

Urban forests form isolated archipelagos

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Submitted: 1 November 2017; Received (in revised form): 18 March 2018; Accepted: 22 March 2018

Abstract

Urbanization decreases native species diversity by converting natural landscapes to anthropogenic cityscapes, and it indirectly degrades native species diversity in remaining natural patches by fragmenting and isolating them. Remnant forest patches embedded in an urban matrix may act as ‘islands’ separated from large populations of trees in rural ‘mainland’ forests. As such, native species richness should increase with forest patch size within the urban landscape and increased connectivity to other urban forest patches and rural forests. Our objective was to link urban land cover with forest patch richness and recruitment. We used U.S. National Park Service (NPS) data from parks in the Eastern USA to examine forest patchiness and connectivity in relatively large, intact landscapes. We applied a similar approach to field data collected along an urban–rural gradient in Western New York (WNY). We predicted that urban forest patches are isolated habitats with tree seedling and canopy richness driven by patch size and connectivity with surrounding forest patches. The WNY forest patches were surrounded by much less forest cover compared to NPS forests, and native tree species richness and abundance were negatively impacted by urban land cover. In all parks, we found increased tree seedling richness with park area, and decreasing species richness with the incursion of non-native species. Urban land-limited forest patch connectivity, particularly with rural forests, and the patches were increasingly limited to bird- and wind-dispersed trees with distance from rural areas. Our data support a conceptual model of urban forest patches behaving as island archipelagos in an anthropogenic ocean of less suitable habitat.

Key words: archipelagos, dispersal limitation, forest fragmentation, island biogeography, tree recruitment

Introduction

Urbanization generally coincides with decreases in native species diversity and abundance with the conversion of natural landscapes to anthropogenic cityscapes (Falcucci, Maiorano, and Boitani 2007; McKinney 2008) and the resulting fragmentation and degradation of remaining less-disturbed habitats (Gibbs 1998; McKinney 2002; Vila and Ibanez 2011; Brearly et al. 2012). In temperate forest biomes, spontaneous and remnant forest patches embedded in an urban matrix may be thus imagined as ‘islands’ separated from large populations of trees in rural ‘mainland’ forests. As such, 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 1993). According to island

biogeography, species richness tends to increase with island size and decrease with distance from mainland source populations. In the urban ecology subdiscipline, these concepts often are embedded in the concepts of ‘patch size’ and ‘connectivity’. Hence, species richness should increase with forest patch size within the urban landscape and increased connectivity to other urban forest patches and rural forests.

Tree seedling recruitment (seedling establishment) is a key indicator of forest demography (Grubb 1977; Eriksson and Ehrlén 1992; Clark, Macklin, and Wood 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, Macklin, and Wood 1998), and seedlings can determine plant population dynamics and community composition (Clark et al. 2007; Warren

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and Bradford 2011; Oldfield et al. 2013). Tree seedlings may establish in urban forests from local canopy trees (Runkle 2000) or through long-distance dispersal from other forests (Clark, Macklin, and Wood 1998). However, long-distance dispersal may be uncommon for many tree species in urban environments unless facilitated by forest management practices such as tree planting (Labatore et al. 2017). Whereas trees within an urban landscape may produce seeds, and seeds may arrive from afar, few opportunities exist for successful tree seedling recruitment with most urban land use (Oldfield et al. 2013). As such, relatively intact forest patches may act as woodland islands within a sea of urbanization, and tree species richness should increase with forest patch size and connectedness with other patches and peripheral rural forests. Urbanization not only alters and isolates forest habitat, but it also appears to degrade persistent forest patches by facilitating the establishment of non-native species (Holway and Suarez 2006; McKinney 2006). Urban population centers may be sources for non-native species while urbanization causes increasing fragmentation of remaining forest patches further promoting non-native incursions (McKinney 2006; La Paix and Freedman 2010; Vila and Ibanez 2011).

The detrimental effects of urbanization on native species, habitat quality and biodiversity are well studied (Brooks and Rowntree 1984; Jim 1998; Pickett et al. 2001; McKinney 2006; Pouyat et al. 2007), but the successional trajectories of spontaneous and remnant urban forests fragments, and the ecological linkages urban forest fragments and the surrounding city share are less well characterized (Labatore et al. 2017). Whereas some sources consider all trees in an anthropogenic landscape an 'urban forest', and urban forestry often is considered the planning and development of recreational areas for humans to maximize the use of resources and amenities while reducing environmental impacts (Pickett et al. 2001), in this paper, we focus on urban forest patches as our unit of analysis.

Our objective was to link urban land cover with urban forest tree recruitment and species richness. Our hypothesis was that urban forests are poorly linked with contiguous forest systems and instead form isolated archipelagos in an anthropogenic landscape. We first analyzed publicly available data for canopy and tree seedling abundance and richness in U.S. National Park Service (NPS) lands to establish a 'baseline' for forest patchiness and connectivity as functions of land cover in relatively large, intact landscapes. We then 'ground-truthed' those data using field data collected along an urban-rural gradient in Western New York (WNY) State (USA). If urban forests are poorly linked with contiguous forest systems, we expected that adjacent urban land use would exhibit relatively greater negative impacts on native tree richness and abundance in urban forests relative to more intact systems. Moreover, if urban forests are isolated habitats in urban landscapes, we predicted that decreased patch size would correspond with decreased native tree seedling and canopy richness and abundance—any decreases offset by increased connectedness with other forested patches. Finally, if urban forests are isolated habitats in urban landscapes, we predicted that they would contain relatively more bird- and wind-dispersed trees given that these dispersal modes can transcend spatial boundaries.

Methods

Urban land cover

We classified land cover surrounding the NPS and WNY study areas using digital satellite maps by randomly selecting eight

survey plots 1 km outside of the park boundaries in eight cardinal and inter-cardinal directions. Each survey plot had a circular area of 100 m² and was created using Google Earth Pro (v7.1) and converted into shapefiles (Zonum Solutions; <http://www.zonums.com/online/kml2shp.php>). Shapefiles were uploaded into i-Tree Canopy (<http://www.itreetools.org/canopy/index.php>), which was used to generate 25 random points in each 100 m² plot at which land cover was observed and classified. Seven parameters were used to define land cover: (1) tree cover ('trees') as an obvious indicator, (2) turf, such as lawns, golf courses and sports fields ('turf') that deters tree recruitment (Bryant 2006; De Chant et al. 2010), (3) disturbed shrub and herbaceous plant cover ('field') that may inhibit tree colonization (Sullivan et al. 2009; Labatore et al. 2017), (4) residential clusters like suburban or apartment housing ('residential') that interrupt reproduction or successful juvenile tree growth (Luck and Wu 2002; Bryant 2006), (5) industrial and commercial properties ('industry') that 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 2006), (6) agriculture fields ('agriculture') that may allow limited recruitment, but generally limit species diversity (Hendrickx et al. 2007; Vellend et al. 2007; Gámez-Virués et al. 2015) and (7) roads, parking lots and impermeable surfaces ('paved') that provide no suitable habitat.

Given that urbanization often is defined by human population density (McDonnell et al. 1997; Theobald 2001; Wandl et al. 2014), and in order to justify our urban land cover parameters, we calculated population density (census tract population · census tract area⁻¹) for each census tract in which plots (NPS and WNY) were located using 2010 U.S. Census data (Census 2010).

U.S. National Park data

We used U.S. National Park data (NPS) to provide a 'baseline' for relatively intact/contiguous eastern deciduous forest response to urbanization, population and non-native species. NPS forest data were compiled from U.S. NPS vegetation surveys in the late 1990s/early 2000s (<http://science.nature.nps.gov/im/inventory/veg/products.cfm>) from 2752 plots 20 × 20 m (400 m²) in size located in 48 urban and rural parks across the Eastern USA (Supplementary Fig. S1a). Data used from these surveys were native canopy tree seedling cover (%) and richness, native canopy tree cover (%) and richness, and non-native herbaceous-layer cover (%).

Western New York forest patch data

We further investigated the impact of urban patch size and connectedness on urban forest recruitment and native richness by establishing plots in spontaneous and remnant forest patches in the WNY region (USA). We defined a forest patch as a tree-dominated, closed canopy stand where tree seedling recruitment could occur (i.e., unmowed/unmanaged understory). In May–August 2015, we conducted urban forest field surveys along three transects in WNY, each beginning at Buffalo's city center (42.88666 N, 78.87936 W). The WNY transects ended at 'rural' points where the habitat reflected a generally continuous mix of forest and agriculture. 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. The transect bearings were selected to sample different portions of the urban landscape and capture forest patches. We sampled all publicly accessible (n = 21) forest

patches along these transects on local, county and state-owned lands from the city center to rural areas outside of the city (Supplementary Fig. S1b). We surveyed the WNY sites in a random order to eliminate temporal bias along the transects.

We assigned the number of survey plots in each forest patch according to forest patch area (1 plot per patch ha, max = 20 plots per patch; $n = 302$ plots across 21 forests). To estimate native tree species richness and density, we sampled tree canopy (DBH > 10 cm) and sub-canopy (DBH < 10 cm) species using the point-centered quarter (PCQ) method (Dix 1961). We sampled tree seedling and sapling abundance by species, total herbaceous percent cover and non-native species percent cover within two quadrats per plot. Each quadrat was 1 m², located 5 m west and 5 m east of the PCQ center point. Quadrats that fell on unmeasurable land (e.g., obstructed by an object such as a fallen tree) were placed an additional 5 m farther in the same direction. In addition, we measured percent of woody shrub canopy cover by species using the line intercept method (Canfield 1941). A transect spanned 10 m from the center of each quadrat, and shrub canopies intersecting the line were measured according to species for canopies > 1 m tall.

In order to investigate potential regional connectivity between forest patches and biogeography, we measured forest area (ha), distance to city center and distance to nearest forested neighbor using Google Earth Pro v7.1. We identified tree species with wind- (anemochory) and bird- (endozoochory) dispersed seeds using the Royal Botanical Gardens KEW Seed Information Database (SID 2008).

Data analysis

Principal components analysis

We used principal component analysis (PCA) to examine variation among native tree seedling richness and cover (%), native tree canopy richness and cover (%), population density (population · m⁻²) and land cover (%) for field, agriculture, paved, residential and industry categories for NPS (Supplementary Fig. S2a) and WNY (Supplementary Fig. S2b) data. We used the 'prcomp' method and 'scale' option (standardizes all variables to unit length) in the R statistical package (R Core Team Version 3.3.2 2016). We used the PCA analyses to assess how the estimated land-cover types covaried with each other and the direct field measurements. We used the covariation patterns to compile some of the land-use proxies as independent variables for hypothesis testing and to reduce potential overparameterization.

National Park Service and Western New York patch data

We examined NPS and WNY forest parameters (tree seedling abundance, tree seedling richness and canopy tree richness) with regression models in the R statistical program (R Core Team Version 3.3.2 2016). For both NPS and WNY studies, plot-level data was aggregated by mean patch values for analysis. We evaluated tree seedling cover and richness as functions of non-native species cover, urban and open land cover, and park area. We evaluated species richness using generalized linear models (GLMs) assuming a Poisson error distribution and abundance using a linear model assuming a Gaussian error distribution. We evaluated canopy tree richness as a function of urban and open land cover and park area with a GLM assuming a Poisson error distribution. In all models, parameters were reduced from the full model if $\Delta AIC > 2.0$. We included *a priori* patch size (park area) × connectivity (urban and open), and park area × non-native species interaction terms, but removed them if not statistically significant. We also investigated WNY forest

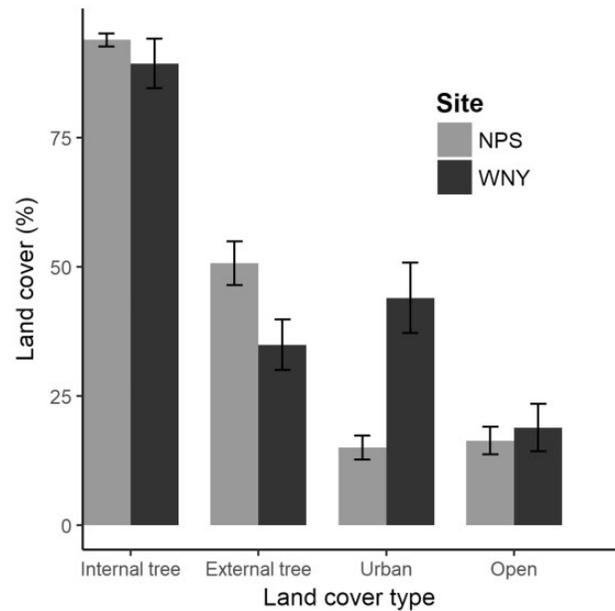


Figure 1: Mean (\pm SE) land cover (%) for U.S. NPS and WNY forested parks and patches. Tree cover is given for the landscape inside the forested parks and patches (internal tree) as well as for the landscapes immediately outside the forested parks and patches (external tree). External land cover includes residential, industry and paved (urban), and agriculture and fields (open).

patch biogeography using GLMs for tree seedling and canopy tree richness (Poisson error), and a linear model for dispersal mode (Gaussian error), as functions of forest patch area, nearest forest neighbor, nearest forest neighbor patch size and distance to rural forests.

In all regression models, potential collinearity between predictor variables was evaluated using variance inflation factors generated in the (*car*) package (Fox and Weisberg 2011). The variance inflation factors for the predictor variables all were < 2.0, indicating they independently predicted variance, except where noted above. We applied a quasi-Poisson error distribution when the data were over-dispersed ($\phi > 2.0$).

Results

Tree cover was similar inside both U.S. National Parks and WNY parks (89–94%; Fig. 1) as was open habitat (field and agriculture) adjacent to the parks (16–19%). Tree cover surrounding the parks was higher in NPS (51%) compared to WNY (35%), and urban land cover surrounding the parks was higher in WNY (44%) compared to NPS (15%). The most common tree seedling and canopy species at all sites was *Acer rubrum*, and it dominated the WNY canopy in particular (Supplementary Fig. S2). In general, the most common NPS and WNY tree seedlings and canopy are similar, except that more than half the WNY plots contain the early successional *Populus deltoides* in the canopy, but its seedlings are not common. Moreover, WNY forest patches were dominated by wind-dispersed trees whereas the NPS forests include more animal-dispersed trees, particularly *Quercus* species.

Principal components analysis

PCA analysis of NPS variables (Supplementary Table S3a) indicated that the PC1 axis explained 37% of the covariation and included a negative relationship between 'urban' parameters

(population, industry, residential, paved) and 'open' parameters (field, agriculture). Seedling and canopy tree richness also covaried with the open parameters. The PC2 axis explained 20% of the covariation and included a negative relationship between the richness variables and canopy cover. PCA analysis of WNY variables (Supplementary Table S3b) indicated that the PC1 axis explained 53% of the covariation and included a negative relationship between 'urban' parameters (population, industry, residential, paved) and 'open' parameters (field, agriculture). Seedling abundance and richness also covaried with the open parameters. The PC2 axis explained 18% of the covariation and included a negative relationship between industry and canopy cover. Based on similar covariation patterns in the PCA, we combined industry, residential and paved into an 'urban' parameter and field and agriculture into an 'open' parameter for hypothesis testing in regression models.

U.S. National Park data

The best-fit model for NPS tree seedling abundance only included open habitat, and tree seedling abundance declined with increased open habitat (Table 1a). The best-fit tree seedling richness model included non-native cover, urban land cover, open habitat and park area. Seedling richness declined with open habitat (Table 1b, Fig. 2A), and a significant interaction term indicated that seedling richness decreased with non-native species cover and increased with park area, but increased less with park area where non-native species were most abundant (Fig. 2B). The best fit for canopy tree richness included urban land cover, open habitat and park area, and canopy tree richness increased with park area (Table 1c, Fig. 3A).

Western New York patch data

The best-fit model for WNY tree seedling abundance included non-native cover, urban land cover and park area, and seedling abundance decreased with urban land cover (Table 2a, Fig. 4A). The best-fit model for seedling richness also non-native cover, urban land cover and park area, and seedling richness also decreased with urban land cover (Table 2b, Fig. 4B). Tree seedling richness also decreased with non-native species and increased with park area (Table 2b). The best-fit canopy tree richness model only included park area, and richness increased with park area (Table 2c, Fig. 3B).

We used biogeographic parameters to further analyze the forest patches in the context of greater metropolitan land cover patterns. The best-fit model for tree seedling richness retained distance from nearest forest patch and distance from rural forests. Tree seedling richness decreased with distance to the nearest patch (Table 3a, Fig. 5A) and with distance from rural forests (Fig. 5B). The best-fit canopy tree richness model retained nearest forest patch area and distance from the nearest forest patch. Tree richness decreased with the distance from the nearest forest patch (Table 3b, Fig. 5C). The best-fit model for the percent of trees dispersed by wind and birds only retained the distance from rural forests, and wind- and bird-dispersed trees species increased with distance to rural forests (Table 3c, Fig. 5D).

Discussion

Our data support a conceptual model of urban forest patches behaving as island archipelagos in an anthropogenic ocean of less suitable habitat. In the NPS and WNY data sets, tree

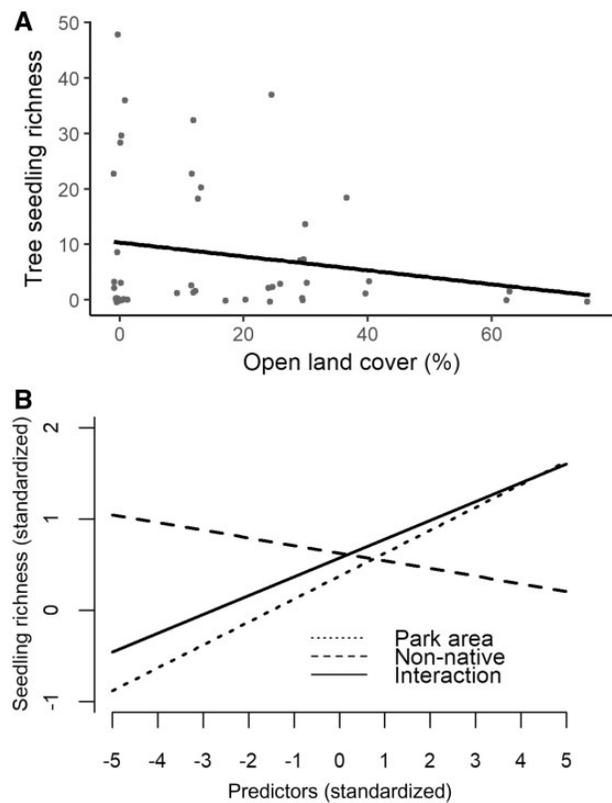


Figure 2: (A) U.S. NPS tree seedling richness in park forests as a function of open land cover (field and agriculture) surrounding the parks. (B) Interaction plot indicating that tree seedling richness decreased with non-native species cover and increased with park area, but increased less with park area where non-native species were most abundant.

seedling richness increased with park area and decreased with the incursion of non-native species. Further supporting the archipelago model was evidence that urban land use segregates the forest patches. Akin to classic island biogeography theory, with more contiguous rural forests representing a mainland, tree seedling richness in urban forest patches increased with proximity to neighboring forest patches and rural forests, and canopy tree richness increased with proximity to rural forests.

Urbanness has been defined by human population density and land cover classifications, but these proxies alone often do not provide clear links to ecological function (Pickett et al. 2001; Theobald 2001; Wandl et al. 2014), and human population density decreases in habitats both suitable and unsuitable for native communities (Warren et al. 2018). We used native tree seedling richness as an indicator of recruitment (e.g., regeneration potential) and native canopy tree richness as an indicator of community intactness. We linked these indicators with land cover categories and used principles from classic island biogeography theory to test our hypothesis that urban forests are poorly linked with contiguous forest systems and form isolated archipelagos in an anthropogenic landscape. In WNY forest patches, tree seedling richness increased with proximity to the nearest forest patch and with proximity to rural forests. Tree canopy richness also increased with proximity to rural forests. These findings are consistent with expectations from island biogeography if the forest patches act as 'archipelagos' and rural forests as a 'mainland' seed source. These results suggest that urban forest islands form an archipelago of loosely connected islands in an ocean of urbanized landscape.

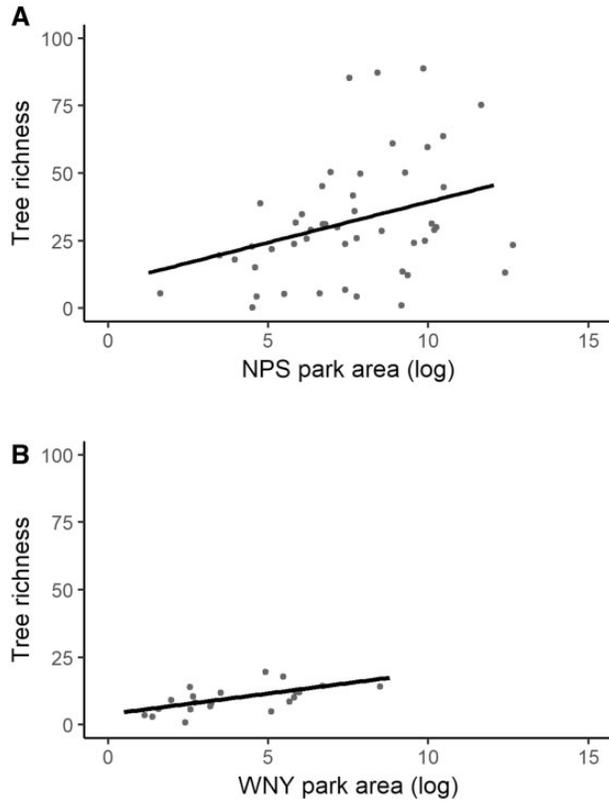


Figure 3: Canopy tree species richness increased with area in U.S. NPS parks (A) and WNY (B) forest patches.

Table 1: U.S. National Park data for (a) tree seedling abundance (% cover; Gaussian), (b) tree seedling richness (quasi-Poisson) and (c) canopy tree richness (quasi-Poisson)

	Coefficient	SE	Test stat.	P-value
a. Tree seedling abundance				
Open habitat	0.855	0.214	3.981	<0.001
b. Tree seedling richness				
Nonnative	-1.314	0.478	-2.753	0.009
Urban	0.014	0.012	1.112	0.274
Open habitat	-0.033	0.017	-1.867	0.071
Park area	-0.195	0.152	-1.283	0.208
Nonnative × park area	0.158	0.056	2.819	0.008
c. Canopy tree richness				
Urban land use	0.003	0.0	0.6	0.533
Open habitat	-0.009	0.005	-1.679	0.100
Park area	0.111	0.041	2.688	0.010

Predictor variables were herbaceous-layer nonnative species (% nonnative species cover), urban land use adjacent to park (% urban), field and agriculture land use adjacent to park (% open) and park area (log ha, park area). AIC was used to select reduced best-fit models from the full models (all predictor variables) with best-fit coefficients shown.

We assumed that urbanization fragments suitable habitat for native tree species, and hence the focus on island biogeography, but fragmentation may be considered a process of both habitat loss and subsequent sectioning of remaining habitat (Fahrig 2003). Indeed, some question the island/sea analogy for a fragmented landscape (Haila 2002). We found that the urban landscape specifically filters tree species by dispersal ability. Urban forest patches increasingly contained greater proportions

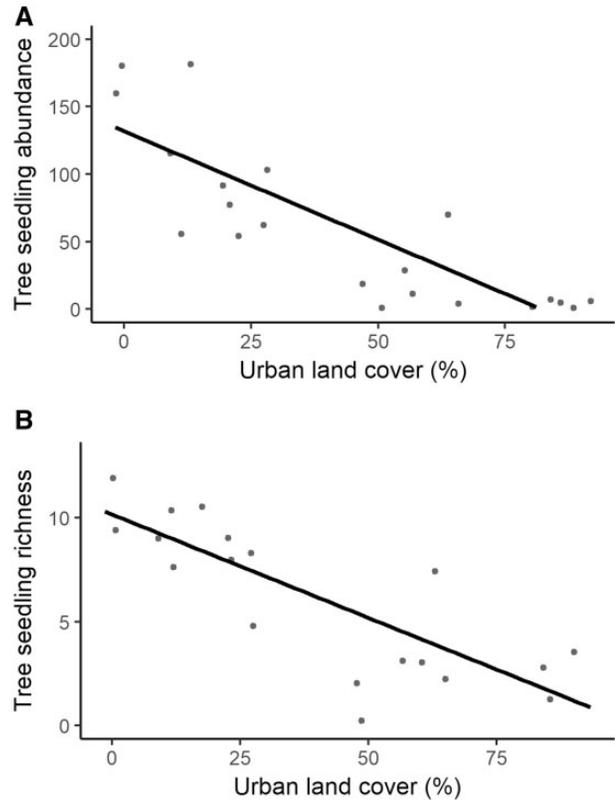


Figure 4: Tree seedling abundance (A) and richness (B) decreased with urban land cover surrounding WNY forest patches.

Table 2: WNY (USA) data for (a) tree seedling abundance (% cover; Gaussian), (b) tree seedling richness (Poisson) and (c) canopy tree richness (quasi-Poisson)

	Coefficient	SE	Test stat.	P-value
a. Tree seedling abundance				
Non-native	-0.961	0.992	-0.969	0.346
Urban	-1.370	0.382	-3.581	0.002
Park area	1.781	5.413	0.329	0.746
b. Tree seedling richness				
Non-native	-0.033	0.017	-1.866	0.062
Urban	-0.015	0.005	-2.845	0.004
Park area	0.014	0.063	0.221	0.082
c. Canopy tree richness				
Park area	0.129	0.034	3.785	<0.001

Predictor variables were herbaceous-layer nonnative species (% nonnative species cover), urban land use adjacent to park (% urban), field and agriculture land use adjacent to park (% open) and park area (log ha, park area). AIC was used to select reduced best-fit models from the full models (all predictor variables) with best-fit coefficients shown.

of wind- and bird-dispersed tree species (e.g., *P. deltooides*, *Fraxinus pennsylvanica*) with distance from rural forests, suggesting that dispersal-limited plants did not successfully cross the fragmented urbanized landscape and unsuitable habitat within. However, these results may also indicate a degradation of forest patches whereby progressively degraded natural forests patches become less resistant to ‘weedy’ incoming seeds (Cadenasso and Pickett 2001). Whereas park area consistently coincided with higher native tree species richness in NPS and WNY parks, the NPS parks were much larger and more diverse than the

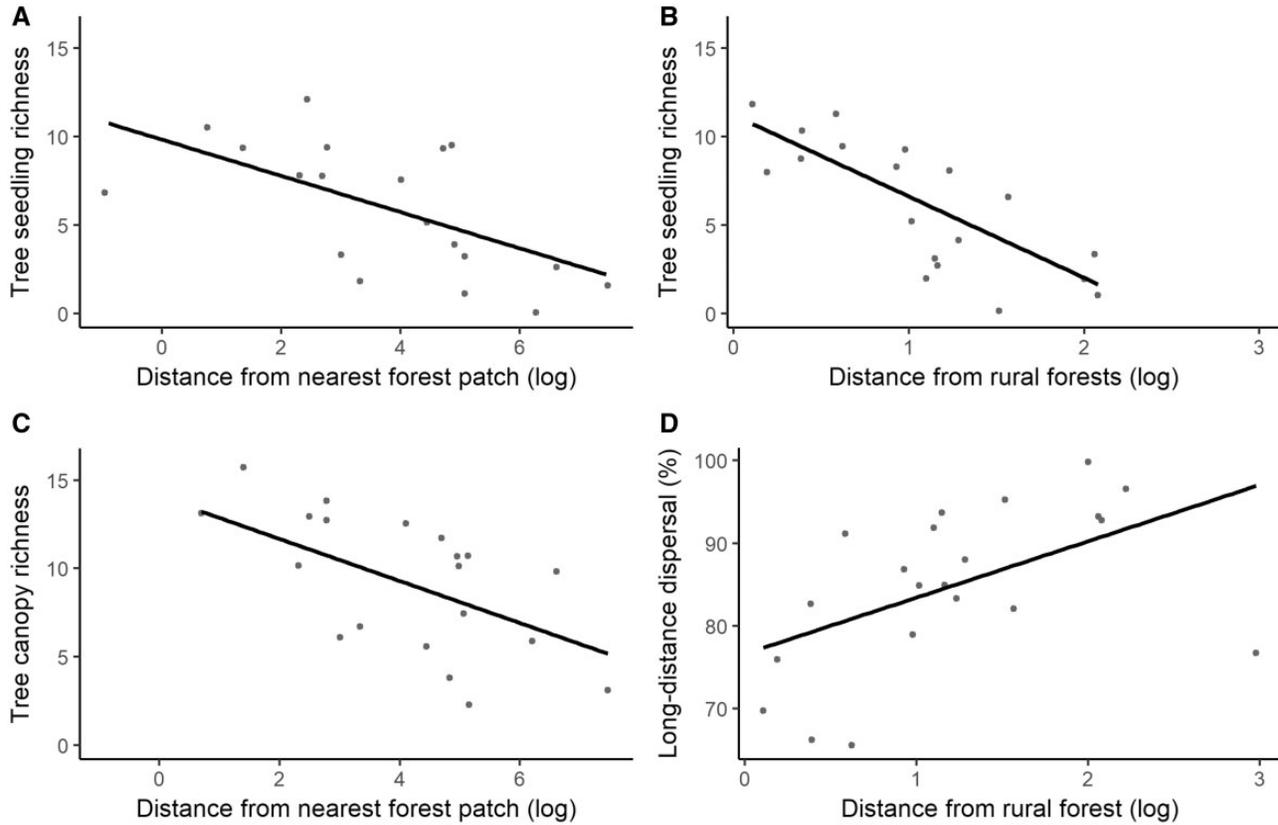


Figure 5: Scatterplots for WNY urban forest patch seedling richness as a function of the distance from the nearest urban forest patch (A) and the distance from rural forests (B), and scatterplots of canopy tree richness with distance from the nearest forest patch (C) and the percent of wind- and bird-dispersed trees with distance from rural forests (D).

Table 3: WNY (USA) data from forested urban patches in the greater Buffalo, NY metropolitan area (USA) for (a) tree seedling richness (Poisson), (b) canopy tree richness (Poisson) and (c) the percent of forest trees dispersed by wind and birds (Gaussian)

	Coefficient	SE	Test stat.	P-value
a. Tree seedling richness				
			z-value	
Distance from nearest forest patch	-0.110	0.057	-1.919	0.055
Distance from rural forests	-0.866	0.174	-4.974	<0.001
b. Canopy tree richness				
			z-value	
Nearest forest patch area	0.064	0.044	1.457	0.145
Distance from nearest forest patch	-0.12	0.036	-3.278	0.001
c. Dispersed by wind and birds				
			t-value	
Distance from rural forests	6.805	2.640	2.578	0.018

WNY parks. The NPS parks were surrounded by much greater forest cover and much less urban land cover and human population density. The negative effects of urban land use on native tree species richness and abundance may be directly attributable to landscape fragmentation and associated deleterious impacts on forest function (Brooks and Rowntree 1984; Jim 1998; Pickett et al. 2001; McKinney 2006; Pouyat et al. 2007). Fragmented forest patches may lack native tree propagule immigration and instead receive copious input from non-native, edge-adapted species, thus limiting the likelihood of the recruitment and regeneration of native tree species.

Native habitat fragmentation not only decreases the abiotic suitability of altered habitat, but it also promotes native and

non-native species that can negatively impact native species richness. We found that urban land cover correlated with higher population density, and human population often corresponds with greater non-native abundance and richness (Pysek et al. 2010; Spear et al. 2013), likely because humans both transport non-native species and create altered habitat conducive for their establishment and capability to spread. Non-native species also limit habitat availability for tree seedlings by filling in canopy gaps or inhibiting germination (Klionsky, Amatangelo, and Waller 2011; Labatore et al. 2017). We found that non-native species negatively corresponded with tree seedling richness (they interact in the herbaceous layer of the forest understory) in both NPS and WNY parks, but urban land cover only negatively impacted the WNY parks. Non-native species respond positively to disturbance, particularly tree canopy disturbance (Byers 2002; Chytry et al. 2008; Warren, Potts, and Frothingham 2015), and fragmentation increases edge habitat which often harbors non-native plant reservoirs (Lockwood, Cassey, and Blackburn 2005; Von Holle and Simberloff 2005; Warren et al. 2013). In addition to promoting non-native plant species, urban landscapes may promote herbivore abundance further impacting urban forest patches (Klionsky, Amatangelo, and Waller 2011; Oldfield et al. 2015; Labatore et al. 2017). Granivorous herbivores limit seed recruitment (Côté, Ferron, and Gagnon 2003) and browsing herbivores curb seedling establishment (Salk et al. 2011; Nuttle et al. 2013), thereby greatly restricting canopy tree regeneration (Labatore et al. 2017). Abundant herbivores generally have the greatest impact on forest patches in fragmented urban areas (Barrett and Stiling 2006; Urbanek and Nielsen 2013).

Urban fragmentation reduces suitable habitat for native trees and breaks up connectivity between forest patches (Brooks and Rowntree 1984; Cordeiro et al. 2009; Sullivan et al. 2009). The effects of fragmentation may be blurred between habitat isolation and habitat loss/degradation, as we noted here, but the island biogeography model holds up for native species if we expand the ‘ocean’ to not only include the abiotic effects of less suitable land cover, but also the increased negative biotic influences of native and non-native competitors and predators. If persistence and diversity are the management goals for urban forest patches, the obvious implication of this work is that larger parks near to one another and/or near to city outskirts are most desirable. A more realistic intervention scenario, particularly given that isolated forest fragments are less likely to receive new species through dispersal (McEuen and Curran 2006; Oldfield et al. 2013; Labatore et al. 2017), is the use of green corridors and native tree planting in existing urban forests. Urban habitat may be suitable for far more native species than are found in it (Labatore et al. 2017; Shepack, Freidenburg, and Skelly 2017), possibly a consequence of historical land use and current dispersal limitations. Green corridors may increase regional forest connectivity, particularly if linked with rural forests, and native tree planting may offset limited native tree immigration and heightened non-native input.

Supplementary data

Supplementary data are available at JUECOL online.

Acknowledgements

The authors thank the U.S. National Park Service for providing vegetation data; New York State and Erie County parks, and the Iroquois National Wildlife Refuge for site access and three anonymous reviewers for helpful suggestions for the manuscript.

Conflict of interest statement. None declared.

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