coeff.	SE	t	p
Intercept	1.29	1.47	0.88	0.38
log(Income)	-0.05	0.14	0.37	0.71
log(Urbanization metric)	-0.05	0.03	-1.74	0.08
Proportion edge forest	**0.93**	**0.20**	**4.67**	**0.00**
Proportion of core forest	0.29	0.19	1.50	0.13

R-squared = 0.06

$F_{(4,195)}$ = 4.425.79, p = < 0.002

LWR

	Coeff.	SE	t	p
Intercept	**5.78**	**2.28**	**2.54**	**0.01**
log(Income)	**-0.51**	**0.22**	**-2.30**	**0.02**
log(Urbanization metric)	-0.04	0.05	-0.94	0.35
Proportion edge forest	0.85	0.61	1.40	0.16
Proportion of core forest	**0.68**	**0.29**	**2.33**	**0.02**

R-squared = 0.02

$F_{(4,195)}$ = 2.351, p = 0.0556

LDMC

	Coeff.	SE	t	p
Intercept	**6.48**	**0.89**	**7.27**	**8.7e-12**
log(Income)	-0.05	0.09	-0.61	0.54
log(Urbanization metric)	-0.00	0.02	-0.42	0.67
Proportion edge forest	**-0.75**	**0.24**	**-3.17**	**0.00**
Proportion of core forest	-0.06	0.11	-0.50	0.62

R-squared = 0.04

$F_{(4,192)}$ = 79.36, p = 0.018

Leaf Thickness

	Coeff.	SE	t	p
Intercept	**-4.15**	**1.00**	**-4.14**	**0.00**
log(Income)	**0.22**	**0.10**	**2.28**	**0.02**
log(Urbanization metric)	**0.05**	**0.02**	**2.41**	**0.02**
Proportion edge forest	-0.52	0.27	-1.95	0.05
Proportion of core forest	-0.25	0.13	-1.97	0.05

R-squared = 0.05

$F_{(4,195)}$ = 3.733, p = 0.006

Leaf area

	Coeff.	SE	t	p
Intercept	**9.35**	**3.51**	**2.66**	**0.01**
log(Income)	**-0.71**	**0.34**	**-2.10**	**0.04**
log(Urbanization metric)	0.10	0.07	1.47	0.14
Proportion edge forest	0.83	0.93	0.89	0.37
Proportion of core forest	-0.04	0.45	-0.09	0.93

R-squared = 0.9351

$F_{(13,186)}$ = 221.4, p = <2.2e-16

Table 9A-8. Results from multiple linear regression models of SLA, LWR, LDMC, leaf thickness and leaf area on continuous measures of urbanization and socioeconomics, including species. Significant predictors are in bold. The codes are as follows, listed by growth form and rural/urban pairing: trees: ACPL = A. platanoides, AIAL = A. altissima; shrubs: BETH = B. thunbergii, ELUM = E. umbellata; vines: CEOR = C. orbiculatus, SODU = S. dulcamara; forbs: A. petiolata, ARVU = A. vulgaris; grasses: MIVI = M. vimineum, BRTE = B. tectorum.

SLA

	Coeff.	SE	t	p
Intercept	0.11	0.73	0.15	0.89
AIAL	**-0.22**	**0.08**	**-2.59**	**0.01**
ALPE	**1.11**	**0.08**	**14.53**	**< 2e-16**
ARVU	-0.04	0.07	-0.54	0.59
BETH	**0.18**	**0.08**	**2.36**	**0.02**
BRTE	**0.24**	**0.07**	**3.29**	**0.00**
CEOR	**0.42**	**0.08**	**5.57**	**0.00**
ELUM	**-0.55**	**0.07**	**-7.46**	**0.00**
MIVI	**1.00**	**0.08**	**13.11**	**< 2e-16**
SODU	**0.48**	**0.07**	**6.40**	**0.00**
log(Income)	0.05	0.07	0.77	0.44
log(Urbanization metric)	**-0.04**	**0.01**	**-3.10**	**0.00**
Proportion edge forest	**0.93**	**0.20**	**4.67**	**0.00**
Proportion of core forest	0.04	0.09	0.50	0.62

R-squared = 0.8356

F(13,186) = 78.79, p = < 2.2e-16

LWR

	Coeff.	SE	t	p
Intercept	-0.43	0.50	-0.86	0.39
AIAL	**1.05**	**0.06**	**18.08**	**< 2e-16**
ALPE	**0.19**	**0.05**	**3.51**	**0.00**
ARVU	**0.73**	**0.05**	**14.29**	**< 2e-16**
BETH	**0.81**	**0.05**	**15.60**	**< 2e-16**
BRTE	**3.00**	**0.05**	**59.60**	**< 2e-16**
CEOR	**0.48**	**0.05**	**9.11**	**< 2e-16**
ELUM	**0.90**	**0.05**	**17.55**	**< 2e-16**
MIVI	**1.80**	**0.05**	**34.02**	**< 2e-16**
SODU	**0.56**	**0.05**	**10.96**	**< 2e-16**
log(Income)	0.01	0.05	0.22	0.83
log(Urbanization metric)	0.01	0.01	1.17	0.24
Proportion edge forest	0.11	0.14	0.82	0.41
Proportion of core forest	**0.28**	**0.06**	**4.52**	**0.00**

R-squared = 0.9662

F(13,186) = 438.1, p = <2.2e-16

LDMC

	Coeff.	SE	t	p
Intercept	**6.71**	**0.43**	**15.44**	**< 2e-16**
AIAL	**-0.25**	**0.05**	**-5.02**	**0.00**
ALPE	**-1.06**	**0.05**	**-23.56**	**< 2e-16**
ARVU	**-0.40**	**0.04**	**-9.13**	**< 2e-16**
BETH	**-0.48**	**0.04**	**-10.85**	**< 2e-16**
BRTE	**-0.38**	**0.04**	**-8.40**	**0.00**
CEOR	**-0.66**	**0.04**	**-14.82**	**< 2e-16**
ELUM	-0.07	0.04	-1.61	0.11
MIVI	**-0.37**	**0.05**	**-8.14**	**0.00**
SODU	**-0.67**	**0.04**	**-15.22**	**< 2e-16**
log(Income)	-0.05	0.04	-1.18	0.24
log(Urbanization metric)	**0.02**	**0.01**	**1.96**	**0.05**
Proportion edge forest	**-0.65**	**0.12**	**-5.48**	**0.00**

Leaf Thickness

	Coeff.	SE	t	p
Intercept	**-1.83**	**0.44**	**-4.12**	**0.00**
AIAL	**0.50**	**0.05**	**9.70**	**< 2e-16**
ALPE	**0.19**	**0.05**	**3.98**	**0.00**
ARVU	**0.53**	**0.05**	**11.68**	**< 2e-16**
BETH	**0.76**	**0.05**	**16.56**	**< 2e-16**
BRTE	**0.33**	**0.04**	**7.43**	**0.00**
CEOR	**0.50**	**0.05**	**10.87**	**< 2e-16**
ELUM	**0.76**	**0.05**	**16.84**	**< 2e-16**
MIVI	**-0.46**	**0.05**	**-9.84**	**< 2e-16**
SODU	**0.29**	**0.05**	**6.30**	**0.00**
log(Income)	-0.04	0.04	-0.84	0.40
log(Urbanization metric)	0.01	0.01	1.23	0.22
Proportion edge forest	-0.05	0.12	-0.44	0.66

Proportion of core forest	-0.03	0.05	-0.60	0.55

R-squared = 0.8386

$F_{(13,183)} = 79.36$, p = <2.2e-16

Proportion of core forest	-0.06	0.05	-1.09	0.28

R-squared = 0.867

$F_{(13,186)} = 100.8$, p = <2.2e-16

Leaf area

	Coeff.	SE	t	p
Intercept	**5.63**	**1.08**	**5.19**	**0.00**
AIAL	**-0.98**	**0.13**	**-7.83**	**0.00**
ALPE	**-0.85**	**0.11**	**-7.49**	**0.00**
ARVU	**-1.77**	**0.11**	**-16.10**	**< 2e-16**
BETH	**-4.09**	**0.11**	**-36.48**	**< 2e-16**
BRTE	**-3.99**	**0.11**	**-36.76**	**< 2e-16**
CEOR	**-1.25**	**0.11**	**-11.10**	**< 2e-16**
ELUM	**-2.13**	**0.11**	**-19.32**	**< 2e-16**
MIVI	**-3.12**	**0.11**	**-27.43**	**< 2e-16**
SODU	**-2.06**	**0.11**	**-18.57**	**< 2e-16**
log(Income)	-0.12	0.11	-1.09	0.28
log(Urbanization metric)	-0.02	0.02	-1.06	0.29
Proportion edge forest	**1.47**	**0.29**	**4.99**	**0.00**
Proportion of core forest	**0.28**	**0.13**	**2.11**	**0.04**

R-squared = 0.9351

$F_{(13,186)} = 221.4$, p = <2.2e-16

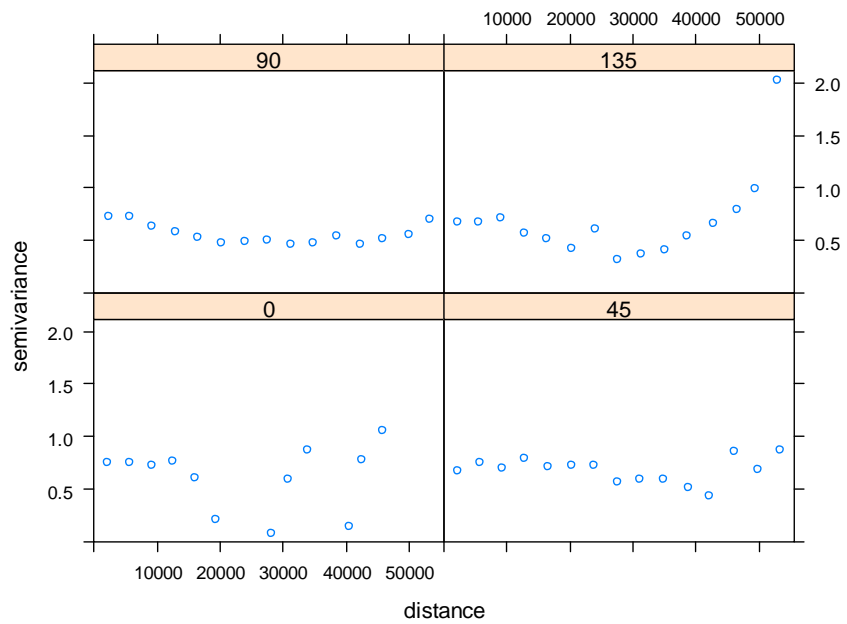Appendix 10. *Checking spatial autocorrelation in glm models*.

With any data including a spatial component, spatial autocorrelation in models can lead to a violation of model assumptions of independence (Dormann et al. 2007). I checked for spatial autocorrelation in the three distribution models using bubble plots and variograms of the residuals, according to methods suggested by Zuur et al. Variograms were produced using the function variogram in the R package gstat. The residual value associated with each point was then exported to ArcGIS to use this programs Moran's I function.

In the bubble plots clustering of similar residuals, for example, positive residuals of similar magnitude appearing in the same portion of the graph, would indicate spatial autocorrelation. In the variograms there is clearly no spatial pattern in the *C. orbiculatus* model, based on the lack of slope in the points, but there do appear to be some small patterns in the *S. dulcamara* and *B. thunbergii* model (Figures A4-1, A4-2, A4-3). The Moran's I test found no evidence of spatial autocorrelation at neighborhoods 4 km around each point, testing the null of randomly distributed residuals (*C. orbiculatus*: Moran's Index = -0.22, z = -1.12 , p = 0.26, *S. dulcamara*: Moran's Index = -0.094, z = -0.47, p = 0.64, *B. thunbergii*: Moran's Index = 0.09 , z = 0.48 , p = 0.63). Spatial autocorrelation was also not evident at larger scales.

Some of the patterns in the variograms in the "urban" and "rural" species models may be driven by data points in Boston. Removing those points from the two models does not remove the spatial pattern in the variograms, but Moran's I statistics still indicate a lack of statistically significant spatial autocorrelation. The urban species variogram without Boston points shows increasing correlation at larger distances while the rural species variogram shows increasing correlation at smaller distance. These trends may be reflective of the rural distribution of *B. thunbergii*, since most rural plots were clustered towards the center of the sampling range; and the urban distribution of *S. dulcamara*, since urban plots were located towards the western and eastern parts of the sampling range in Hartford and Boston. A few points in the northeast near Putnam, CT and southeast in Norwich were also urban and may have also added to some small spatial patterns in the residuals.

Figures A10-1a, b and c. Bubble plot, overall variogram and directional variogram of the *S. dulcamara* model. 0 is north, 45 is northeast, 90 is east, and 135 is southeast.
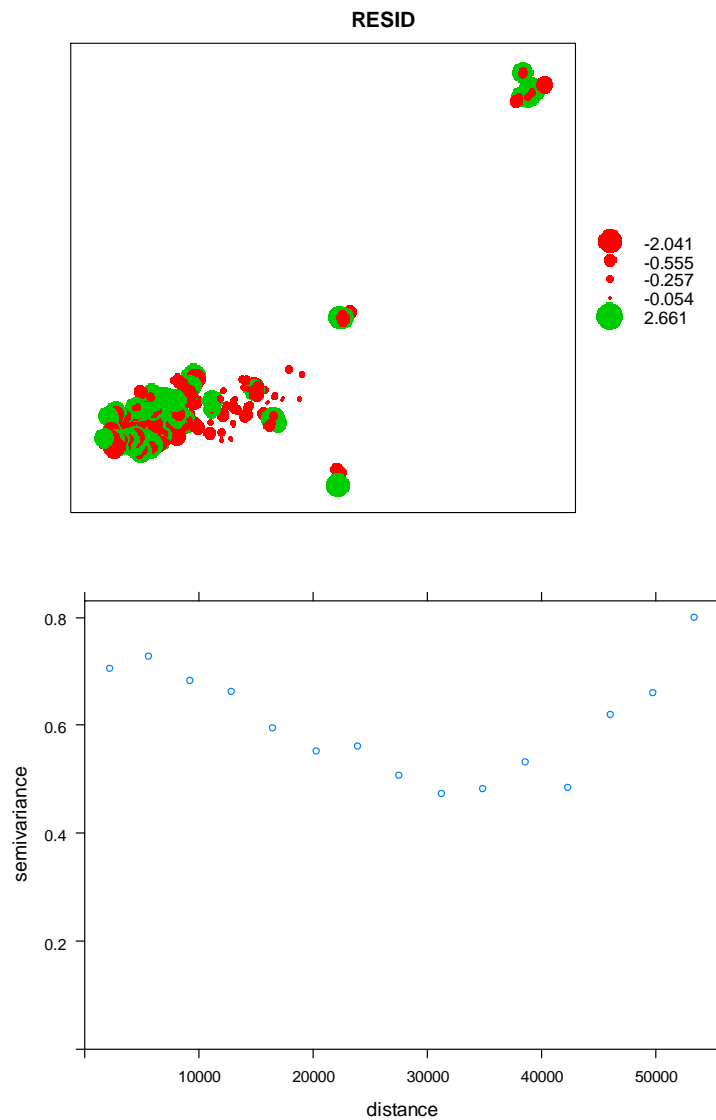
Figures A10-2a, b and c. Bubble plot, overall variogram and directional variogram of the *C. orbiculatus* model. 0 is north, 45 is northeast, 90 is east, and 135 is southeast.
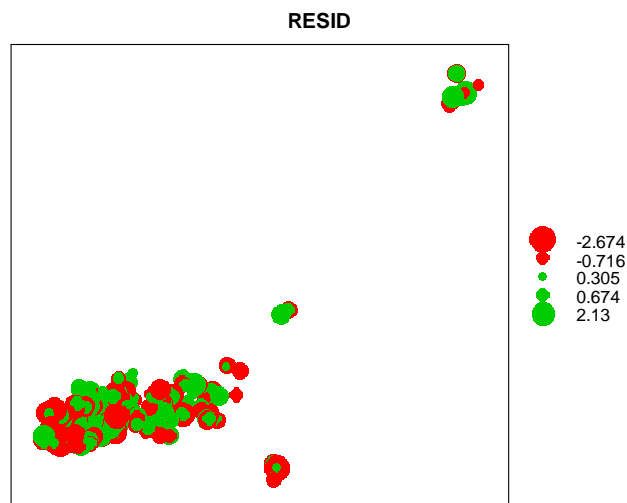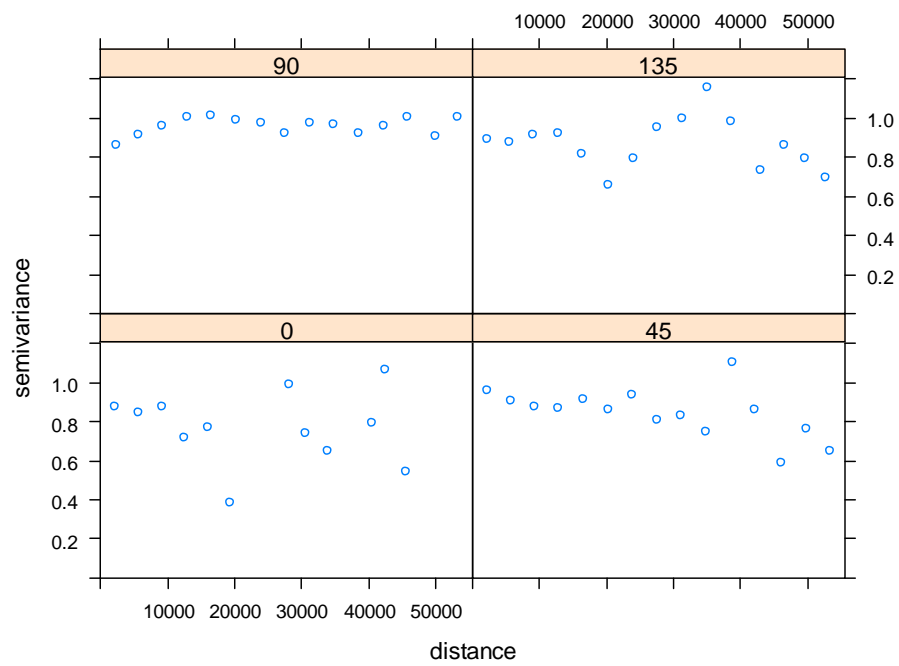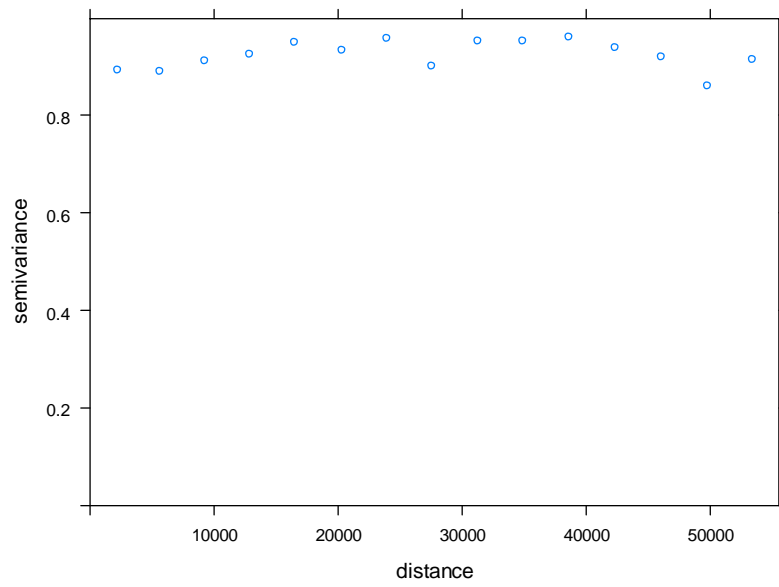
Figures A10-3a, b and c. Bubble plot, overall variogram and semivariogram of the *B. thunbergii* model. In the semivariogram directions, 0 is north, 45 is northeast, 90 is east, and 135 is southeast.

Appendix 11. *Leaf nutrient content data.*

Dried leaf samples were sent to the UCONN Soil Analysis Laboratory for analysis of leaf nutrient content. Leaves were re-dried, ground using a mill grinder and combined to provide enough samples for analysis. For most species, enough plant material was available to analyze both nitrogen content and ppm of a suite of elemental nutrients for two rural samples and two urban samples. 37 samples for percent N, percent C and C:N and 24 samples for leaf parts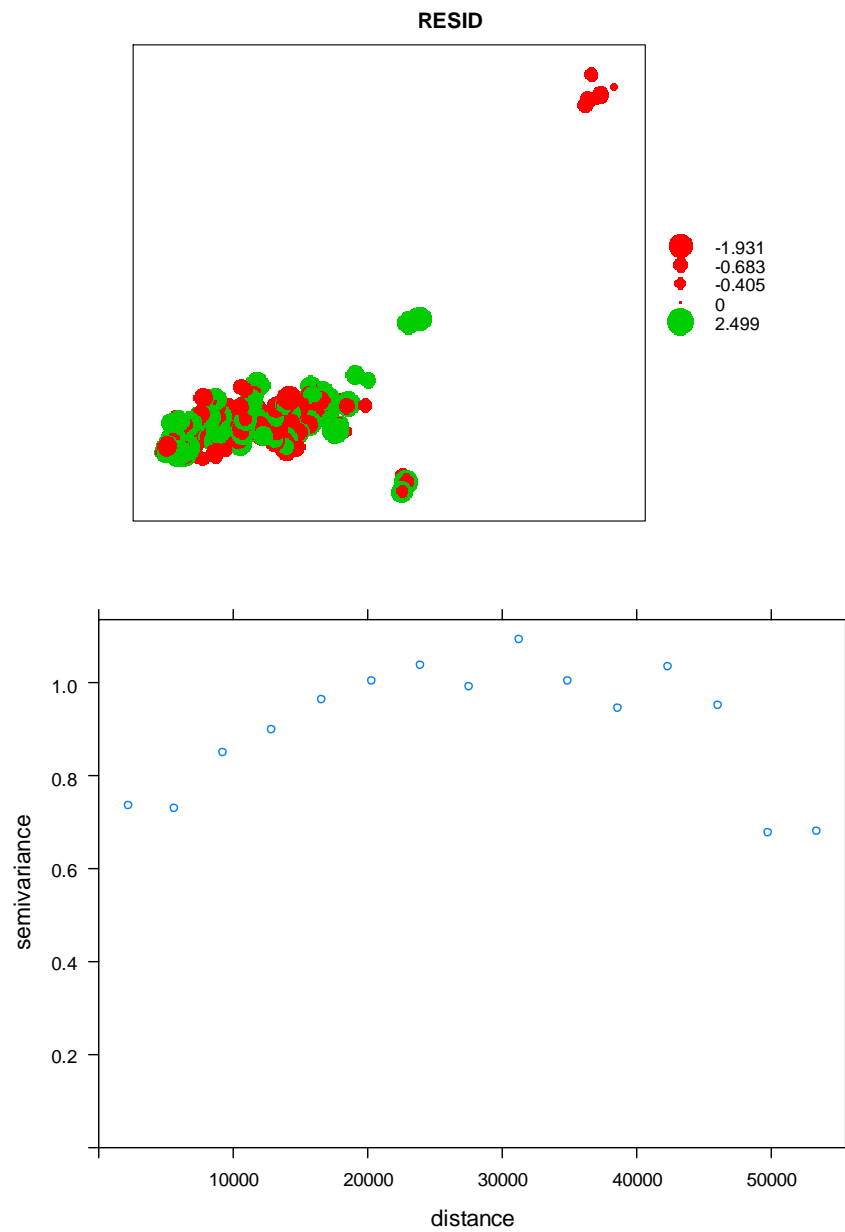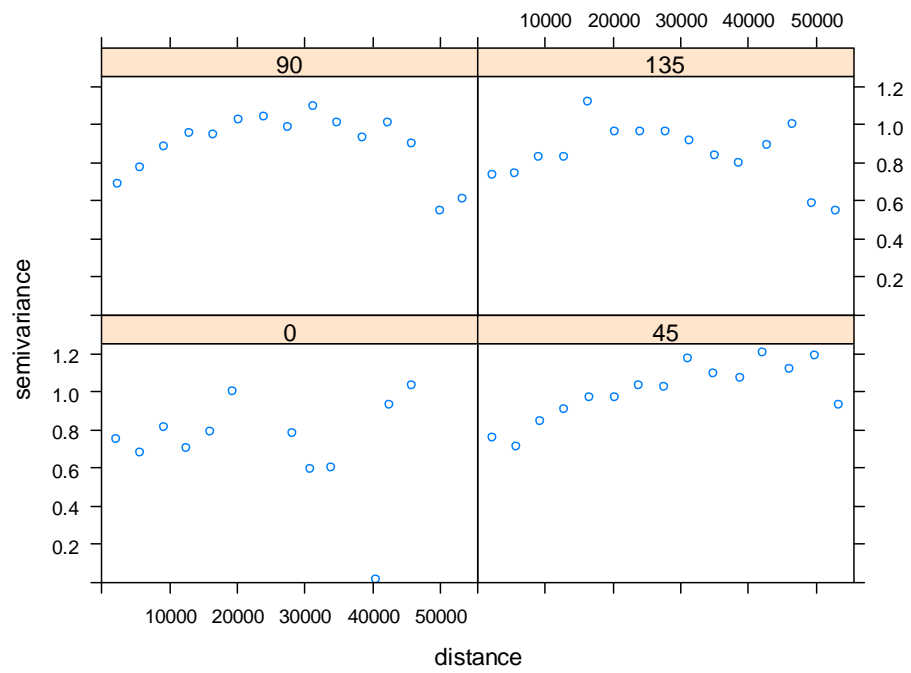 per million of Al, Fe, Mn, Na, Zn, Pb, B, Cu, and percent P, K, Ca and N:P were entered into separate analyses. One-way multivariate analyses of variance (MANOVA) were employed for exploring the effect of urban /rural classified species or urban/rural sites across several leaf nutrient levels. Appropriateness of MANOVA was checked with histograms and boxplots of dependent variables and model residuals; and checking for correlations between these variables. Correlations were moderate between many variables (Appendix 11), and the log transformation ensured normality. Separate MANOVA analyses were used for %C, %N and C:N because of the different sample sizes. Means and standard deviations for all leaf contents, and additional information on leaf nutrient content, are presented in Appendix 11.

The one-way MANOVA with parts per million of Al, Fe, Mn, Na, Zn, Pb, B, Cu, and percent P, K, Ca, N and N:P as dependent variables revealed significant effects of species association on the dependent variables ($F(11,12)$ = 4.9946, *p* = 0.004974). Univariate ANOVA analyses on each response separately showed that these results were significant for Al (p = 0.01), marginally for Zn (*p* = 0.05), Cu (*p* = 0.003516), and % Ca (*p* = 0.002275). Leaf % Ca content was higher for the rural associated species in all cases; while Ca content in urban soils was higher than that of rural soils. The same MANOVA with %N, %C and C:N also showed a significant effect of species association ($F(3,33)$ = 5.0469, *p* = 0.005), though %C was the only significant variable (*p* = 0.004). Levels of Al, Zn, Cu and Pb were higher for *A. platanoides* than *A. altissima*. Levels of Al and Zn were higher for *A. petiolata*, while levels of Cu and Zn were higher for *S. dulcamara*. Ultimately, no one unifying pattern of leaf heavy metal content emerged.

The effect of site in the same sets of one-way MANOVA models did not reveal significant differences, though individual ANOVA analyses showed that Fe was significantly higher in leaves collected from urban sites (*p* = 0.0114). Leaf Pb content was slightly higher in urban sites, however this difference was not significant (*p* = 0.6668). Copper was significantly greater in urban associated species (*p* = 0.0035), but not significantly greater in leaves collected from urban sites (*p* = 0.2812). The forb *A. vulgaris* had by far the greatest leaf copper content of all the species tested. Iron content was greater in rural soils, greater in leaves from urban sites, and highest in *A. petiolata*.

Table 11A-1. Correlation matrix of the log transformed leaf nutrient measurements (N = 24). Untransformed means and standard deviations are also listed. Significant correlations are in bold.

	Al	Fe	Mn	Na	Zn	Pb	Cu	%P	%K	%Ca	N:P
Al											
Fe	**0.55**										
Mn	-0.33	-0.26									
Na	**0.62**	**0.65**	-0.57								
Zn	0.21	0.03	0.35	-0.18							
Pb	0.15	-0.03	-0.04	-0.05	0.25						
Cu	-0.04	0.3	0.09	0.05	0.26	0.23					
%P	**0.47**	**0.49**	-0.4	0.77	0.09	0.03	0.17				
%K	**0.71**	**0.61**	**-0.58**	**0.9**	0.06	0.15	0.1	**0.84**			
%Ca	**0.49**	0.3	-0.34	0.37	-0.18	-0.09	-0.64	0.19	0.3		
N:P	**-0.42**	-0.35	0.32	**-0.46**	-0.1	-0.32	-0.18	**-0.7**	**-0.68**	-0.13	
Mean	80.4	83.7	142.2	75.8	47.4	2.2	13.7	0.2	1.9	2.7	13.2
SD	64.7	41.6	119.9	38	34.5	2.1	4.8	0.1	1.1	1.5	4.1

Table 11A-2. Correlation matrix of the log transformed leaf nutrient measurements (N = 37). Untransformed means and standard deviations are also listed. Significant correlations are in bold.

	%N	%C	C:N
N.perc			
C.perc	0.02		
CtoN	**-0.97**	0.14	
Mean	3.0	45.4	16.4
SD	0.9	2.4	4.9

Table 11A-3. Means and standard deviations for leaf nutrient data. Species codes are as follows, listed by growth form and rural/urban pairing: trees: ACPL = A. platanoides, AIAL = A. altissima; shrubs: BETH = B. thunbergii, ELUM = E. umbellata; vines: CEOR = C. orbiculatus, SODU = S. dulcamara; forbs: A. petiolata, ARVU = A. vulgaris; grasses: MIVI = M. vimineum, BRTE = B. tectorum.

	%N		%C		%P		%K		%Ca		%Mg	
	MEAN	SD	MEAN	SD	MEAN	SD	MEAN	SD	MEAN	SD	MEAN	SD
ACPL	2.61	0.30	47.23	1.09	0.17	0.02	0.9	0.20	1.855	0.69	0.17	0.05
R	2.51	0.47	48.10	0.71	0.17	0.02	0.945	0.32	1.27	0.04	0.13	0.01
U	2.71	0.07	46.35	0.07	0.18	0.01	0.855	0.08	2.44	0.21	0.21	0.00
AIAL	2.78	0.36	46.25	0.70	0.18	0.02	1.0175	0.20	2.9025	1.08	0.28	0.08
R	2.99	0.16	46.60	0.00	0.20	0.01	1.02	0.34	2.35	0.98	0.30	0.12
U	2.57	0.42	45.90	0.99	0.17	0.01	1.015	0.02	3.455	1.15	0.27	0.04
BETH	2.27	0.16	45.63	0.06	NA	NA	NA	NA	NA	NA	NA	NA
R	2.38	0.04	45.64	0.11	NA	NA	NA	NA	NA	NA	NA	NA
U	2.16	0.16	45.63	0.03	NA	NA	NA	NA	NA	NA	NA	NA
ELUM	3.78	0.29	48.56	0.25	0.22	0.03	1.4175	0.26	1.305	0.43	0.22	0.06
R	3.59	0.30	48.38	0.12	0.20	0.03	1.325	0.36	1.235	0.56	0.22	0.01
U	3.97	0.07	48.74	0.20	0.23	0.04	1.51	0.20	1.375	0.46	0.23	0.10
CEOR	2.52	0.72	42.62	1.38	0.20	0.03	1.77	0.12	4.5375	0.67	0.27	0.05
R	3.03	0.06	43.65	0.78	0.20	0.01	1.685	0.11	4.12	0.81	0.27	0.07
U	2.01	0.71	41.60	0.93	0.20	0.06	1.855	0.06	4.955	0.09	0.28	0.06
SODU	4.72	0.73	45.49	0.97	0.25	NA	2.17	NA	2.72	NA	0.45	NA
R	5.21	0.67	46.17	0.13	NA	NA	NA	NA	NA	NA	NA	NA
U	4.24	0.47	44.81	0.99	0.25	NA	2.17	NA	2.72	NA	0.45	NA
ALPE	3.54	0.77	40.45	0.97	0.39	0.12	3.9475	0.53	4.3825	0.51	0.51	0.09
R	4.07	0.81	40.60	0.85	0.45	0.13	4.135	0.56	3.975	0.29	0.58	0.01
U	3.02	0.08	40.30	1.41	0.33	0.11	3.76	0.62	4.79	0.18	0.44	0.07
ARVU	2.18	0.49	46.58	0.48	0.29	0.08	2.4175	0.36	1.255	0.19	0.20	0.06
R	2.24	0.79	46.40	0.57	0.31	0.07	2.395	0.09	1.285	0.32	0.18	0.04
U	2.11	0.28	46.75	0.49	0.26	0.10	2.44	0.61	1.225	0.01	0.22	0.09
MIVI	3.18	0.38	46.03	0.23	NA	NA	NA	NA	NA	NA	NA	NA
R	3.37	0.27	46.09	0.29	NA	NA	NA	NA	NA	NA	NA	NA
U	2.81	NA	45.92	NA	NA	NA	NA	NA	NA	NA	NA	NA
BRTE	2.19	0.21	44.67	1.16	NA	NA	NA	NA	NA	NA	NA	NA
R	2.04	NA	45.49	NA	NA	NA	NA	NA	NA	NA	NA	NA
U	2.33	NA	43.85	NA	NA	NA	NA	NA	NA	NA	NA	NA

	C:N		N:P		Cu		B		Al		Fe	
	MEAN	SD	MEAN	SD	MEAN	SD	MEAN	SD	MEAN	SD	MEAN	SD
ACPL	18.34	2.72	15.10	0.70	12.175	1.41	79.05	17.45	44.275	5.14	58.35	12.19
R	19.58	3.99	15.12	0.93	11.65	1.20	64.25	5.73	43.15	5.30	54.4	11.88
U	17.11	0.47	15.09	0.79	12.7	1.84	93.85	2.19	45.4	6.79	62.3	15.56
AIAL	16.87	2.48	15.45	1.35	10.925	1.60	84.65	40.21	29	14.02	62.925	16.36
R	15.61	0.81	15.36	1.35	11.95	1.77	66.3	58.97	18.85	12.09	57.2	16.12
U	18.14	3.38	15.53	1.91	9.9	0.57	103	5.09	39.15	5.59	68.65	20.29
BETH	20.21	1.53	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
R	19.18	0.39	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
U	21.23	1.62	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
ELUM	12.91	1.01	17.87	2.93	17.2	3.05	56.375	29.81	42.35	19.63	83.85	21.73
R	13.54	1.18	18.21	4.10	14.8	1.70	53.95	24.11	30	22.91	68.25	19.16
U	12.28	0.27	17.53	2.93	19.6	1.41	58.8	45.40	54.7	4.53	99.45	8.70
CEOR	18.25	6.14	12.55	3.17	10.125	1.18	34.25	5.22	121.375	77.58	79.25	37.91
R	14.44	0.56	15.17	1.39	10.35	0.78	31.9	6.93	165.9	100.13	56.55	6.29
U	22.06	7.40	9.92	0.77	9.9	1.84	36.6	3.39	76.85	9.97	101.95	47.02
SODU	9.80	1.44	15.64	NA	14.1	NA	66.5	NA	61.5	NA	85.5	NA
R	8.95	1.18	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
U	10.65	1.41	15.64	NA	14.1	NA	66.5	NA	61.5	NA	85.5	NA
ALPE	11.79	2.24	9.85	3.42	11	1.66	70.35	14.92	171.225	78.75	132.65	81.72
R	10.21	2.25	9.86	4.80	9.9	0.28	57.55	0.78	134.95	85.91	77.6	16.55
U	13.36	0.12	9.84	3.45	12.1	1.84	83.15	3.46	207.5	77.22	187.7	87.40

ARVU	**22.26**	**5.03**	**8.05**	**2.86**	**20.975**	**6.09**	**57.2**	**20.96**	**78.9**	**10.40**	**85.025**	**12.97**
R	22.14	8.08	7.12	0.93	15.8	0.28	54.75	8.84	80.65	15.91	75.3	3.11
U	22.37	3.23	8.97	4.50	26.15	2.05	59.65	34.86	77.15	7.71	94.75	10.82
MIVI	**14.60**	**1.73**	**NA**	**NA**	**NA**	**NA**	**NA**	**NA**	**NA**	**NA**	**NA**	**NA**
R	13.72	1.18	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
U	16.34	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
BRTE	**20.56**	**2.46**	**NA**	**NA**	**NA**	**NA**	**NA**	**NA**	**NA**	**NA**	**NA**	**NA**
R	22.30	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
U	18.82	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA

	Mn		Zn		Na		Pb	
	MEAN	SD	MEAN	SD	MEAN	SD	MEAN	SD
ACPL	**327.725**	**72.26**	**98.1**	**9.64**	**32.75**	**7.94**	**2.1**	**1.55**
R	268.8	39.46	98.55	14.92	33.81	11.24	1.5	1.13
U	386.65	14.78	97.65	7.42	31.69	7.62	2.7	2.12
AIAL	**84.9**	**50.86**	**15.275**	**4.40**	**48.56**	**5.67**	**1.35**	**0.90**
R	71.35	23.69	14.2	0.57	48.28	5.97	1.55	0.92
U	98.45	80.40	16.35	7.28	48.84	7.78	1.15	1.20
BETH	**NA**	**NA**	**NA**	**NA**	**NA**	**NA**	**NA**	**NA**
R	NA	NA	NA	NA	NA	NA	NA	NA
U	NA	NA	NA	NA	NA	NA	NA	NA
ELUM	**182.025**	**70.57**	**28.875**	**13.94**	**72.355**	**11.81**	**1.85**	**2.50**
R	143	89.24	34.15	21.71	62.74	6.93	2.75	3.89
U	221.05	29.77	23.6	0.71	81.97	0.58	0.95	0.64
CEOR	**64.125**	**17.81**	**23.525**	**10.87**	**76.145**	**4.87**	**2.4**	**3.30**
R	65.4	29.27	27.4	16.40	76.49	3.63	0.55	0.64
U	62.85	9.40	19.65	5.02	75.8	7.58	4.25	4.31
SODU	**384.8**	**NA**	**121.2**	**NA**	**83.14**	**NA**	**1.9**	**NA**
R	NA	NA	NA	NA	NA	NA	NA	NA
U	384.8	NA	121.2	NA	83.14	NA	1.9	NA
ALPE	**56.425**	**29.29**	**47.65**	**10.16**	**147.2**	**30.17**	**2.05**	**2.41**
R	58.25	50.56	52.6	3.96	143.18	9.11	3.45	3.04
U	54.6	1.98	42.7	14.00	151.22	50.83	0.65	0.64
ARVU	**77.3**	**73.71**	**52.65**	**33.13**	**76.16**	**9.99**	**3.55**	**1.97**
R	104.05	115.89	27.4	2.40	75.85	17.10	2.05	0.21
U	50.55	2.05	77.9	27.15	76.47	2.53	5.05	1.63
MIVI	**NA**	**NA**	**NA**	**NA**	**NA**	**NA**	**NA**	**NA**
R	NA	NA	NA	NA	NA	NA	NA	NA
U	NA	NA	NA	NA	NA	NA	NA	NA
BRTE	**NA**	**NA**	**NA**	**NA**	**NA**	**NA**	**NA**	**NA**
R	NA	NA	NA	NA	NA	NA	NA	NA
U	NA	NA	NA	NA	NA	NA	NA	NA

For *S. dulcmara*, *B. thunbergii* and both grass species only percent nitrogen was analyzed. One sample of *S. dulcamara* was analyzed for the full suite of variables, but was not entered into analyses beyond %N due to lack of replication. Additionally, only one rural sample and one urban sample were available for *B. tectorum*, and both urban *M. vimineum* samples were combined together.

Two-way MANOVA for both sets of variables using site and species association as factors did not reveal any significant interactions, or individual effects of site on leaf nutrient values. Two-way MANOVA using growth form and species association as factors did reveal both a significant interaction and significant main effects (growth form: $F(3,18) = 5.3342$, $p = 6.324e\text{-}06$; association: $F(1,18) = 4.9631$, $p = 0.0157$; interaction: $F(1,18) = 7.3799$, $p = 0.0044$). ANOVA analyses for individual nutrients show that growth form has an effect on Al, Mn, Na, Zn, Cu, % P, %K, %Ca, and N:P. The interaction between growth form and species association was only significant for Mn, Na, Zn, Cu, %K, and % Ca, indicating that for these variables differences exist

between the urban and rural associated species. Differences are primarily driven by the trees and forbs, since missing data meant that species pairs for the shrubs, vines and grasses were missing or incomplete. The mean values of variables for trees and forms do not reveal any patterns.

Leaf % N was also not significantly different between urban and rural site leaves, as was found in the soils. High leaf nitrogen content correlates positively with mass-based maximum photosynthetic rate and SLA, indicating fast growth and fast nutrient uptake strategies (Pérez-Harguindeguy et al. 2013). Among species, the highest % N concentration was found in *S. dulcamara*. The lowest was found in the forb *A. vulgaris*. Average leaf % N was slightly higher in rural sites. N and P are both critical limiting elements in plant growth, and the ratio of the two can reveal which is most limiting in a given environment (Pérez-Harguindeguy et al. 2013). No significant differences between urban and rural sites or urban and rural species were found for this ratio. Differences do exist between species, though not between growth forms. *E. umbellata* had the highest values for this ratio, followed by the trees, then *C. orbiculatus*, and the two forb species.