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Forest Islands in a Sea of Urban Habitat

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by

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ABSTRACT OF THESIS

Urban forests are poorly defined as ecological communities. Substantive links between anthropogenic landscape features and forest ecology are lacking. 'Urbaness' is commonly defined by human population density or land use classifications, but their use is inconsistent throughout the literature, and rarely is linked with ecological processes. Furthermore, it is unknown whether urban forests are functioning parts of a patchy urban woodland system or isolated islands amidst an ocean of unsuitable habitat. I first used digital satellite imagery and publicly available U.S. National Park data to link urban land use with forest processes. I then linked those land use classifications with the potential for urban forests to regenerate by investigating tree recruitment in the greater Buffalo, NY (U.S.) metropolitan area. If urban forests link with the greater regional forest ecosystem, then tree species richness should resemble the regional forests. However, if the urban forest patches are isolated, they should contain a subset of the regional forest richness with recruitment limited by forest patch size. Heavy urban cover predicted reduced tree and seedling richness and abundance. Moreover, tree seedling richness decreased with increasing urban land use. Tree seedling richness and abundance both declined when invasive species were present, suggesting invasive species may act as a barrier to tree recruitment. Tree recruitment was more strongly linked with forest patch size than the regional species pool, and active dispersal was limited to wind-dispersed species between urban forests. These results suggest that urban forests are isolated forest islands surrounded by an ocean of urban habitat.

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Introduction

Urban forests are poorly defined ecological communities (Theobald 2001, Raciti et al. 2012, Wandl et al. 2014). Several parameters (e.g., population density) used to define urbaness lack substantive links between anthropogenic land use and urban forest ecology (McDonnell and Pickett 1990, Theobald 2001, Wandl et al. 2014). Indeed, urban forestry often is described as the planning and development of recreational areas for humans that maximize the usage of resources and amenities while reducing environmental impacts (Pickett et al. 2001). Although the many detrimental effects of urbanization on habitat quality and biodiversity are well studied (Brooks and Rowntree 1984, Jim 1998, Pickett et al. 2001, McKinney 2005, Pouyat et al. 2007), it is unknown whether urban forest patches are stable, regenerating forests, part of a greater urban ecosystem, or isolated islands in an urban ocean.

Urbaness is commonly defined by human population density; however, its use is very inconsistent (McDonnell et al. 1997, Theobald 2001, Wandl et al. 2014). For example, the U.S. Census Bureau defined urban as > 620 people km^{-2} in 1980 (McDonnell and Pickett 1990) and > 2,590 people km^{-2} in 2010 (Raciti et al. 2012), whereas the European Union classified urban as continuous areas and cities with > 20,000 people in 2011 (Wandl et al. 2014). Moreover, U.S. state census agencies often classify entire counties as either urban or rural based on total population estimates even though human settlement often is aggregated into urban clusters (Theobald 2001, Raciti et al. 2012, Wandl et al. 2014). Consequently, 'urban' includes suburban, exurban, and even rural areas. Human population density is rarely used to delineate these categories (Pickett et al. 2001), and the ambiguity presents difficulties in distinguishing different levels of urbaness (Wandl et al. 2014). Population density is also an indirect measure of urbaness, as different urban areas may have similar populations but different land uses (Raciti et

al. 2012). Hence, population density poorly defines urbaness (Pickett et al. 2001, Raciti et al. 2012, but see Klotz 1990).

Land use classification systems are another way to define urban areas (McDonnell and Pickett 1990, Blair and Launer 1997, Luck and Wu 2002, Raciti et al. 2012, Wandl et al. 2014). For example, Luck and Wu (2002) used four coarse-scale cover classes to identify patterns of urbanization, whereas McDonnell and Pickett (1990) used 16 "structural features" to define urban. However, land use classifications, like population density, can be inconsistent. For example, in different classification schemes, paved ground cover was included as 'impermeable surface area' (McDonnell and Pickett 1990), 'urban' (Luck and Wu 2002), or in both 'business' and 'residential' cover classes (Blair and Launer 1997). Urban land use classifications all distinguish urban from rural, but few link land use with key ecological processes such as tree recruitment.

An alternate possibility is that urbaness itself, regardless of land use type, forms a landscape of habitat unsuitable for tree recruitment. That is, regardless of urban land use type, none of it provides suitable habitat for tree seedlings to germinate and survive. Forest patches in an otherwise urban landscape may form islands of suitable habitat, surrounded by a 'concrete ocean' and separated from rural 'mainland' populations outside the city. Hence, species richness of urban forests may be understood through the lens of island biogeography as a way to understand ecological processes in isolated habitats (MacArthur and Wilson 1967, Kadmon and Pulliam 1995). According to island biogeography, species richness tends to increase with island size and decrease with distance from mainland source populations. From an 'urban biogeography' perspective, urban forests may be isolated islands in a sea of unsuitable urban

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habitat separated from rural mainland populations. If so, tree recruitment and tree species richness would likely be greater in larger parks and lesser in isolated, urban parks.

Tree seedling recruitment is a key indicator of forest stability (Grubb 1977, Eriksson and Ehrlen 1992, Clark et al. 1998, McEuen and Curran 2006, Clark et al. 2007). Canopy trees must be replaced by seedlings for a forest ecosystem to regenerate (Grubb 1977, Clark et al. 1998), and seedlings have been shown to have a strong impact in determining plant population dynamics (Clark et al. 2007, Oldfield et al. 2013). Seeds can be introduced locally by existing adult populations (Runkle 1981) or through long-distance dispersal (Clark et al. 1998), though long-distance dispersal is rare in urban forests (Clark et al. 1998, Cordeiro et al. 2009, Herrera and Garcia 2010). McEuen and Curran (2006) found that failed dispersal can account for recruitment failure in isolated forest fragments. Tree recruitment is rare in urban forests (McEuen and Curran 2006, Oldfield et al. 2013), and may be due to isolation from larger rural population. Even if local dispersal is plentiful, tree seedlings may fare poorly due to increased invasive species and high herbivory in urban forests (Klionsky et al. 2011, Labatore 2015, Oldfield et al. 2015).

The objective of this study was to investigate tree recruitment in urban forests. I used publicly available U.S. National Park forest data and additional field-collected forest data in the greater Buffalo, NY (U.S.) metropolitan area to examine how well urban forest composition, surrounding urban land use and urban biogeography predicted tree seedling recruitment. I expected that heavy urban land use would correspond with greater declines in tree recruitment and species richness than light urban land use. If the urban forest patches connect with the greater regional forest ecosystem the tree species identities and seed recruitment should resemble the regional forests with a weak link between patch size and species richness. If the urban forest

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patches are isolated islands they should instead contain a subset of the regional forest richness with recruitment limited to strong dispersers, such wind-dispersed propagules, and species richness linked strongly with patch size.

Methods

Urban parameters

The following eight parameters are the land use types used in defining urban land cover. Tree cover ('Trees') is an obvious indicator of urban forest whereas other urban parameters may correspond with reduced or eliminated tree recruitment (see Table 1). Mowed grass, such as cemeteries, golf courses and sports fields ('Lawn') deter tree seedling survival (Bryant 2004, De Chant et al. 2010), and shrub and herbaceous plant cover ('Vegetation') may inhibit tree colonization (Gorchov and Trisel 2003, Fagan and Peart 2004, Sullivan et al. 2009, Labatore 2015). Residential clusters like suburban or apartment housing ('Residential') have effects that can vary with size (i.e. heat islands, increased mowing, small-scale pesticide application, and increased runoff) and may interrupt reproduction or successful juvenile tree growth (Luck and Wu 2002, Bryant 2004). Industrial and commercial properties ('Industrial/commercial') are strong germination barriers due to altered soil composition, poor air and water quality, and the presence of toxins or heavy metals (McDonnell et al. 1997, Pickett et al. 2001, McKinney 2005). Agriculture fields ("Agriculture') can allow for limited recruitment, but practices that alter the landscape (e.g. plowing or intense grazing) might eliminate recruitment. Ponds, lakes and rivers ('Water') are common land types and are included to improve the accuracy of classifying land use, but are not direct measurements of urbaness and therefore were excluded from final analysis. Roads, parking lots, and impermeable surfaces ('Paved') provide no suitable habitat for

trees. I grouped these eight parameters into urban categories based on how strongly they likely suppress tree recruitment. Accordingly, 'heavy urban' ('Paved,' 'Residential,' and 'Industrial/Commercial') can represent land use where natural tree recruitment is highly unlikely, whereas 'light urban' ('Lawn,' 'Vegetation,' and 'Agriculture') can represent land use in which recruitment may occur, though not in appreciable numbers.

National Parks Data

Forest data was compiled from U.S. National Park Service vegetation surveys (http://science.nature.nps.gov/im/inventory/veg/products.cfm) for 50 urban and rural parks across the U.S. These data were used to test which urban parameters best predicted tree seedling abundance and species richness. Data used from these surveys were park area (ha), distance to edge (m), tree species identity, tree seedling abundance, canopy tree cover, understory tree cover, and herbaceous cover. The National Park Service (NPS) surveys vary in number of plots per park (e.g., Saugus Iron Works National Historic Site, *n = 4*; New River Gorge National River, *n = 708*), as well as the size of each park (e.g., Saugus Iron Works National Historic Site, size = 5.1 ha; Great Smoky Mountains National Park, size = 200,000 ha). Each park can be broadly classified as temperate deciduous forest.

I generated land use classification surveys for the 50 national parks using digital satellite imagery. I surveyed eight randomly selected plots (from the park vegetation plot locations) within the boundaries of each park as well as an additional eight fixed plots 1 km outside of the park boundaries in eight cardinal directions (N, NE, E, SE, S, SW, W, NW). Each plot covered a circular area of 100 m^2 (radius = 5.64 m). The circular plots were created using Google Earth Pro (v7.1) and converted into shape files using Zonum Solutions

(http://www.zonums.com/online/kml2shp.php). Shape files then were uploaded into i-Tree

Canopy (http://www.itreetools.org/canopy/index.php) and land use was analyzed by identifying

the eight land use types (Table 1) at 25 random points per plot.

Field Data

In May-August 2015, I conducted field surveys along three transects in western New York, U.S.,

each beginning at the city center of Buffalo (42.88666N, 78.87936W). Transect 1 traveled

northeast at 45°N for approximately 45 km; transect 2 traveled east at 85°E for approximately 40

km; transect 3 traveled south at 158°SE for approximately 52 km. Each transect covered an urban

to rural gradient, and I sampled state, county and town forest patches that fell on the transects

(Table 2). I defined 'forest' as unmanaged habitat dominated by canopy tree species where the

potential existed for tree seedling recruitment to occur in the understory.

I randomly surveyed the field sites to eliminate temporal bias along the transects. The

number of plots for each field site varied by forest patch size (1 plot ha^{-1}, max = 20 patch^{-1}; $n =$

302). Tree canopy (DBH > 10 cm) and sub-canopy (DBH < 10 cm) species were sampled using

point-centered quarter (PCQ) method (Dix 1960) at each plot to find canopy and sub-canopy

density as well as tree species richness. Tree seedling and sapling abundance by species, total

herbaceous percent cover and invasive species percent cover by species were sampled within two

subplots. Each subplot was 1 m^2, located 5 m west and 5 m east of the PCQ center point.

Subplots that fell on unmeasurable land (e.g., obstructed by an object such as a fallen tree or

permanent body of water) were placed an additional 5 m further in the same direction. The

percent of woody shrub cover by species was also measured using the line intercept method

(Canfield 1941). A transect spanned 10 m from the center of each subplot, and all shrub cover

intersecting the line was measured per woody species for all individuals > 1 m.

Biogeography Data

In order to measure larger-scale, urban forest biogeography, I recorded the distance (km) of each

field site to the city center of Buffalo, as well as the distance from each field site to the nearest

forested neighbor. I measured distance to neighbor as the minimum distance between each forest

boundary. I also obtained total forest area (ha) for each park and nearest forested neighbor. All

biogeography measurements were gathered using Google Earth Pro v7.1.

After the field surveys and biogeography measurements, I then conducted land use

surveys using i-Tree Canopy following the protocol for the NPS data (25 random points per plot

for all internal park plots measured *in situ*; 8 fixed plots located 1 km outside of park boundary in

each cardinal direction).

Data Analysis

All statistical analyses were done in the R statistical program (R Core Team 2016). Heavy urban,

light urban and urban (heavy + light urban) land uses were examined to determine which best

linked with tree recruitment using Akaike information criterion (AIC, $\Delta > 2$). In order to examine

local seed recruitment, the 'match' between adult and seedling/sapling tree species identities in

the same plot was calculated as a proportion of all species in the plot.

Principal component analysis (PCA) was used to examine covariation among the urban

predictors, human population density, adult tree density and dominance, subcanopy tree density

and dominance, shrub cover, invasive species cover, herbaceous cover, park size, proximity to

city center and nearest forested neighbor. Loadings were then used to indicate the most important

variables, and only those variables were used in each model. Given that the PCA cannot handle

missing variables, and does not provide a test of hypotheses, I tested adult tree and seedling

richness as a function of the best predictors using generalized linear mixed models (GLMM) for

plot-level analysis and generalized linear models (GLM) for park-level analysis. I used the GLM

and GLMM models for both national park and field data assuming a Poisson error distribution. I

included park as a random effect at the plot level as plots within a park are likely autocorrelated.

Model selection was based on AIC, and a quasipoisson error distribution was used to account for

overdispersion where necessary. The "lme4" package in the R statistical program was used to

evaluate GLMMs. The "car" package in the R statistical program was used for variance inflation

factors. A linear model (LM) was run for all significant results to find goodness of fit.

Coefficients with *p-value* < 0.05 were considered significant, and coefficients with *p-value* <

0.10 were considered marginally significant (*sensu* Hurlbert and Lombardi 2009).

Results

National Parks Data – Plot Level Analysis

The PCA loadings indicated that canopy tree richness, species match, seedling abundance,

understory tree cover, human population density, distance to edge, internal urban cover, and

external heavy urban cover most covaried with seedling richness. However, the only statistically

significant predictor was match (Table 3; Fig. 1). Urban cover negatively covaried with tree

species richness, canopy tree cover, and understory tree cover. The PCA loadings indicated that

distance to edge, match, human population density, internal urban cover, canopy tree cover, and

understory tree cover most covaried with seedling abundance. Whereas there was no significant

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predictor of seedling abundance, human population density and external heavy urban cover negatively covaried with seedling abundance. Distance to edge, human population density, internal urban cover and external urban cover most covaried with canopy tree richness. Canopy tree richness decreased with internal urban cover (Fig. 2), but had no relationship with distance to edge, human population, or external heavy urban cover (Table 4).

National Parks Data – Park Level Analysis

The PCA loadings indicated that park area, canopy tree richness, match, canopy tree cover, understory tree cover, human population density, distance to edge, and external heavy urban cover most covaried with seedling richness. Canopy tree cover and understory tree cover were removed from the GLM after AIC model selection ($\Delta > 2$). Seedling richness was significantly predicted by match (Fig. 3) as well as park area (Table 5). The PCA loadings indicated that seedling richness, external heavy urban cover, human population density, and match most covaried with seedling abundance. Only match significantly predicted tree seedling abundance (Table 6). Seedling abundance did not positively covary with any predictors, however it negatively covaried strongly with human population and external heavy urban cover (Fig. 4). Distance to edge, park area, internal light urban cover, and external heavy urban cover most covaried with canopy tree richness. Canopy tree richness was significantly predicted by park area, whereas external heavy urban cover was a marginally significant predictor of canopy tree richness (Table 7; Fig. 5).

Field Data – Plot Level Analysis

The PCA loadings indicated that canopy tree density, match, herbaceous cover, invasive species cover, shrub cover, subcanopy density, subcanopy dominance, and external heavy urban cover most covaried with seedling richness and abundance. Subcanopy density was removed from the GLMM after AIC model selection ($\Delta > 2$). Canopy tree density, match, and external heavy urban cover all significantly predicted seedling richness, whereas invasive species cover was a marginally significant predictor of seedling richness (Table 8; Fig. 6). Herbaceous cover, shrub cover, and subcanopy dominance did not predict seedling richness, and weakly covaried with seedling richness in biplot analysis. The PCA loadings indicated that canopy tree density, herbaceous cover, match, invasive species cover, shrub cover, subcanopy tree dominance, and external heavy urban cover most covaried with seedling abundance. Canopy tree density, match, subcanopy tree dominance, and external heavy urban cover all significantly predicted seedling abundance (Table 9; Fig. 7). Canopy tree richness at the plot level most covaried with canopy tree density, match, invasive species cover, subcanopy tree dominance and density, external urban cover, internal urban cover, and internal heavy urban cover. Only match was marginally significant in predicting canopy tree richness (Table 10), however the goodness of fit between these two variables was very low ($R^2 = 0.02$). Subcanopy tree dominance and subcanopy tree density were the only two variables to be even moderately correlated (Pearson's correlation coefficient > 0.50).

Field Data – Park Level Analysis

The PCA loadings indicated that canopy density, canopy dominance, canopy richness, subcanopy dominance, subcanopy richness, match, herbaceous cover, invasive species cover, and external heavy urban cover most covaried with seedling richness. Canopy density, canopy

dominance, canopy richness, subcanopy dominance, herbaceous cover, and invasive species cover were removed from the GLM after AIC model selection ($\Delta > 2$). Match (coeff. = 23.6009, SE = 9.489, z value = 2.487, p value = 0.013, R^2 = 0.59) and external heavy urban cover (coeff. = -2.9694, SE = 0.7017, z value = -4.232, p value < 0.001, R^2 = 0.74) both significantly predicted tree seedling richness (Fig. 8), whereas subcanopy tree richness (coeff. = 0.0261, SE = 0.0622, z value = 0.420, p value = 0.6744) did not. Canopy density, subcanopy density, match, and external heavy urban cover all covaried with tree seedling abundance. All four variables significantly predicted seedling abundance, although canopy tree density was only marginally significant (Table 11). Seedling abundance increased with subcanopy density and match, and increased marginally with canopy tree density, whereas seedling abundance decreased with external heavy urban cover. External heavy urban cover strongly correlated (Pearson's correlation coefficient > 0.70) with decreased canopy tree density and increased invasive species cover. Invasive species cover also strongly negatively correlated with tree density. Interestingly, this was the only test where match was significant but not the best predictor.

Biogeography Analysis

Park area, distance to city center, distance to nearest forested neighbor, and area of nearest forested neighbor were the predictors used in biogeography analysis. Distance to city center and neighboring forest patch area were removed from the GLM for canopy tree richness after AIC model selection ($\Delta > 2$), however an interaction effect between park area and distance to nearest neighbor was added to the model. Park area significantly predicted canopy tree richness (coeff. = 0.09896, SE = 0.0385, z value = 2.569, p value = 0.010, R^2 = 0.36) [Fig. 9], whereas distance to nearest forested neighbor did not (coeff. = -0.1868, SE = 0.1478, z value = -1.264, p value =

0.206). There was no interaction effect (coeff. = 0.0195. SE = 0.0806, z value = 0.242, p value = 0.809).

Park area and area of nearest forested neighbor were removed from the GLM for canopy tree density after AIC model selection ($\Delta > 2$). Canopy tree density increased with both distance to city center (coeff. = 0.4362, SE = 0.0938, t value = 4.651, p value < 0.001, $R^2 = 0.44$) [Fig. 10] and proximity to nearest forested neighbor (coeff. = 0.3458, SE = 0.1474, t value = 2.347, p value = 0.031, $R^2 = -0.03$). Increasing distance from the city center also strongly correlated (Pearson's correlation coefficient > 0.70) with increasing park area and increasing area of nearest forested neighbor. Hence, forest cover became denser and more diverse as a patch increased in size and moved farther away from urban clusters.

Discussion

Urbaness is typically defined by human population density (McDonnell and Pickett 1990, Theobald 2001, Raciti et al. 2012, Wandl et al. 2014) or land use classifications (McDonnell and Pickett 1990, Blair and Launer 1997, Luck and Wu 2002, Raciti et al. 2012, Wandl et al. 2014), but inconsistencies with these definitions often lead to a lack of connectivity between ecological function and what is considered 'urban' (Pickett et al. 2001, Theobald 2001, Wandl et al. 2014). I found that urban forest patches were less functional compared to rural forests via isolation and reduced tree recruitment. However, there are many ways in which a forest can be "functional." My research focused on the aspect of forest regeneration by way of tree recruitment. Tree recruitment decreased with increasing urban land use (defined by the urban parameters found in Table 1). Whereas human population density covaried with several predictors of tree recruitment (e.g. distance to edge or urban land use), it failed to predict both adult tree and tree seedling

richness and abundance. Tree recruitment increased with forest patch size as well as with

distance from the city center, although the best predictor of seedling richness and abundance was

matching adult tree species with tree seedling species. Furthermore, adult tree and seedling

richness found in urban forest patches were only a small subset of the regional pool, which

suggests long-distance dispersal between forest patches was limited (Cordeiro et al. 2009,

Herrera and Garcia 2010). My findings are consistent with predictions from island biogeography

in which I conceptualized urban forest patches as isolated islands amidst an urban sea of

unsuitable habitat.

The theory of island biogeography (MacArthur and Wilson 1967, Kadmon and Pulliam

1995) states that species richness should increase with both increasing island area and decreasing

distance from mainland source populations. The urban forest patches of the greater Buffalo, NY

(U.S.) metropolitan area are analogous to the models within island biogeography theory. Park

area limited adult tree and tree seedling species richness. Canopy tree and seedling richness

increased with park area, and canopy tree density and abundance were greatest in parks farthest

from the city center, or nearest to the 'mainland' rural forest population. Incidentally, increasing

park area correlated with increasing distance from the city center. That is, functioning forest

patches tended to be larger and farther away from the city. Hence, biogeography measurements

such as park area or distance from city centers can be used to predict urban forest tree

recruitment.

Forest fragmentation is known to have deleterious impacts on ecosystem function

(Brooks and Rowntree 1984, Cordeiro et al. 2009, Sullivan et al. 2009, Herrera and Garcia

2010). I investigated whether urban forest fragments are functioning patches within a greater

urban ecosystem or are isolated from one another. Functioning patches should share a similar

species richness representative of the whole system, yet I found urban parks to have a very limited subset of the regional tree species. Increasing proximity of forested neighbors failed to predict adult tree and tree seedling richness, indicating that if any propagule dispersal was occurring between urban parks, it was likely limited to long-distance, wind-dispersed species (e.g. *Populus deltoides* or *Fraxinus pennsylvanica*). Adult tree abundance increased when forest neighbors were nearby, however increasing distance from city center was a stronger predictor of tree abundance.

Anthropogenic land use is commonly used to delineate urban from rural, often along an urban to rural gradient (McDonnell and Pickett 1990, Blair and Launer 1997, McDonnell et al. 1997, Raciti et al. 2012, Wandl et al. 2014). Species richness (Blair and Launer 1997), stem density (McDonnell et al. 1997), changing landscape patterns (Luck and Wu 2002), and carbon stocks (Raciti et al. 2012) have all been shown to vary along urban to rural gradients, yet none of these ecological measures were linked to any direct urban indices. I found tree recruitment decreased with several urban indices. Tree recruitment consistently decreased with heavy urban cover (i.e., Industrial/commercial, Residential, Paved) surrounding parks at both the national and local scale. Tree recruitment also decreased with light urban cover (i.e., Agriculture, Lawn, Vegetation), however only when it was found within national park boundaries. Interestingly, heavy urban land uses were the only urban indices to significantly limit tree recruitment in local parks. The Buffalo, NY (U.S.) metropolitan region has a rich and lengthy history of industrial manufacturing, which may have contributed to these findings. Nevertheless, heavy urban cover seemed to limit tree seedling richness and tree seedling abundance despite all of the intrinsic qualities of an otherwise functioning forest. In other words, natural processes within forest canopies and subcanopies all the way down to the woody shrub and herbaceous ground layers

shape forest form and function, yet all of these natural processes were overshadowed by the detrimental effects of heavy urban land use.

Urban land use positively correlated with invasive species cover. Invasive species can disrupt or prevent germination of native plants (Klionsky et al. 2011, Labatore 2015, Oldfield et al. 2015). Once such species, European buckthorn (*Rhamnus cathartica*), has been found to limit germination via allelochemicals (Klionsky et al. 2011). I found that tree seedling richness was reduced at the plot-level with invasive species cover, whereas there was no effect at the park level. This is a bit surprising given that invasive species were present in 86% of my local field sites and common in 50%. Although anthropogenic habitat may simply be conducive to disturbance-adapted invasive species (Glasby et al. 2007, Westphal et al. 2008), and the effects of invasive species cover on tree recruitment might be eliminated with a rich mature canopy or limited urban land use. This would certainly require further investigation.

The greatest predictor of tree seedling richness and tree seedling abundance, however, was the matching of adult tree and tree seedling species. Tree seedling richness and abundance were the highest when the forest canopy consisted of the same species. This trend was much more pronounced at the local scale, suggesting that these urban forest boundaries are real, further highlighting the lack of dispersal between urban forest patches. Local urban forest patches were isolated, and ample recruitment occurred only at large parks found relatively far from the city center – parks that had a diverse enough and dense enough mature forest canopy for active recruitment to occur. Tree recruitment was less limited at the national scale. Match and park area were strong predictors of increased tree seedling richness and abundance for U.S. National Parks, particularly when urban land use was minimal and failed to limit tree recruitment.

The deleterious effects of forest fragmentation and urbanization have been well studied (Brooks and Rowntree 1984, Jim 1998, Pickett et al. 2001, McKinney 2005, Pouyat et al. 2007). Isolated forest patches lack propagule migration, which in turn limits the likelihood of ongoing forest recruitment and regeneration. Urban land use reduces the amount of suitable habitat within a forest patch via fragmentation (Brooks and Rowntree 1984, Cordeiro et al. 2009, Sullivan et al. 2009), and eliminates the connectivity between forest patches (Bryant 2004). My results demonstrate that urban land use can be used to identify specific anthropogenic attributes that interfere with ecological processes such as tree and seed dispersal and recruitment. Furthermore, limited tree recruitment in urban forest ecosystems can lead to a decline in old-growth canopy structure which might pave the way for increased disturbance, nonnative species colonization, or even a widespread reduction in overall forest richness and composition.

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Tables

Table 1: List of urban land use parameters used in i-Tree surveys.

Urban driver	Abbreviation	Description
Trees	Tr	Tree cover
Lawn	La	Mowed grasses, ball fields, cemeteries, golf courses, etc.
Vegetation	Ve	Vegetation other than trees (e.g., grasses or shrubs)
Paved	Pa	Roads, lots, and any impermeable surfaces
Water	Wa	Body of water appearing to be permanent
Agriculture	Ag	Any crop or cattle-grazing land, whether planted or empty
Residential	Re	Houses or apartments
Industrial/Commercial	IC	Businesses and factories

Table 2: List of 21 field sites surveyed across greater Buffalo, NY (U.S.) metropolitan area. Included are park names, identifying number, order in which parks were surveyed, location (GPS), area, and municipality in charge of each property.

Site Name	Park No.	Order	Transect	Latitude	Longitude	Area (ha)	Municipality
Alden Town Park	1	9	East	42.9077	-78.5032	35.95	Town
Audubon Town Park	2	14	Northeast	42.9969	-78.7663	11.13	City
Boston Forest County Park	3	5	South	42.6221	-78.7901	293.26	State
Botanical Gardens	4	12	South	42.8336	-78.8301	12.73	City
California Road Recreational Area	5	6	South	42.7574	-78.7802	16.86	County
Casey-Paradise Park	6	18	Northeast	43.0217	-78.7155	10.3	Town
Cheektowaga Town Park	7	1	Northeast	42.913	-78.7941	1.48	State
Chestnut Ridge Park	8	13	South	42.717	-78.7533	438.07	Town
Como Lake County Park	9	17	East	42.8916	-78.6487	62.09	Town
Darien Lakes State Park	10	3	East	42.9118	-78.4112	738.9	Private
East Otto State Forest	11	15	South	42.4281	-78.7903	1362.23	Town
Garnet Playground	12	20	Northeast	42.9775	-78.7969	3.23	City
Great Baehre Conservation Park	13	7	Northeast	43.0077	-78.7335	39.9	County
Iroquois National Wildlife Refuge	14	10	Northeast	43.132	-78.388	3944.75	Town
Red Jacket Riverfront Park	15	4	South	42.8652	-78.8531	13.84	State
Seneca Bluffs	16	2	East	42.8656	-78.8108	14.42	Town
Sprague Brooke Park	17	19	South	42.5915	-78.6313	322.81	County
Stiglmeier Park	18	21	East	42.8885	-78.7332	33.83	Town
Tim Russert Park	19	16	East	42.8572	-78.7996	12.51	State
Westwood Park	20	11	East	42.9048	-78.6148	15.2	Town
Yates Park	21	8	South	42.75891	-78.7527	6.57	Town

Table 3. List of variables in GLMM predicting tree seedling richness. Data is from U.S. National Park, plot-level data.

	Coefficient	SE	z value	p value
Distance to edge	0.0004	0.0004	1.120	0.263
Match	26.6482	5.5846	4.772	< 0.001
Human population density	0.0362	0.0413	0.875	0.381
Internal urban	0.0155	0.0191	0.813	0.416
Seedling abundance	-0.0031	0.0134	-0.229	0.819
Canopy tree cover	-0.0038	0.0042	-0.895	0.371
Understory tree cover	0.0058	0.0049	1.180	0.238

Table 4. List of variables in GLMM predicting tree canopy richness. Data is from U.S. National Park, plot-level data.

	Coefficient	SE	z value	p value
Distance to edge	0.0001	0.0001	1.104	0.27
Human population density	-0.0152	0.0137	-1.106	0.269
Internal urban	-0.0716	0.0059	-12.023	< 0.001
External urban	0.0009	0.0012	0.744	0.457

Table 5. List of variables in GLM predicting tree seedling richness. Data is from U.S. National Park, park-level data.

	Coefficient	SE	*t* value	*p* value
Park area	0.2541	0.0709	3.585	< 0.001
Match	124.9777	19.7303	6.334	< 0.001
Human population density	0.0226	0.0527	0.428	0.67
Distance to edge	0.0839	0.1015	0.826	0.413
External heavy urban	0.003	0.0063	0.480	0.633

Table 6. List of variables in GLM predicting tree seedling abundance. Data is from U.S. National Park, park-level data.

	Coefficient	SE	*t* value	*p* value
Match	-275.8609	87.5316	-3.152	0.003
Understory tree cover	0.0309	0.0238	1.300	0.202
Distance to edge	0.0667	0.1371	0.487	0.629
Human population density	-0.1877	0.3699	-0.507	0.315
Internal light urban	-0.0201	0.0479	-0.420	0.677
External heavy urban	-0.0414	0.0281	-1.474	0.149
Park area	0.1153	0.1189	0.969	0.339

Table 7. List of variables in GLM predicting canopy tree richness. Data is from U.S. National Park, park-level data.

	Coefficient	SE	t value	p value
Distance to edge	0.0733	0.0459	1.598	0.117
Internal light urban	-0.0176	0.1286	-1.370	0.178
External heavy urban	0.0039	0.0021	1.823	0.075
Park area	0.1118	0.0256	4.360	< 0.001

Table 8. List of variables in GLMM predicting tree seedling richness at the plot-level. Data was collected from local field sites around the greater Buffalo, NY (U.S.) metropolitan region.

	Coefficient	SE	z value	p value
Canopy density	0.0003	0.0001	2.279	0.023
Match	7.6971	0.9119	8.440	< 0.001
Herb cover	0.0011	0.0022	0.488	0.625
Invasive cover	-0.0148	0.0083	-1.775	0.076
Shrub cover	-0.0085	0.0066	-1.296	0.195
Subcanopy dominance	0.0000	0.0000	1.567	0.117
External heavy urban	-1.6574	0.5601	-2.959	0.003

Table 9. List of variables in GLMM predicting tree seedling abundance at the plot-level. Data was collected from local field sites around the greater Buffalo, NY (U.S.) metropolitan region.

	Coefficient	SE	z value	p value
Canopy tree density	0.0008	0.0002	4.012	< 0.001
Match	13.3933	1.3504	9.918	< 0.001
Herbaceous cover	-0.0013	0.0031	-0.404	0.686
Invasive species cover	-0.0144	0.0089	-1.610	0.107
Shrub cover	-0.0113	0.0079	-1.420	0.155
Subcanopy tree dominance	0.000	0.000	3.049	0.002
External heavy urban	-2.551	0.7589	-3.362	0.001

Table 10. List of variables in GLMM predicting canopy tree richness at the plot-level. Data was collected from local field sites around the greater Buffalo, NY (U.S.) metropolitan region.

	Coefficient	SE	z value	p value
Canopy tree density	-0.0001	0.0001	-0.487	0.626
Match	1.0355	0.6166	1.679	0.093
Invasive species cover	-0.0011	0.0028	-0.375	0.708
Subcanopy tree dominance	-0.0000	0.0000	-0.356	0.722
Subcanopy tree density	0.0000	0.0000	1.11	0.267
External urban	0.1652	0.2008	0.822	0.411
Internal urban	-0.0166	0.1737	-0.096	0.924
Internal heavy urban	0.3884	0.5692	0.682	0.495

Table 11. List of variables in GLM predicting tree seedling richness at the park-level. Data was collected from local field sites around the greater Buffalo, NY (U.S.) metropolitan region.

	Coefficient	SE	t value	p value
Canopy tree density	0.0015	0.0007	2.091	0.053
Subcanopy tree density	0.0003	0.0001	3.309	0.004
Match	29.7341	10.8847	2.732	0.015
External heavy urban	-3.0487	1.0971	-2.779	0.013

Figures
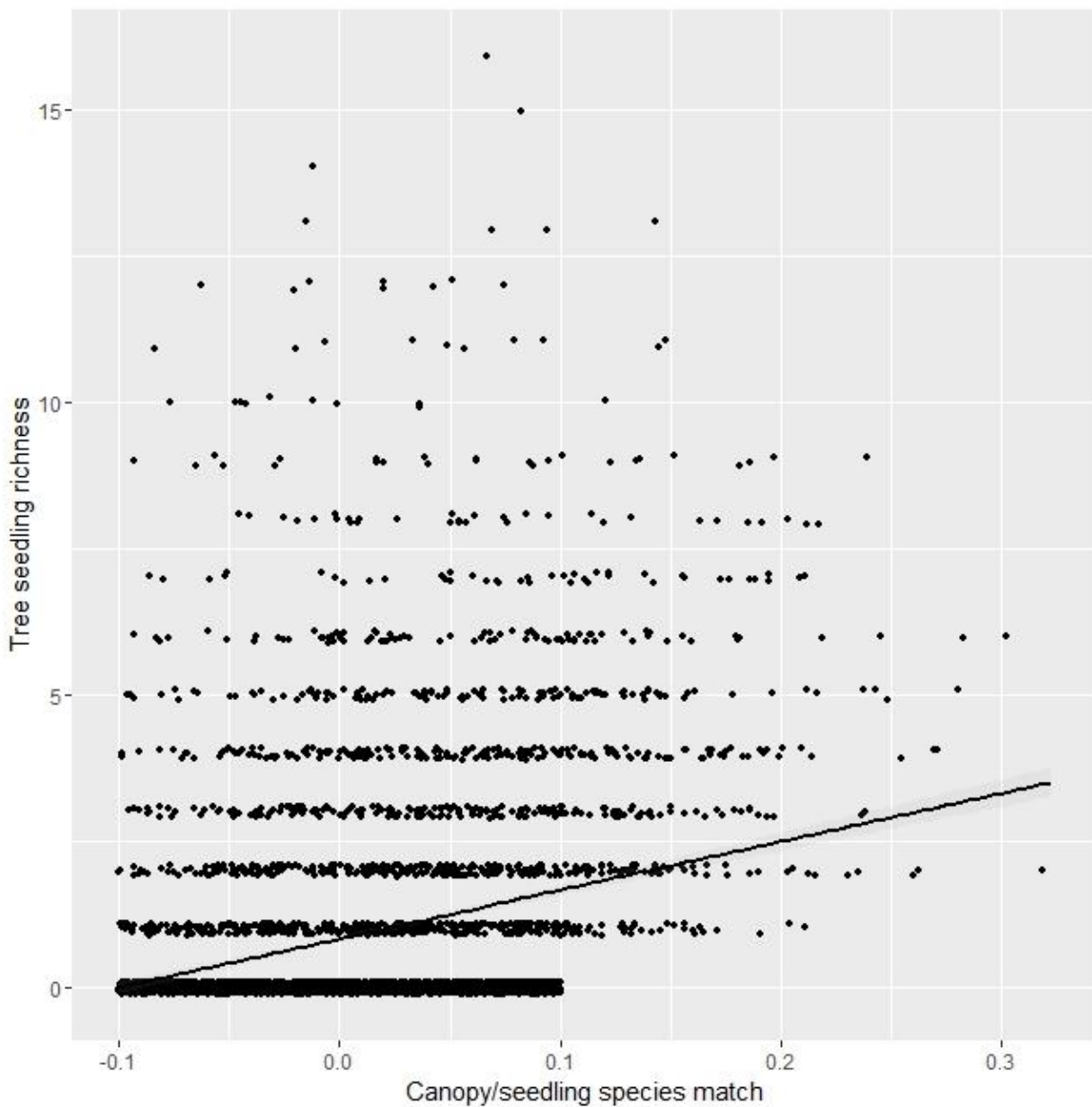
Fig. 1. Tree seedling richness as a function of species match between adult and seedlings. Data is from U.S. National Park, plot-level data. Tree seedling richness increased with increasing species match. $R^2 = 0.33$
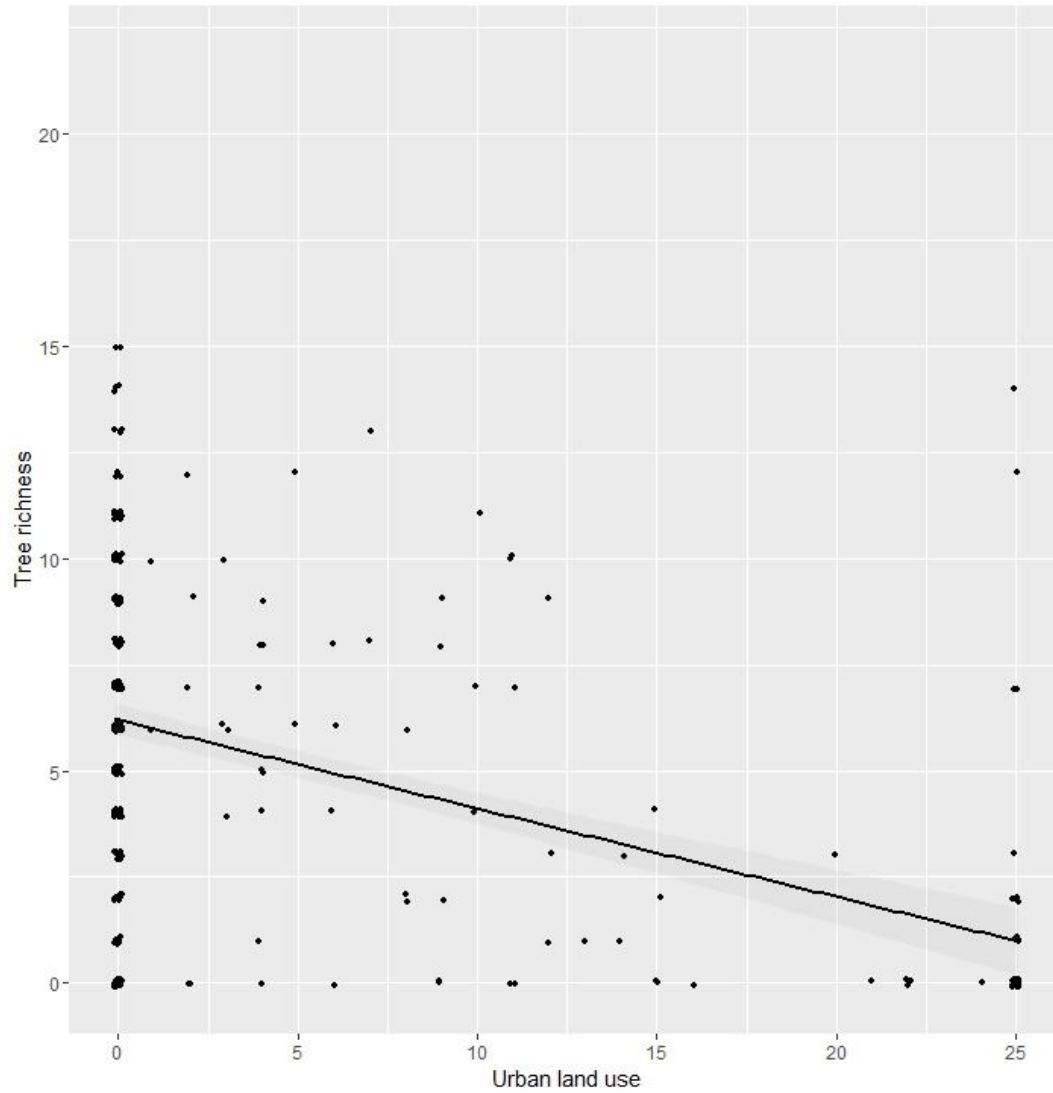
Fig. 2. Canopy tree richness as a function of internal urban cover for U.S. National Park, plot-level data. Tree richness significantly decreased with urban land use. $R^2 = 0.25$
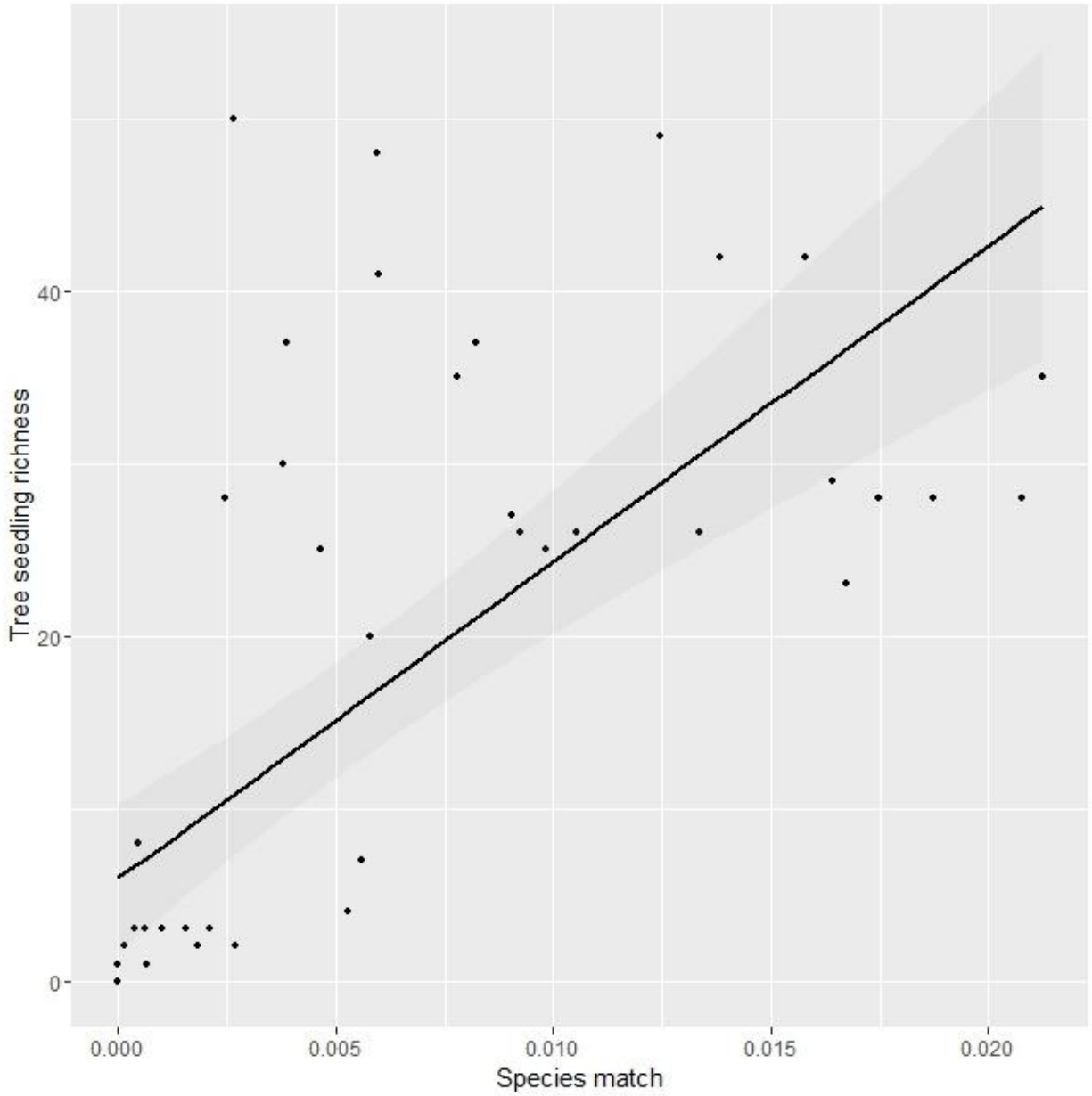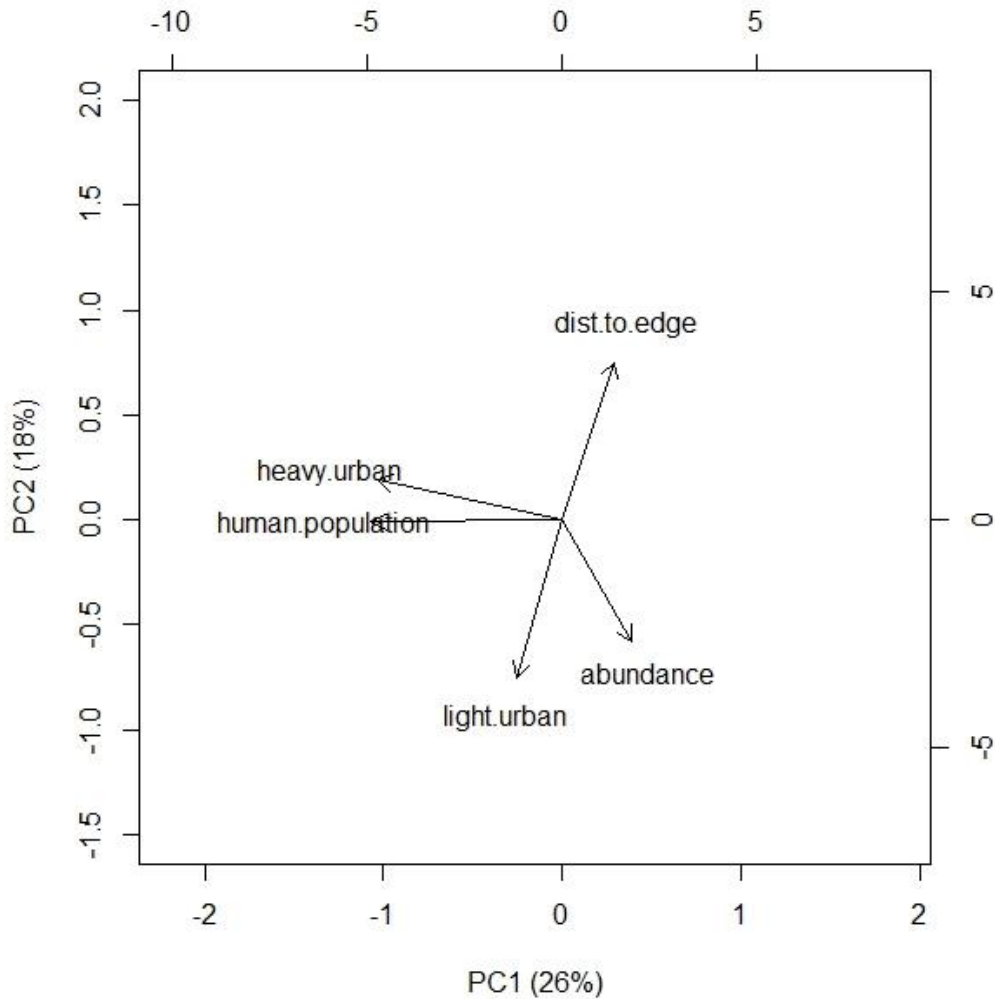
Fig. 3. Tree seedling richness as a function of species match between adult and seedlings. Data is from U.S. National Park, park-level data. Tree seedling richness increased with increasing species match. $R^2 = 0.48$

Fig. 4. Principal component analysis of urban predictors. The biplot represents covariation among tree seedling abundance, internal light urban cover, human population, external heavy urban cover, and distance to edge. A longer line in the biplot indicates greater variation in a component. Lines pointing in the same direction indicate a positive correlation between components, whereas opposite lines indicate a negative correlation. The biplot indicates that seedling abundance negatively covaried with heavy urban cover (i.e. industrial/commercial, residential, pavement) surrounding parks, and negatively covaried with increasing human population density. There was a slight negative covariation between seedling abundance and distance to edge, and a slight positive correlation between seedling abundance and light urban cover (i.e. lawns, other vegetation, agriculture) within parks.
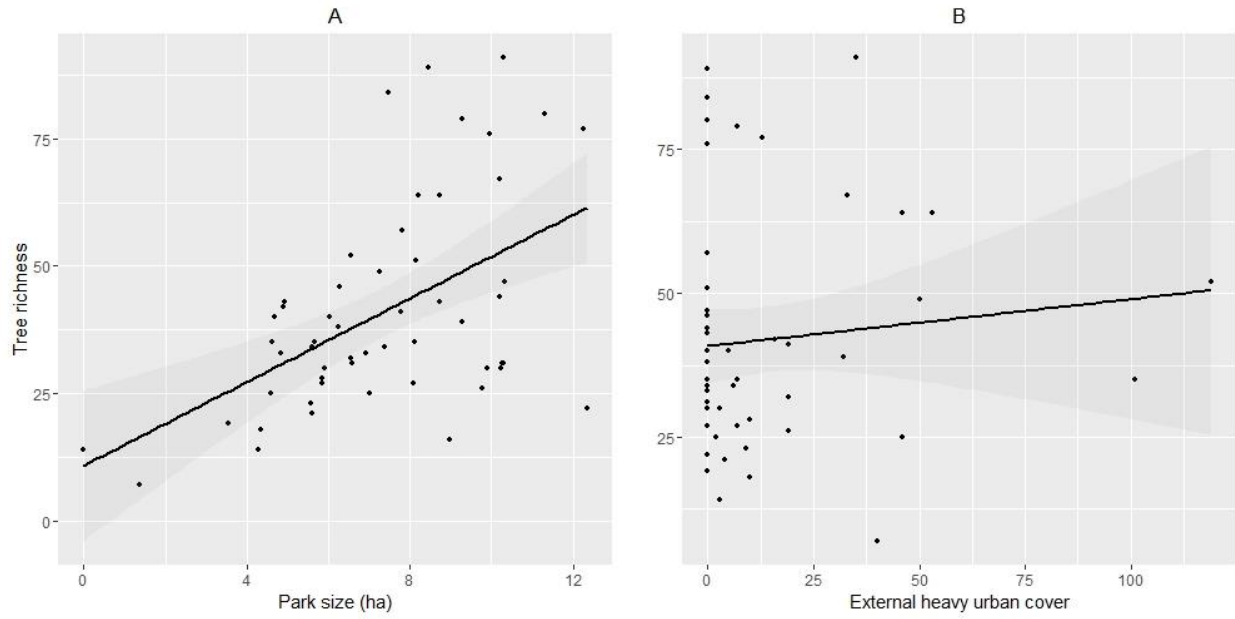
Fig. 5. Tree richness as a function of (a) park size (ha) [significantly increased; $R^2 = 0.25$], and (b) external heavy urban cover [marginally significant increase; $R^2 = 0.01$]. Data is from the U.S. National Park, park-level analysis.
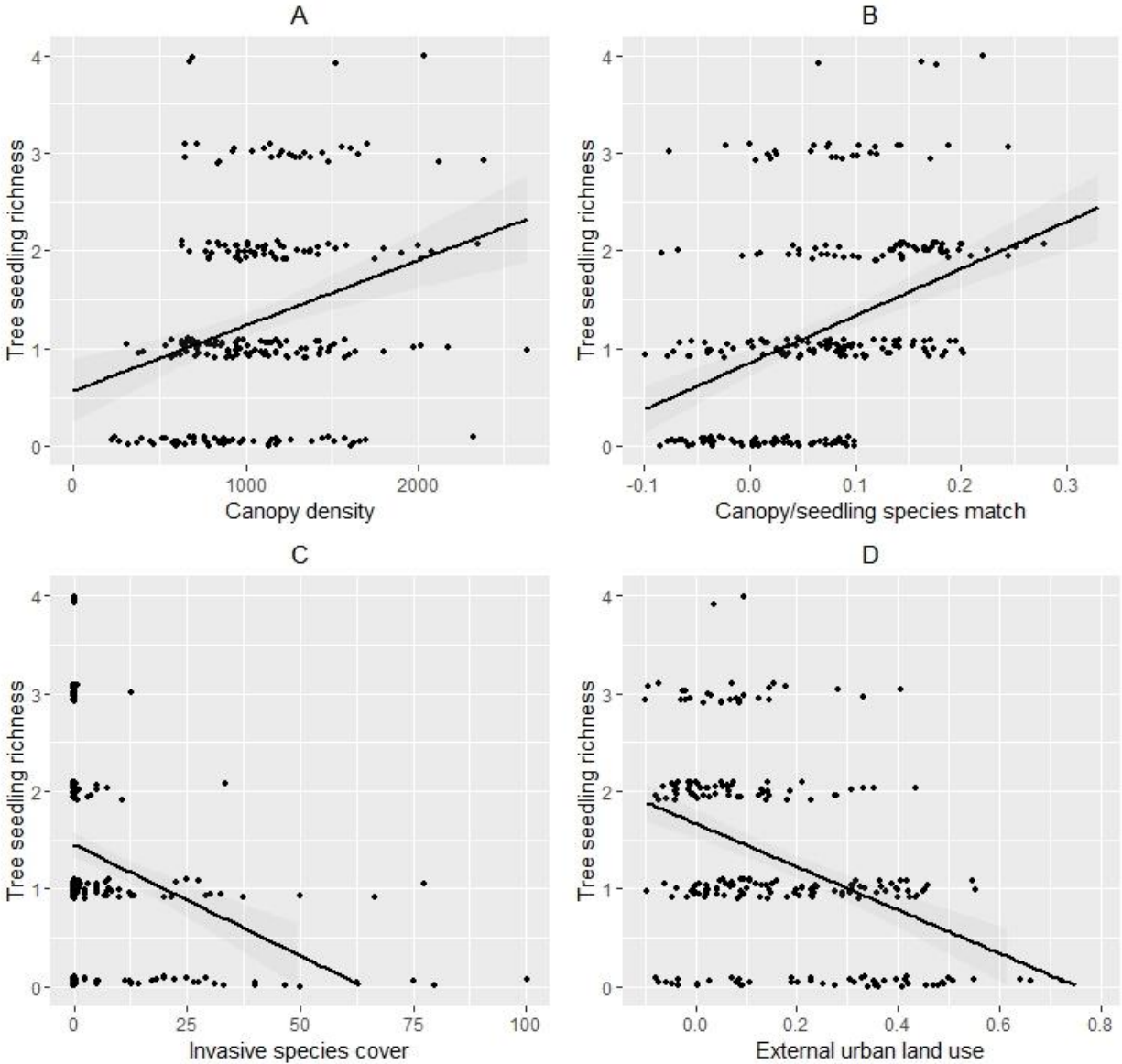
Fig. 6. Multi-panel plot of four predictors of tree seedling richness: (a) seedling richness significantly increased with canopy tree density, $R^2 = 0.11$; (b) seedling richness significantly increased with the proportion of species matches between canopy trees and seedlings, $R^2 = 0.41$; (c) seedling richness significantly decreased with invasive species cover, $R^2 = 0.10$; (d) seedling richness significantly decreased with external heavy urban land use, $R^2 = 0.18$; Data was collected from local field sites around the greater Buffalo, NY (U.S.) metropolitan region. Seedling richness increased with canopy density and species match, whereas richness decreased with invasive species and increased urban land cover. Invasive species cover and urban land use were highly correlated at the plot-level.
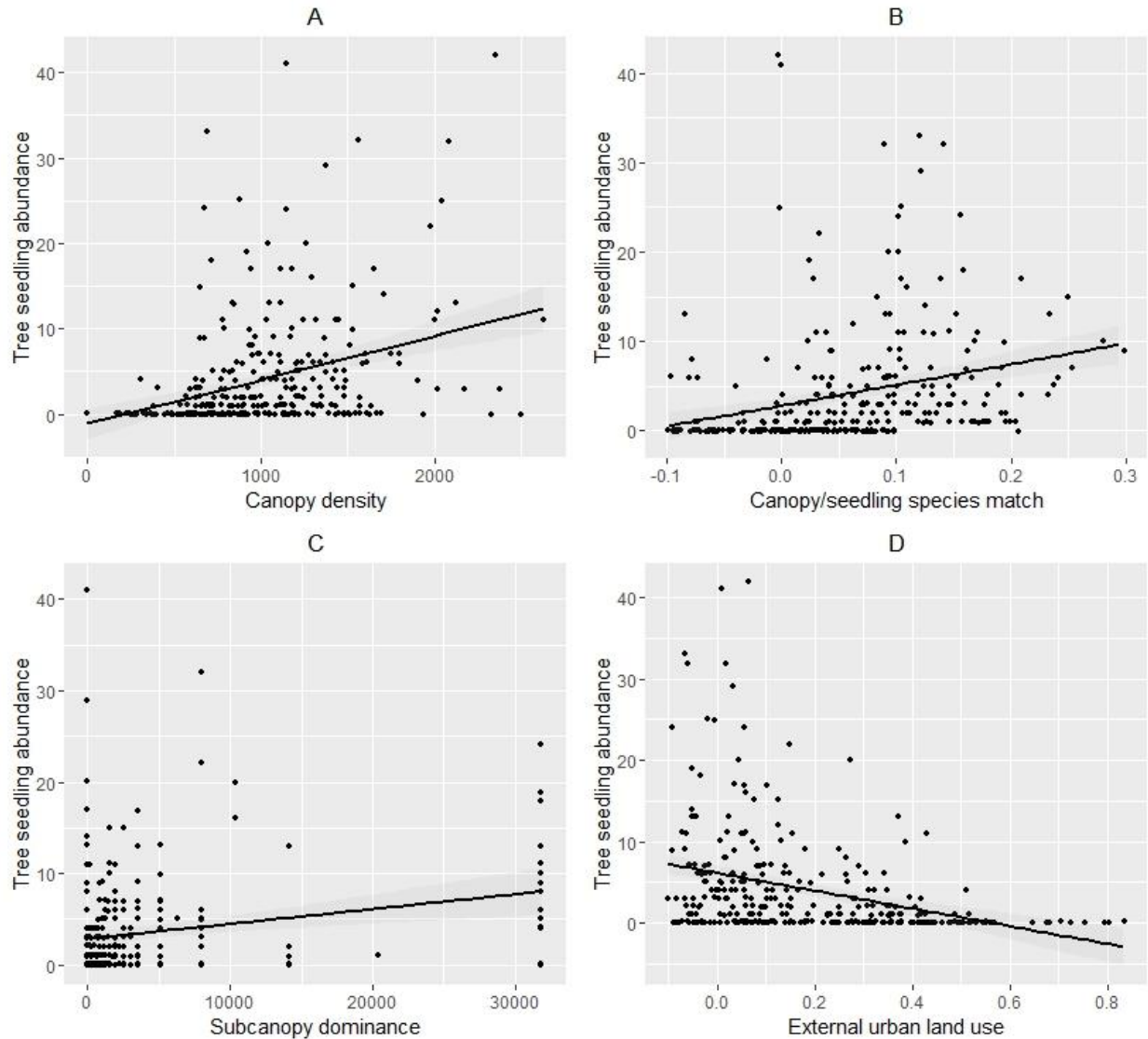
Fig. 7. Multi-panel plot of four predictors of tree seedling abundance: (a) seedling abundance significantly increased with canopy tree density, $R^2 = 0.11$; (b) seedling abundance significantly increased with the proportion of species matches between canopy trees and seedlings, $R^2 = 0.19$; (c) seedling abundance significantly increased with subcanopy dominance, a common measure of basal area per hectare, $R^2 = 0.04$; (d) seedling abundance significantly decreased with external heavy urban land use, $R^2 = 0.12$; Data was collected from local field sites around the greater Buffalo, NY (U.S.) metropolitan region at the plot-level. Seedling abundance increased with canopy density and species match, as well as subcanopy dominance. Urban land use is the only predictor that significantly decreased seedling abundance.
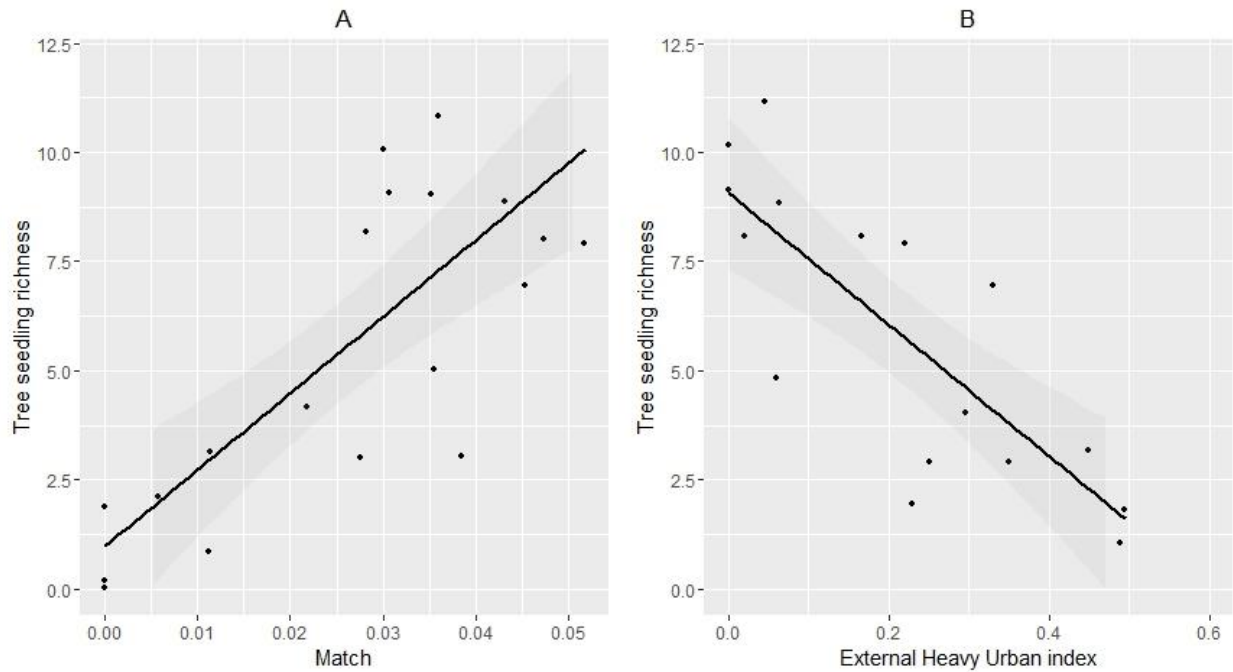
Fig. 8. Tree seedling richness as a function of (a) the proportion of species matches between canopy trees and seedlings (significantly increased; $R^2 = 0.59$), and (b) external heavy urban land use (significantly decreased; $R^2 = 0.74$) at the park-level. Data was collected from local field sites around the greater Buffalo, NY (U.S.) metropolitan region.
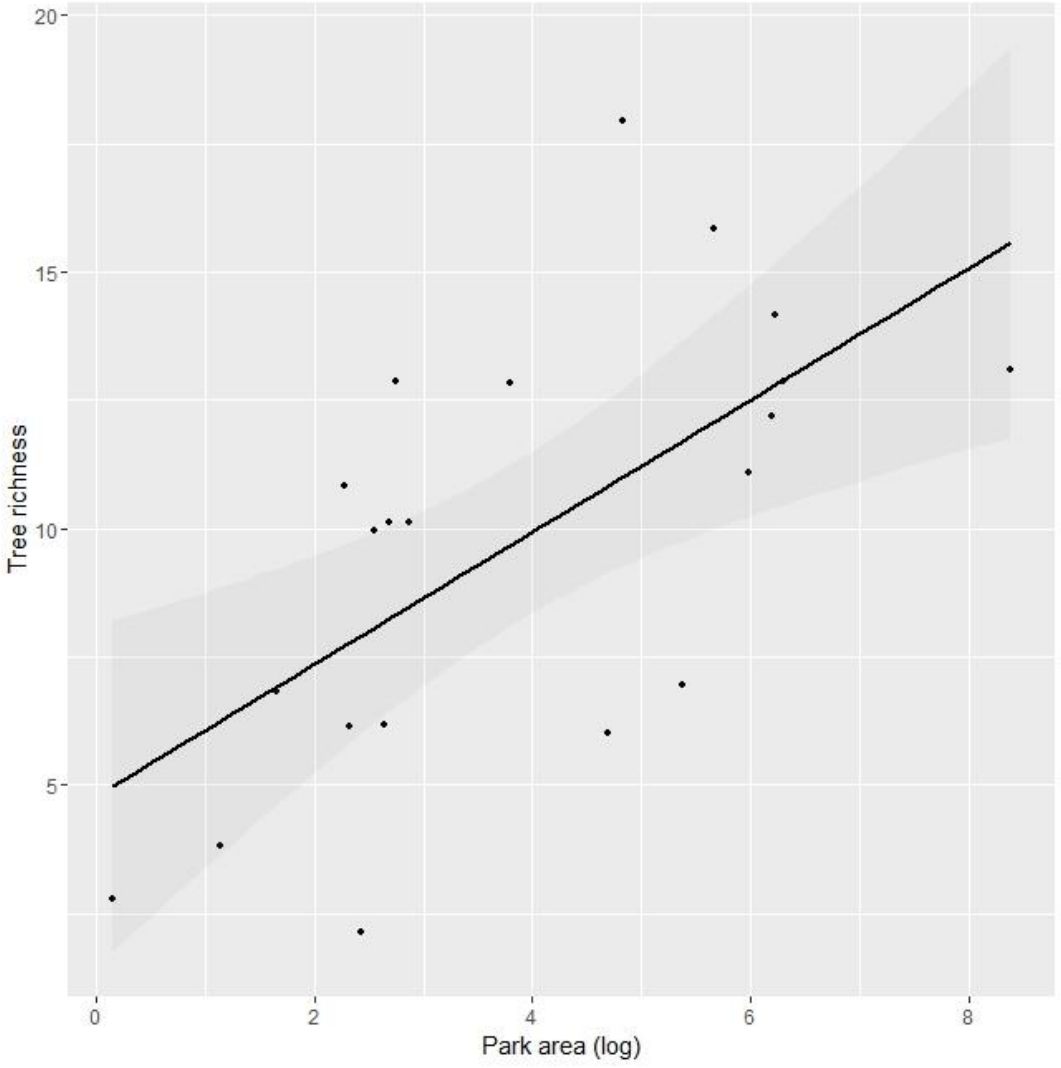
Fig. 9. Tree richness as a function of park area (ha) log transformed, for biogeography measurements at the park-level. Data was collected from local field sites around the greater Buffalo, NY (U.S.) metropolitan region. $R^2 = 0.36$
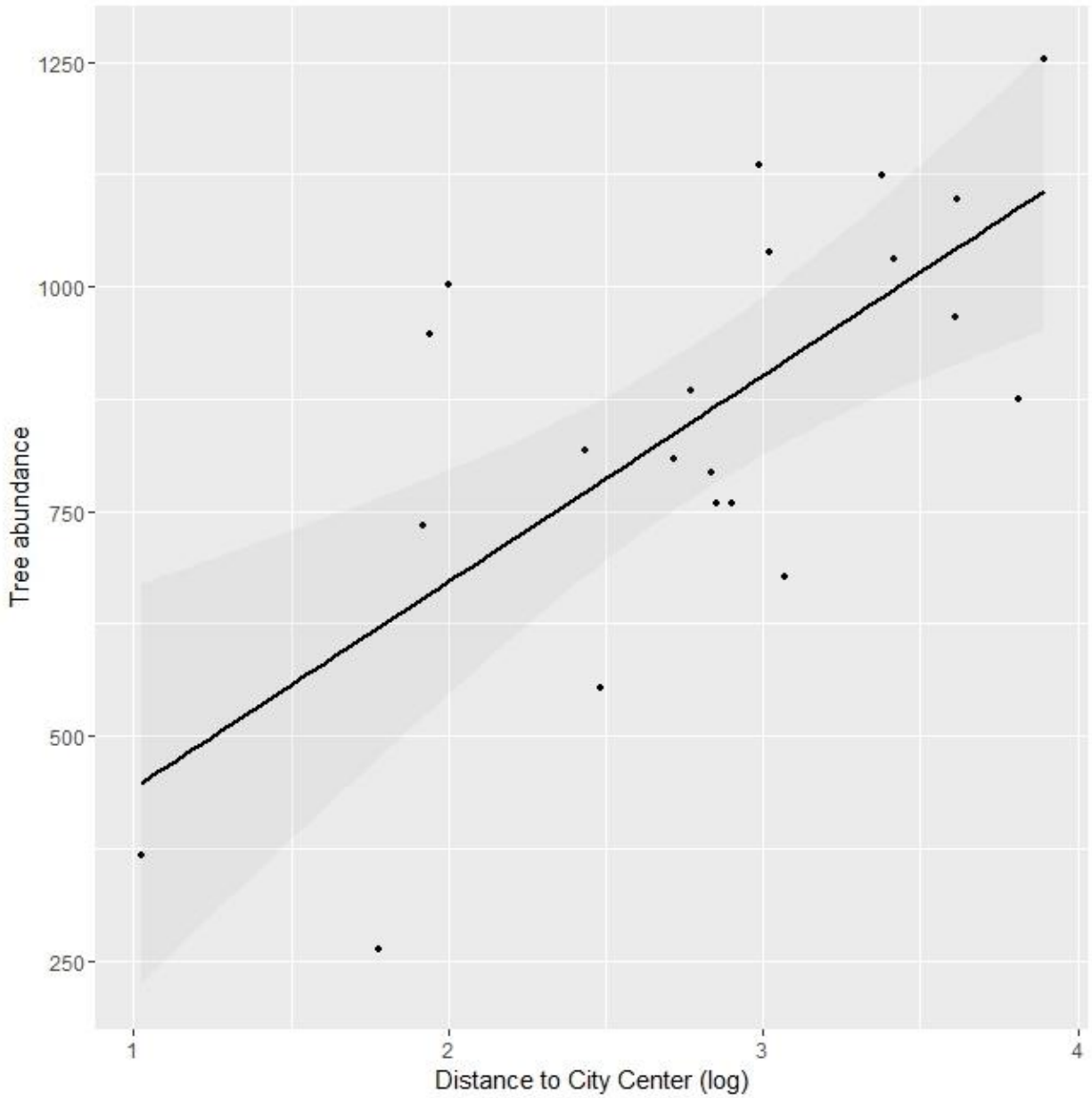
Fig. 10. Tree abundance as a function of distance (km) from the city center of Buffalo, NY (log transformed) for biogeography measurements at the park-level. Data was collected from local field sites around the greater Buffalo, NY (U.S.) metropolitan region. $R^2 = 0.44$