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Natural regeneration in urban forests is limited by early-establishment dynamics: implications for management

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Abstract. Urban forested natural areas are valuable ecological and social resources, but long-term sustainability of these habitats is challenged by environmental and social factors associated with urban ecosystems. Advances in city-scale assessments of urban forests have increased the resolution of forest community types and conditions, allowing for improved understanding of ecological function, such as natural regeneration, in these urban habitats. By applying metrics of tree regeneration that are commonly used for the management of rural forests, urban ecologists can test the potential for traditional forest management strategies within our cities. In this study, we compare urban and rural oak–hickory forest composition and structure and the capacity for natural regeneration in the New York metropolitan area. Specifically, we use two metrics of advance regeneration that describe the abundance of seedlings and saplings at different size classes to test whether this management for natural regeneration is a viable option. We found differences in recruitment dynamics between urban and rural forests that have implications for the sustainability of these forests and new management strategies. First, after controlling for forest community type, species composition in urban and rural sites was significantly different across multiple strata and within the seed bank. Species-specific capacity for natural regeneration was different in urban and rural sites, signaling the possibility of divergent successional trajectories. Second, while differences in species composition exist, both urban and rural sites were dominated by native species across all forest strata except for urban seed banks. Third, despite finding significantly lower average annual seedling abundance in urban (1.9 seedlings/m^2) compared to rural (7.1 seedlings/m^2) sites, we observed greater density of saplings in urban forests, and no significant difference in stocking index between sites. These findings suggest that early-establishment barriers to recruitment are greater in urban forest sites. However, once established, seedling transition into advance regeneration stages may not be different between site types, and advance regeneration may, in some cases, be more viable in urban forested natural areas. These results highlight functional differences between urban and rural forest recruitment dynamics that may impact on the future community composition of oak–hickory forests in the two landscape settings.

Key words: advance regeneration; forest management; forest structural diversity; natural regeneration; plant recruitment dynamics; restoration ecology; seed rain; seed bank; urban biodiversity; urban forestry.

Introduction

Urban forested natural areas are an important component of the total urban tree canopy (UTC) and overall sustainability for cities located in forested biomes. These green spaces provide valuable ecosystem services for residents (e.g., Haase et al. 2014), and habitat for local and regional biodiversity (e.g., Ives et al. 2016, Lepczyk et al. 2017). In the United States, natural areas make up approximately 85% of municipal parkland (Trust for Public Land 2017), and forested natural areas are common in many of the world's largest and densest cities (e.g., Lawrence et al. 2013). For example, in New York City (NYC), there are 4,250 ha of urban forested natural areas, which represent 5% of the total land area, nearly 25% of all parkland, and more than 70% of the total natural area in the city. Furthermore, 75% of all trees in NYC are found in forested natural areas (Pregitzer et al.

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2018). Consequently, these forests may provide a disproportionate amount of ecosystem services generated for the city and are often a priority for environmental managers.

Despite providing many ecological and cultural services, urban forested natural areas often connote degradation, perceived as sites dominated by exotic and invasive species, and different from rural forests both in composition and structure (Huebner et al. 2012, Pregitzer et al. 2019*a*). However, recent research reveals this may not necessarily be the case. Forested natural areas in NYC are characterized by primarily native tree species in the canopy, as well as by forest community types commonly identified in non-urban landscapes (Forgione et al. 2016, Pregitzer et al. 2019*a*). Although native canopies may dominate NYC's urban forested natural areas now, the long-term fate of these forests is uncertain. Some evidence suggests that natural regeneration and recruitment of woody species in the understory and midstory may be negatively influenced by urban conditions and are divergent from rural forest systems. Comparing plant communities between urban and rural plots and across an urban-rural gradient, researchers report greater nonnative seedling species richness in urban forests (Airola and Buchholz 1984, Guntenspergen and Levenson 1997, Zipperer 2002, Cadenasso et al. 2007) and reduced native seedling abundance (Burton et al. 2005, Cadenasso et al. 2007, Pennington et al. 2010, Trammell and Carreiro 2011, Overdyck and Clarkson 2012, Wallace et al. 2017). These trends are not absolute, as some other studies have found no relationship between urbanization and species-specific recruitment (Michalak 2011).

There is a need to increase the resolution with which we examine differences in urban and rural communities and ecosystem function. For urban forested natural areas, this includes studying tree seedling recruitment within different forest community types and conditions. Early life stages in plants, from seed dispersal to seed banking and seedling establishment, are important in determining future forest composition and structure (Hurtt and Pacala 1995, McConkey et al. 2012). Improved understanding of urban-driven changes in tree recruitment and regeneration potential can direct management approaches that sustain native forest communities in cities (Piana et al. 2019). In rural forests of the northeast United States, managers often rely on natural regeneration, leveraging early recruitment processes from seed dispersal, seed banking, and early establishment. These strategies are fundamental to ecological forest management and silviculture (Ashton and Kelty 2018) and are guided by data commonplace to rural systems, such as advance regeneration and stocking indices. Advance regeneration is defined as all tree seedlings that are established in the understory, often for more than 1 yr (Ashton et al. 2018), while stocking indices account not just for seedling or sapling abundance, but size classes within these stages. Such data are used to inform management prescriptions implemented at the stand scale, a spatial unit that identifies site by forest composition, structure, and condition.

These data are often not available for forests in cities and their absence represents a barrier to implementing operational scale silviculture and ecological forest management practice (Piana et al., *in press*). Natural regeneration is a dominant process in urban forested natural areas, but occurs passively, and is often not the focus of land management activities (e.g., Pregitzer et al. 2019*b*). Instead, urban forest managers in North America, often employ a combination of invasive plant removal and direct planting; approaches that are resource-intensive (Johnson and Handel 2016, DiCicco 2014, Pregitzer et al. 2019*b*, 2018). The implementation of these approaches is financially prohibitive for many municipalities. Therefore, a fundamental question for applied ecologists is, what is the potential to manage for natural regeneration in urban forested natural areas?

In this study, using common ecological and forestry metrics, we investigate whether urban forested natural areas can sustain themselves through natural regeneration processes. In addition, we examine the potential for seed rain and seed banks to play a role in urban natural area restoration. We compared oak–-hickory forest stands in urban and rural sites of the NYC region and ask: (1) What is the difference in composition and abundance for canopy trees, saplings, and seedlings, as well as seed rain and seed bank in urban and rural forests? (2) Do regeneration patterns in urban and rural forests differ in tree species identity and abundance in early and advance regeneration stages relative to canopy species? We focus on oak–hickory forests because they are common throughout the Northern Piedmont, Northeastern Highlands and Upland Province, and Coastal Zone ecoregions of the northeastern United States and are the most common forest community type in NYC natural areas (Forgione et al. 2016). Understanding these regeneration patterns and processes can advance sustainable management solutions for urban and rural forests in one of the most densely populated regions of the United States.

Methods

Study location

This study was conducted in six mature oak–hickory forests located in the NYC metropolitan area (Fig. 1; Appendix S1: Fig. S1). Urban sites (n = 3) were located in forested natural areas within Van Cortlandt Park (VCP) and Pelham Bay Park (PBP) in the Bronx, and Inwood Hill Park (IHP) in Manhattan. These sites are all publicly owned parkland managed by New York City Department of Parks and Recreation and have a long history of study by urban ecologists (e.g., Pickett and McDonnell 1989, Johnson and Handel 2016). Rural sites (n = 3) were in the New York Highlands region at

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Sterling Forest State Park (SFSP), Blue Lake Park (BLP), and Black Rock Forest (BRF). All sites were located more than 15 km apart and within the southernmost region of the Northeastern Upland Province (Broughton et al. 1966). Each of the rural sites is a protected area and part of a region that is the largest contiguous open space near New York City. The surrounding landscape is defined as intermix wildland–urban interface landscape (Martinuzzi et al. 2015). Given the geophysical similarity and proximity, this area has been used in multiple previous ecological studies comparing urban and rural populations, from flora to fauna (e.g., Harris et al. 2013, Sonti et al. 2019). To assure similar conditions, rural sites were characterized by <1% impervious cover and zero human residents within a 500-m buffer and <5% impervious cover and <500 human residents within the 2-km buffer (Appendix S1: Fig. S1 and Table S1).

Six plots were installed in each of the three urban sites (n = 18). Three plots were installed in each of the rural sites (n = 9). We installed extra urban plots to account for potential vandalism. Three urban plots did experience significant human disturbance, for example removal of seed traps and installation of informal encampments, which interfered with data collection. These plots were not included in the final analysis. Sampling density was determined from a review for forest seed rain studies (Clark et al. 1999) and previous urban-rural forest research in region (Pickett and McDonnell 1989, Kostel-Hughes et al. 1998). All plots were randomly located in stands classified as the oak–hickory forest community type by using a grid system and random number generator. All plots were located more than 200 m from the next nearest plot. We used forest type maps in the rural forest and urban site selection was informed by a recent city-scale ecological assessment and urban-specific forest community classification system (Edinger et al. 2016, Forgione et al. 2016). Plots were located in closed canopy (80–95% canopy cover) stands of mature trees 60–100 yr old, >30 m from forest edges and >20 m from trails. Additionally, all plots were confined to areas delineated as Hollis or Charlton soil series (USGS), on slopes <10% grade, and non-hydric conditions. We were unable to obtain site-specific information on the history of management in the rural sites, but given the structural similarity and size class of trees were able to predict that similar harvests occurred approximately 60–100 yr ago. There is no active harvesting or silvicultural prescription for these sites. Neither urban nor rural forests are managed for any specific timber type. Furthermore, throughout the region, the overabundance of white-tailed deer in rural and suburban areas has led to increased herbivory and altered forest composition and structure (Horsley et al. 2003, Rooney and Waller 2003, Côté et al. 2004). The rural sites in this study have a history of deer management and hunting, which could lessen herbivory pressure and allow an understory and midstory to establish. In the urban sites, deer were not present or uncommon in two (IHP and VCP) of the three sites but were common in Pelham Bay Park. Deer are not actively hunted or removed from Pelham Bay Park.

Field methods

Tree species were sampled within three forest strata: canopy, saplings, and understory. Canopy trees were sampled in 35-m fixed radius plots. Canopy trees were defined as all single- and multi-stemmed individuals >10 cm dbh (diameter at breast height, 1.30 m above ground). Midstory saplings were defined as all stems 2–10 cm dbh and sampled in 10-m fixed radius plots. We followed standardized methods for calculating a stocking index by sampling all saplings 1–2.5 cm dbh in three 3 m radius subplots within each plot (McWilliams et al. 2015). Canopy trees and saplings were sampled in July 2016. Seedlings were sampled in 10 1 × 1 m semipermanent quadrats installed at each plot in two parallel 20-m transects, 5 m apart, and at 5 m intervals. An additional two quadrats randomly located within each 10 m radius plot were sampled in 2016 to compute advance regeneration metrics. Two classifications of seedlings were used. Average annual abundance measures included all seedlings <100 cm tall and 1 cm diameter. For the stocking index, we sampled all seedlings that were <1 cm dbh, with no maximum height. We measured the height of all seedlings in 2016. Seedling abundance was sampled in July each year 2016–2018. *Carya* seedlings were identified to the genus only. All other species were identified to species.

Seed rain was monitored from March 2016 to March 2019 using a custom-designed seed trap (0.125 m^2; Appendix S1: Fig. S2). Trap design was tested for seed loss due to bouncing for a range of seed types and sizes. The lowest efficiencies were for *Carya* sp. (0.84 ± 0.6) and *Quercus* sp. (0.87 ± 0.4). These values were comparable to other studies conducted in similar forest types (Clark et al. 1999). Ten seed traps were installed in two parallel transects and adjacent to each seedling quadrat. Seed traps were elevated from the ground and included a screen to minimize seed predation within the trap. Seeds were collected from each trap monthly from January through July, and biweekly, August through December, to minimize seed predation risk during peak dispersal. All captured seeds were identified to species. Only mature and intact diaspores captured in seed traps were considered in our analyses.

The soil seed bank was estimated using soil cores and the seedling emergence method (Price et al. 2010). Two soil cores 5.0 cm in diameter and 10 cm deep (volume per core = 196.35 cm^3) were collected in random locations adjacent to each seed trap and seedling plot. In total, 20 cores were collected at each plot. Leaf litter was not excluded from the soil core sample. The sampling density and depth were within a range determined to be appropriate for sampling woody species in urban and

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FIG. 1. Urban forested natural areas (left, Van Cortlandt Park, Bronx, New York, USA) are green spaces that are characterized by ecological function and processes, such as natural regeneration, commonly associated with rural forest systems (right, Blue Lake Forest Park, New York; photo credit: Max R. Piana).

regional forest sites (Kostel-Hughes et al. 1998, Clark et al. 1999). Sampling took place in April 2018, after the seed bank had been cold stratified in situ. The soil samples were kept in cold storage until planting in greenhouses. Soil cores were pooled by seed trap transect, homogenized, and planted into one greenhouse tray (50.8 × 28.0 cm). The soil core samples were mixed with sterilized greenhouse potting mix to obtain an equal volume of soil per tray. Control flats (n = 5), which contained only sterilized greenhouse potting soil, were placed among the experimental trays to identify any contaminate species. The seedling trays were rotated and stirred monthly to encourage germination and to account for differences in light, temperature, and humidity within the greenhouse. Seedlings were identified, counted, and then removed from the tray upon emergence. If identification was not possible in the emergent seedling stage, then the individual was transplanted and grown until identification was possible. The soil core samples were grown for six months. Again, *Carya* seedlings were identified to the genus only. All other species were identified to species.

Data analysis

All analyses were limited to tree species only; all other woody species, including lianas and shrubs, were excluded. To analyze differences in plant community composition at each life-history stage and between urban and rural forest sites, we used three nonparametric multivariate techniques: NMDS (Kruskal 1964), PERMANOVA (Anderson 2001), and PERMDISP (Anderson 2006). Plot data was used for each analysis and transformed to relative abundance prior to analysis to allow for comparison among strata and seed stages. *Carya* species in all strata were reported as genus only to match sampling resolution with seedling strata. All other taxon was identified to species. We used the Bray-Curtis measure of dissimilarity (Bray and Curtis 1957) as the distance measure for all analyses. To visualize differences in species assemblages between urban and rural forest sites and forest strata, we performed NMDS ordinations, using the metaMDS function of vegan package (Oksanen et al. 2010). Two-dimensional solutions were chosen and final ordinations were generated from 200 random starts.

PERMANOVA analyses were used to test whether community composition varied among forest strata in urban and rural forest site types. PERMANOVA tests for differences in the locations (centroids) of multivariate groups (Anderson 2001). Analyses were performed using the adonis function of vegan. P values for the test statistic (pseudo-F) are based on 999 permutations, and are reported down to, but not below, 0.001. Pairwise comparisons of the dissimilarity among each strata and between site types used function adonis with p-adjust method holm in vegan to adjust for multiple comparisons. We tested for differences in the variability of forest strata assemblages between urban and rural sites with PERMDISP analyses. Multivariate dispersions (mean

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distances of observations to the group centroid) were first calculated using the betadisper function of vegan, with the mean dispersion then compared between groups via Tukey's Honest Significant Differences. All statistical analyses were performed using R 3.6.0 (R Core Team 2019). The critical α level was 0.05 for all tests.

We compared regeneration through two established metrics of advance regeneration used in rural forests. The advance regeneration index (McEwan et al. 2011) was used to test the relative representation of large (dbh> 38.0 cm) trees among saplings (dbh < 13.0 cm). Negative values indicate instances where there is greater representation of the species in the canopy than among small trees and saplings. Positive numbers indicate a larger proportion of smaller trees relative to larger trees for that species. We also calculated a regeneration stocking index (RSI) following methods developed by the U.S. Forest Service (Marquis and Bjorkbom 1982). The RSI computes a total plot score that has been scaled to determine adequate stocking with and without herbivory from white-tailed deer. Scores are determined from a point system based on count data for seedlings (<1 cm dbh) as determined by individual seedling height (15–30 cm, 1 point; 30–100 cm, 2 points; 100–150 cm. 15 points; >150 cm. 30 points) and saplings count data (4.25 points each). For an individual plot to be considered adequately stocked at high deer density (>8 km^2, as determined by Horsley et al. 2003) it must have a score of 115, or at low deer density, a score of 38 (Marquis and Bjorkbom 1982, McWilliams et al. 1995).

We compared total, native, and exotic species richness and abundance, species-specific abundances, and RSI scores between forest types (urban and rural). Canopy and sapling abundances were calculated as basal area and standardized to per hectare estimates. Seedling, seed rain, and seed bank abundances were standardized to 1 m^2. Seed rain and seedling abundances are reported as average abundances from 2016–2018. For each comparison, we tested for normality, using nonparametric tests (Mann–Whitney *U* test) when our data failed to fit a normal distribution.

Results

Forest strata community composition

There were significant differences between these urban and rural oak–hickory forest communities. Nonmetric multidimensional scaling (NMDS) ordination plots (stress = 0.159) indicated that the tree species composition in all forest strata and seed stages differed between urban and rural sites, as well as among strata and seed stages within each site type (Fig. 2); this was supported by permutational multivariate analysis of variance ($R^2 = 0.38$, $P = 0.001$).

Post-hoc pairwise comparisons of Adonis dissimilarity indicated that the composition of urban and rural forest canopy, sapling, seedling, and seed bank were significantly different from each other (Appendix S1: Table S2). However, there was no difference in the composition of urban and rural seed rain. Within rural forests, significant differences were observed between the community composition of the canopy and all other strata and seed stages. Also, the rural seed bank differed significantly from rural seed rain and seedling communities. Within urban sites, significant differences were observed when comparing all strata and seed stages, except between seed rain and canopy and between sapling and both seed rain and seedlings. All other strata comparisons were significantly different.

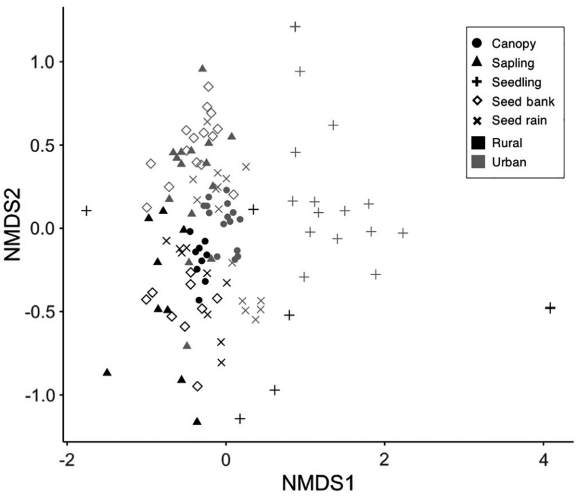


FIG. 2. NMDS ordination plots based on Bray-Curtis dissimilarities (stress = 0.159) of forest tree community composition among forest strata (canopy, sapling, and seedling), seed rain, and seed bank for all urban (gray) and rural (black) forest plots. All data were converted to relative abundance prior to analysis. *Carya* was reported to genus.

The permdisp analysis (Appendix S1: Table S2), a measure of beta diversity, indicated that there are significant differences in group mean dispersions (PERMDISP; $F = 4.29$, df = 9, $P < 0.001$). Post-hoc pairwise comparisons indicated that urban canopy and sapling strata were more statistically dispersed than in rural forests. In other words, in addition to differences in composition, there was greater variability in tree species composition in the urban forest canopy and urban sapling strata. The community composition of rural sapling and seed banks were significantly more dispersed in ordination space than rural canopy (all P values < 0.05). In urban forests, there were no differences in dispersion among urban strata and the seed rain or seed bank.

Forest strata and seed richness and abundance

Fifty-five tree species were recorded. Of these, 24 species were identified in all forest strata but only 6 were observed in all forest strata and seed stages. Of the 55 species, 7 were identified as nonnative to the region

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(*Acer platanoides*, *Ailanthus altissima*, *Morus alba*, *Maclura pomifera*, *Paulownia tomentosa*, *Phellodendron amurense*, *Tilia cordata*). From 2016–2019, more than 40,000 seeds from tree species were captured from the seed rain and 367 tree germinants identified in seed bank analysis. A full list of species-specific abundances for all strata and seed stages is in the supplemental material (Appendix S1: Table S3).

The urban forest canopy was characterized by greater basal area (30.8 ± 0.9 m^2/ha; mean ± SE) than rural sites (25.8 ± 1.5 m^2/ha; Table 1). There were 48 species is the canopy, 6 of which were nonnative. There were no significant differences in canopy species richness between urban and rural sites. However, there were significantly more nonnative tree species in urban canopies. Despite systematically selecting sites with similar communities, differences in species dominance among canopy species were observed. In both urban and rural forests, the canopy was dominated by three species of oak: *Quercus rubra*, *Q. alba*, and *Q. velutina*. Three species of hickory, *Carya tomentosa*, *C. glabra*, and *C. ovata* were common at all sites, but *C. cordiformis* was limited to urban sites. Differences in canopy composition were driven by the greater abundance of *Acer saccharum* and *Q. montana* in rural sites. *Prunus serotina* was dominant in urban forest canopies, but significantly less common in rural forest canopies. Nonnative species were not present in rural canopies, while six of the seven nonnative species identified in this study were present in urban forest canopies.

Urban forests had significantly greater average basal area of saplings (2.0 ± 0.2 m^2/ha) than rural forest sites (1.0 ± 0.1 m^2/ha; Fig. 3). In total, there were 23 species identified in the sapling layer, of which *Morus alba* was the only nonnative species. The dominant species in sapling strata in urban and rural sites were different (Fig. 4). In rural sites, *A. saccharum*, *A. rubrum*, and *Ostrya virginiana* were the most common species. Dominant urban sapling species included *Q. rubra*, *P. serotina*, *C. cordiformis*, and *C. tomentosa*. Similar to the canopy, there were no observed differences in overall or native species richness among sapling strata. The nonnative species was only observed among urban forest saplings.

The average annual density of seedlings was much greater in rural forests (7.1 1.5 seedlings/m^2) than in urban forests (1.9 ± 0.6 seedlings/m^2; Fig. 3). Thirty-one species of tree seedlings were identified in the understory. There was greater seedling species richness in rural forests (10.4 ± 0.9 species, SE = 0.9) than urban sites (4.7 ± 0.4 species). Again, there were no nonnative seedlings present in rural sites and while few were identified in urban sites; these differences were significant (Table 1). Similar to the sapling strata, the dominant seedlings in rural sites included *A. saccharum*, *A. rubrum*, and *O. virginiana*; *Q. rubra* was also present (Fig. 5). In urban sites, *P. serotina* seedlings were by far the most abundant (1.2 ± 0.3 seedlings/m^2). There were significantly fewer total oak seedlings in urban sites (0.1 ± <0.1 seedling/m^2), compared to rural sites (0.9 ± 0.1 seedlings/m^2). These differences were observed across all oak species.

Seed rain was the only life stage that did not differ statistically when comparing total and native species abundances in urban (603.9 ± 211.3 seeds/m^2) and rural sites (239.1 ± 159.4 seeds/m^2; Table 1). This was driven by high variability and the presence of species that produce abundant seed (e.g., *Betula* sp.). There were, however, significantly more nonnative seeds present in urban seed rain (urban = 4.5 ± 2.2 seeds/m^2; rural = 0.03 ± <0.1 seeds/m^2). Overall, there were 35 species identified in the seed rain. Total and native species richness did not significantly differ between site types, but exotic species richness was greater in urban sites. Using a species-specific focus, seed rain corresponded with canopy

Table 1. Species richness and density of forest canopy (all stems ≥ 10 cm dbh), saplings (all stems >2 and <10 cm dbh), understory (all stems <2 cm dbh and <100 cm height), seed rain, and seed bank for two forest types: urban (n = 15) and rural natural (n = 9).

		All Species		Native		Exotic	
Strata and Seed Stage	Site type	Richness	Density	Richness	Density	Richness	Density
Canopy	Urban	12.9 ± 0.8	**30.8 ± 0.9**	11.8 ± 0.8	**30.3 ± 1.0**	**1.3 ± 0.2**	**0.5 ± 0.2**
	Rural	13.8 ± 0.9	**25.8 ± 1.5**	13.8 ± 0.9	**25.8 ± 1.5**	–	–
Sapling	Urban	6.5 ± 0.6	**2.0 ± 0.2**	6.3 ± 0.6	**2.0 ± 0.1**	**0.2 ± 0.1**	**0.01 ± 0.0**
	Rural	4.4 ± 0.8	**1.0 ± 0.1**	4.4 ± 0.8	**1.0 ± 0.1**	–	–
Seedling	Urban	**4.7 ± 0.4**	**1.9 ± 0.6**	**4.4 ± 0.4**	**1.9 ± 0.6**	**0.3 ± 0.1**	**0.0 ± 0.0**
	Rural	**10.4 ± 0.9**	**7.1 ± 1.5**	**10.4 ± 0.9**	**7.1 ± 1.5**	–	–
Seed Rain	Urban	13.3 ± 0.5	603.9 ± 211.3	11.7 ± 0.6	599.5 ± 211.5	**1.6 ± 0.1**	**4.5 ± 2.2**
	Rural	12.3 ± 0.6	239.1 ± 159.4	12.2 ± 0.6	253.3 ± 52.8	**0.1 ± 0.1**	**0.03 ± 0.02**
Seed Bank	Urban	**3.0 ± 0.3**	**151.2 ± 61.4**	1.0 ± 0.2	14.9 ± 3.9	**2.0 ± 0.3**	**136.3 ± 60.0**
	Rural	**1.1 ± 0.3**	**8.5 ± 6.4**	1.0 ± 0.3	7.8 ± 2.3	**0.1 ± 0.1**	**−0.7 ± 0.7**

Notes: Values are mean ± SE. The densities for canopy (basal area, m^2/ha), sapling (basal area, m^2/ha), and seed bank (seeds/m^2) were determined from a single sample collected in 2018. The abundance of seedlings (stems/m^2) and seed rain (seeds/m^2) was the average abundance from 2016–2018. Abundances were standardized from plot measures. Boldface type indicates significant difference between urban and rural sites (P < 0.05 Welch's t-test [1947] and Mann-Whitney U test [Mann and Whitney 1947]).

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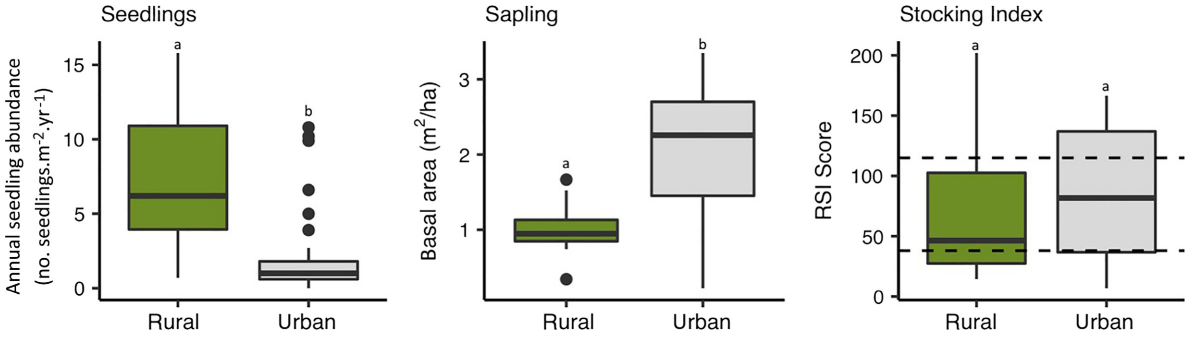


FIG. 3. Mean annual seedling abundance, total sapling basal area, and the natural regeneration stocking index (RSI) for urban (gray) and rural (green) forests. Seedling abundance was greater in rural forests (Mann-Whitney U test, $U = 117.5$, $P < 0.010$), sapling density was greater in urban forests ($U = 29.0$, $P < 0.050$), and there was no difference in RSI ($t = -0.262$, $P = 0.796$). The RSI is derived from abundance of seedling and sapling, and weighted by seedling height (see *Methods* for scoring metric). For an individual plot to be considered adequately stocked at high deer density (>8 km^2) it must have a score of 115, or at low deer density, a score of 38 (dashed lines). Boxes indicate the interquartile range (25th and 75th percentile) and the line shows the median. Error bars show ±1.5 times the interquartile range to the 25th and 75th percentiles. Outlier points are beyond 1.5 times the interquartile range. Different lowercase letters above boxes indicate significant differences ($P \leq 0.05$).

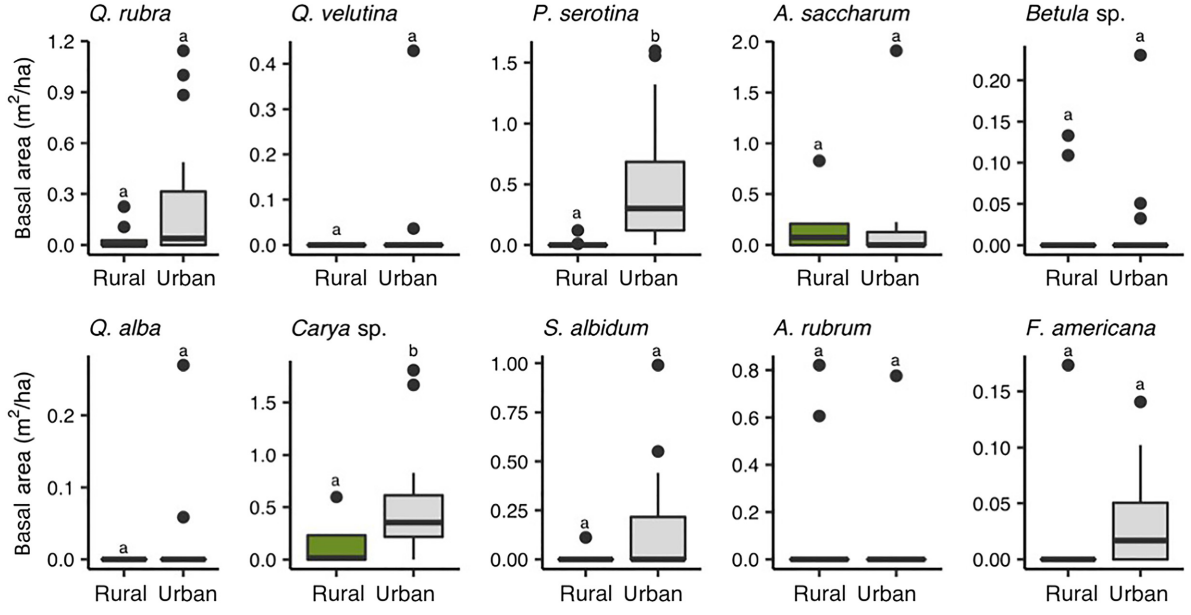


FIG. 4. Sapling basal area (m^2/ha) for canopy-dominant species in urban and rural forests. We found greater density of *P. serotina* ($U = 8.5$, $P < 0.001$) and *Carya* sp. ($U = 27.0$, $P < 0.050$) in urban forests. Note, we did not include *L. tulipifera* in the figure, which was absent in rural forest sapling plots and present in just two urban plots. Boxes indicate the interquartile range (25th and 75th percentile) and the line shows the median. Error bars show ±1.5 times the interquartile range to the 25th and 75th percentiles. Outlier points are beyond 1.5 times the interquartile range. Different lowercase letters above boxes indicate significant differences ($P \leq 0.05$). Abbreviated genera are *Quercus*, *Prunus*, *Acer*, *Sassafras*, and *Fraxinus*.

dominance, with the notable exception of small-seeded species, such as *Betula* sp., which, where present, were prevalent in the seed rain but not common in the overstory. *Ailanthus altissima*, with wind dispersed seeds, was the most common nonnative species in both urban and rural sites.

Urban forests had significantly greater total and nonnative seed abundance in the seed banks than rural sites (Table 1). There was, however, no significant site difference when comparing the abundance of only native species. In total, 13 species were identified, 4 of which were nonnative. As observed in the NMDS ordination, there were strong differences in canopy and seed bank species composition. Despite the low abundance of nonnative species in canopy and sapling strata, urban seed banks were dominated by these species, including *Paulownia*

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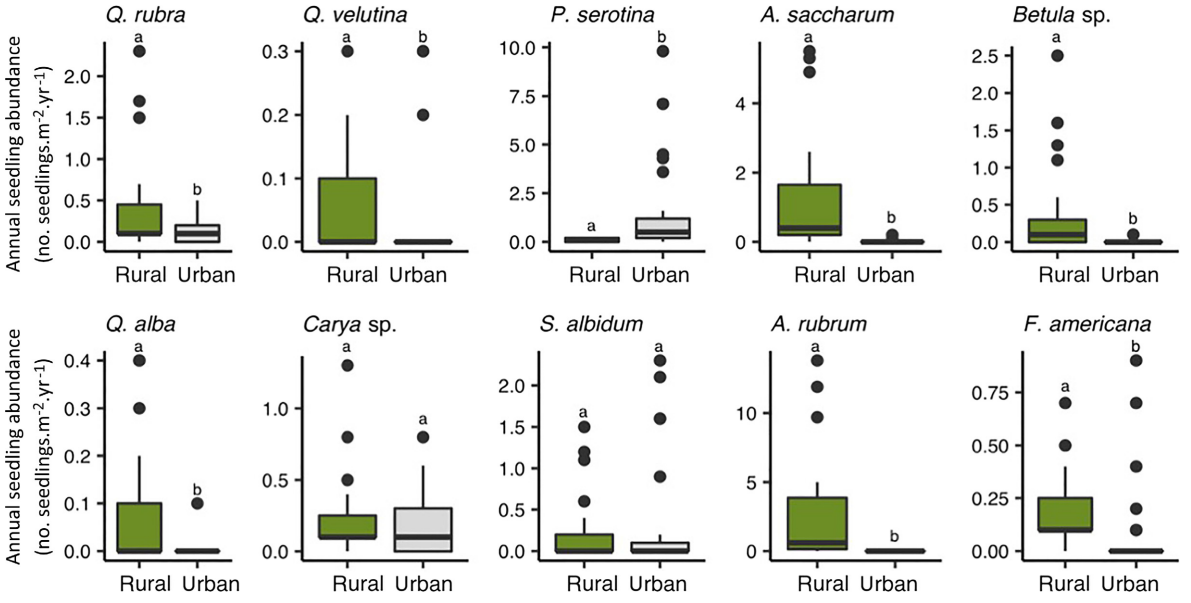


FIG. 5. Seedling abundance (seedling/m^2) for canopy-dominant species in urban and rural forests. Seedling abundances are the plot mean observed across three sampling years (2016–2018). The only species more abundant in urban sites was *P. serotina* ($U = 234.5$, $P < 0.001$) and there was no significant difference in *S. albidum* seedlings. All other species were significantly more abundant in rural forest ($P < 0.05$). Note, we did not include *Liriodendron tulipifera* in the figure; only one seedling was observed among urban plots and none in rural forests. Boxes indicate the interquartile range (25th and 75th percentile) and the line shows the median. Error bars show ±1.5 times the interquartile range to the 25th and 75th percentiles. Outlier points are beyond 1.5 times the interquartile range. Different lowercase letters above boxes indicate significant differences ($P \leq 0.05$). Abbreviated genera are *Quercus*, *Prunus*, *Acer*, *Sassafras*, and *Fraxinus*.

tomentosa and *Morus alba*, and to a lesser extent, *A. altissima*. In rural sites, *A. rubrum* was the most abundant species in the seed bank.

Advance regeneration and regeneration stocking index

There was no significant difference in the RSI between sites ($t = -0.262$, $P = 0.796$; Fig. 3). In fact, urban sites (RSI = 84.0 ± 15.1) were on average greater compared to rural (RSI = 77.2 ± 21.1) forests. The RSI was variable across all rural sites (SFSP, 55.0 ± 18.9; BLP, 149.3 ± 28.9; BRF, 27.4 ± 7.5) and was below the threshold recommended for sites associated with high abundance of deer in two of the three sites. Stocking values for urban sites were also variable. However, in two sites where there are no or few deer. In Van Cortlandt Park (RSI = 111.2 ± 34.2) and Inwood Hill Park (RSI = 96.2 ± 27.5), RSI exceeded baseline thresholds. The other urban site, Pelham Bay Park (RSI = 58.3 ± 19.3), which does have abundant deer, was well below RSI thresholds.

The advance regeneration index also provides insight on the relative dominance of species in the sapling strata, relative to canopy dominants (Fig. 6). In both urban and rural forests, oaks were determined to be less dominant in the midstory than in the canopy. Conversely, *Carya* species increased in relative dominance in the sapling strata in both urban and rural sites. Other canopy sub-dominants, such as *Acer* sp. and *Betula* sp., were similarly represented in both the canopy and midstory. In urban forests, *P. serotina* was relatively more dominant in advance sapling stages.

DISCUSSION

To our knowledge, this study is the first application of advance regeneration and stocking indices to urban forested natural areas. We identify a potentially overlooked difference in urban and rural forest recruitment dynamics for oak–hickory forests in NYC that have important implications for the sustainability and management of these forest communities. Early-establishment barriers to recruitment appear to be greater in urban sites, as seen by the lower total abundance of tree seedlings in urban sites. However, once established, transition to advance regeneration stages such as saplings may not be lower, and advance regeneration may be more viable in urban forested natural areas than previously thought. Furthermore, while native species dominate all forest strata in both urban and rural sites, differences in community composition suggest that urban forests may be on a divergent successional trajectory from their rural counterparts.

Decreased tree seedling abundance in urban forests compared to rural forests may result from multiple barriers to early life-history processes. These include seed production, pre- and/or post-dispersal seed predation, changes in soil structure and chemistry, leaf litter depth, microclimate, and competition with nonnative plants

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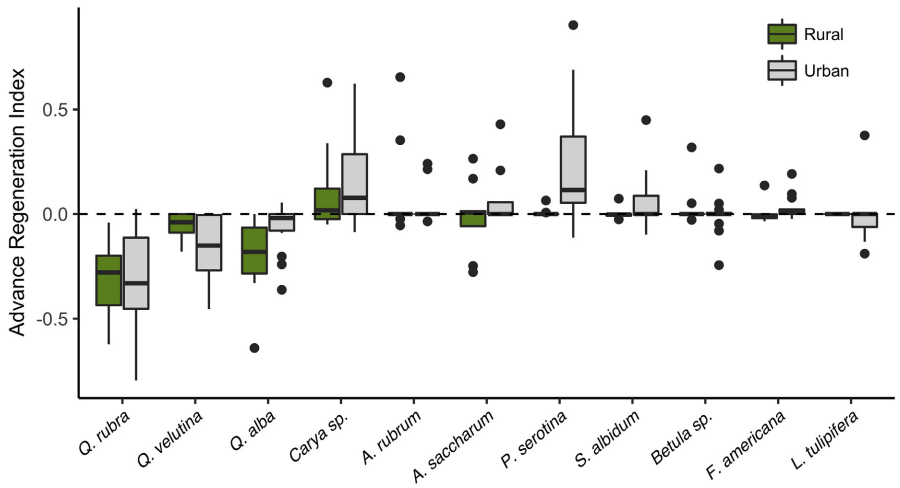


FIG. 6. Advance regeneration index for canopy-dominant species in urban (gray) and rural (green) forests. The index is the difference between relative dominance of large (dbh > 38.0 cm) trees within 35 m radius plots and relative dominance of saplings (dbh < 13.0 cm) within each 10 m radius plot. Negative values indicate instances where there is greater representation of the species in the canopy than among small trees and saplings. Positive numbers indicate a larger proportion of smaller trees relative to larger trees for that species. Abbreviated genera are *Quercus*, *Prunus*, *Acer*, *Sassafras*, *Fraxinus*, and *Liriodendron*.

(Aronson and Handel 2011, Piana 2019). Given the similarity in canopy composition and structure as well as seed availability, differences in seedling abundance in our study are likely the result of post-dispersal factors. In related studies, leaf litter depth was found to decrease with increasing urbanization and, as a result, microclimate conditions and site suitability became less favorable for larger-seeded species, such as oaks (Kostel-Hughes et al. 1998). Post-dispersal factors such as seed predation are not well studied in urban sites, but the negative effects of interspecific competition with invasive plants are better understood (e.g., Gaertner et al. 2017). Species-specific research is required to compare the mechanisms limiting seedling establishment from seed production within different urban forest community types and conditions.

Despite lower annual seedling abundance, sapling abundance was significantly greater in urban sites. Furthermore, the RSI of urban forests was slightly greater than rural forests, although not statistically significant. Multiple factors may contribute to these differences. In our study, herbivory is likely a strong driver of the differences. The overabundance of white-tailed deer herbivory is well documented as a negative influence on woody plant regeneration (Anderson and Katz 1993, Augustine and Decalesta 2003, Aronson and Handel 2011). The stocking indices computed in this study support the conclusion that all rural sites were below sustainable thresholds of advance regeneration in areas with high deer abundance (Marquis and Bjorkbom 1982, McWilliams et al. 1995). The urban sites were on average below this threshold, but several plots did exceed high deer density thresholds for regeneration (e.g., maximum RSI = 166.5). Furthermore, two of the three urban sites are without, or with minimal, deer abundance. In these sites, RSI values are well above recommended thresholds for adequate natural regeneration. In Pelham Bay Park, the urban site with deer, RSI values were below the threshold and similar to rural sites. The findings from our study suggest that when buffered from deer, the long-term fate of advance regeneration may improve and be better than rural forest sites located within the same region. The landscape and land-use structure of cities could be critical drivers of these differences. Disconnected urban forest parks may benefit from the urban matrix. These are essentially "green islands" buffered from deer populations and may actually exceed non-urban sites with respect to advance regeneration. Our findings highlight the complexity of studying urban sites and the need for considering the multiple, co-occurring and often exacerbated disturbances. Future work can address how advance regeneration may vary in urban sites across a continuum of deer abundance, as well as the specific influence of deer on advance regeneration using exclosure experiments.

In addition to gross differences in total seedling abundance and advance regeneration, dissimilarity in community composition in seedling and sapling strata suggests that the future trajectories of these urban and rural oak–hickory forests may be different. Our findings highlight the role of regional ecosystem change and local, urban-driven changes on oak-dominated forests. Oak forests across the eastern United States are undergoing shifts in community composition (McEwan et al. 2011). Specifically, researchers find that, although red oaks are dominant in the canopy, smaller size classes are not as well represented, indicating recruitment limitation (Lorimer 1984, Loftis and McGee 1993, McEwan et al.

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2011). This loss of oaks has been associated with increases in maple species, particularly *A. rubrum* (Abrams 1998, McEwan et al. 2011). Similar to these regional trends, in our study oak species in both urban and rural sites were underrepresented in sapling stages compared to the canopy (Fig. 6).

In rural forests decreased oak regeneration has been explained by the "multiple interaction ecosystem drivers hypothesis," which includes the important role of suppressed fire and burn regimes (e.g., Crow 1988, Abrams 1992, Nowacki and Abrams 2008), as well as changes in regional temperature, moisture and nitrogen dynamics, the loss of keystone tree species such as the American chestnut (*Castanea dentata*), and increased herbivory from deer (McEwan et al. 2011). Certainly, deer are a factor in total seedling abundance; however, without deer, the abundance of *Quercus* sp. seedlings was significantly lower in urban sites. Consequently, while total advance regeneration may be greater in urban sites, local factors associated with the urban ecosystem context act as barriers to recruitment for oak species, and differently affect sub-dominant canopy species.

For example, we found maple species dominating the seedling stages in rural forests, a trend that has been observed throughout the range of *Q. rubra* in the eastern United States (Abrams 1998, McEwan et al. 2011). However, in urban forests, *P. serotina*, not maple, is the most dominant in younger strata (saplings and seedlings). *A. rubrum* and *P. serotina* are both native, early-successional trees, but if they are to transition to canopy dominants, this would create different community types. This difference may be a simple result of source limitation (i.e., there were few *P. serotina* located near our rural plots). Or, these community differences may be the result of functional traits of the two species and divergent community dynamics in urban and rural sites. For example, *P. serotina* is bird dispersed, which may allow for greater vagility and seed availability.

It is important to note that community and population differences may be an artifice of limited plot replicates, the influence of which may be greater in urban sites, which are known to be relatively more heterogeneous in composition. However, the availability of community type mapping in New York City allowed for confidence in our stratified sampling size and design, as well as for implications of interpreting our results. City-scale assessments of urban forested natural areas are relatively new (Pregitzer et al. 2019*a*) and classic forest measures, such as the U.S. Forest Inventory Analysis (FIA), are only now being adapted to urban sites. As work progresses, we will be better equipped to understand the sampling densities required for urban forests. Relatively little is known about the early life stages, from seed production, dispersal, and germination success, for tree species in urban forests. Long-term demographic data collection in urban forest communities, as well as common garden and seed addition experiments, are needed to better understand tree species-specific responses and site limitations. Together, these will define the relationship between drivers of change at global, regional, and local scales, urban forest succession dynamics, and to inform management decisions and strategies.

Managing for natural regeneration

Despite the structural similarity of urban forested natural areas to rural forests located in the same region, traditional methods of ecological forest management, such as silviculture have not been applied to the urban category (Piana et al., *in press*). Silviculture, the science and art of growing trees, is the traditional ecological management framework for rural forests and grounded in a complex understanding of site and silvics, the autecology of species (Ashton and Kelty 2018). Silviculture uses a deep understanding, often grounded in operational scale experiments, of population and community dynamics to prescribe management strategies that often leverage existing seed sources and create site conditions that favor specific species. For example, stand thinning often uses target spacing that is related to seed dispersal distances, as well as light and moisture requirements for desired species (Ashton and Kelty 2018). In the northeast United States, it is common for silviculture treatments to promote natural regeneration and advance regeneration, as opposed to direct planting (e.g., plantation forestry).

The management goals for urban forested natural areas are multiple and complex, however, as is observed in rural systems (e.g., Fahey et al. 2018), resilience and adaptation are emergent overarching objectives (Piana et al., *in press*). Natural and advance regeneration is a critical process that can increase structural and composition diversity in forests. Leveraging natural regeneration may expand the suite of on-the-ground strategies for urban forest management. However, basic metrics of forest stocking and long-term observation of population and community dynamics are lacking in urban contexts. Many forest restoration studies, conducted in degraded sites or in former canopy gaps, highlight the need for planting and resource-intensive management for long-term success, such as on-going removal of invasive plants (Simmons et al. 2016, Sasaki et al. 2018, Johnson and Handel 2019). However, there is a range of forest conditions present in urban forested natural areas, from invaded gaps to intact native canopy, stands that we might term "healthy forest." In New York City, intact native canopy is the dominant forest condition (Pregitzer et al. 2019*a*). We did find that native species were dominant across seedling, sapling, and seed stages, although there were significantly more nonnative species in urban sites. Our findings suggest that in these stands, advance regeneration may be adequate to sustain native forest communities. Given the high cost to restore degraded forested natural areas, or even create new forest in cities (Pregitzer et al. 2018), there is value in focusing on maintaining existing healthy forest. In such cases,

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traditional forest management approaches common in rural settings, complementing more active restoration strategies, may be viable options.

One passive restoration strategy is to rely on seed banks to replenish native plant stock. Seed banks are considered important determinants of succession and gap dynamics in North American eastern deciduous forests (Mladenoff 1990, Hyatt and Casper 2000), but the role of seed banks in regenerating forests may be limited (Pickett and McDonnell 1989, Hopfensperger 2007). Although rural forest seed banks have been extensively studied, there is woefully limited research on urban seed banks. Scattered studies suggest that urban forest seed banks contain more nonnative species when compared to rural forests (Kostel-Hughes et al. 1998, Pyšek et al. 2002, Beauchamp et al. 2013, Overdyck et al. 2013). There is less agreement on the abundance of woody species in the urban seed bank, and therefore, the potential for passive restoration. Some studies indicate that canopy-dominant species have low abundances and importance values in urban forest seed banks (Beauchamp et al. 2013, Wang et al. 2015). On the other hand, a study conducted in the same region as our sites demonstrated the potential for native woody plant recruitment from seed banks (Kostel-Hughes et al. 1998).

Here, we observed low abundances of woody species, and in particular, few dominant canopy species, in both urban and rural seed banks. Not only were few of the species present among forest strata represented in the urban seed bank, the majority of species in the seed bank were exotic invasive species. Of the large-seeded species, such as *Quercus* sp. and *Carya* sp., only two were found in urban soil seed banks despite their abundance in the canopy. Functionally, the importance of seed banks may be greater for smaller-seeded woody species associated with our study sites such as *Acer rubrum*, *Betula* sp., *Liriodendron tulipifera*, *Nyssa sylvatica*, *Robinia pseudoacacia*, and *Sassafras albidum* (e.g., Schiffman and Johnson 1992, Hille Ris Lambers et al. 2005, Hille Ris Lambers and Clark 2005). Our findings suggest that relying on the seed bank for passive restoration may not be a viable management option for urban forest regeneration.

Although the seed bank may not be relied upon, our results suggest that ambient seed rain in urban forested natural areas may be adequate to support natural regeneration and, subsequently, traditional silvicultural approaches. Urban forest seed rain, in particular, has rarely been quantified (e.g., Cutway and Ehrenfeld 2010, Overdyck et al. 2013, Labatore et al. 2016, Ettinger et al. 2017). In the only study to compare urban and rural seed rain, the authors report greater nonnative seed dispersed in urban forests than in rural forests (Overdyck et al. 2013). We found greater nonnative seed abundance in urban sites, but also found no difference in native seed abundance between sites, suggesting that urban sites were no more seed limited than rural sites. However, the entire recruitment natural history must be addressed; seed predation may limit the potential for broadcast seeding (Overdyck et al. 2013, Piana 2019).

Although not measured directly in our study, site factors, not seed availability, may be more limiting for natural regeneration. Specifically, given the high seed rain but lower abundance of seedlings in urban sites, we hypothesize that factors following seed dispersal through germination may be particularly affected. In silviculture, site conditions are frequently modified to promote specific species using techniques such as burning or soil scarification (Ashton and Kelty 2018). In urban sites, other barriers must be addressed to manage for native tree recruitment (Kowarik and Lippe 2018, Piana et al. 2019). For example, site factors might limit seed germination and managers may need to reduce soil contamination, compaction, or supplement organic layers. We found that some urban sites may be protected from deer and, therefore, more likely to support natural regeneration management strategies. In such areas, early herbivory may limit establishment, although there is little direct study of early herbivory in urban forests (Piana 2019). In these cases, strategies to protect seedlings, such as tree guards, may be needed until seedlings reach a self-defended size. Alternatively, urban sites may fundamentally be difficult for seedling establishment, and direct planting may be necessary. Small planting stock may be adequate, reducing costs.

The results from this study challenge the notion that urban forested natural areas are inherently recruitment limited and advance the potential to adapt traditional forest management approaches that may be more cost-effective and sustainable than current planting and restoration practices. This study highlights the need to examine specific drivers and barriers to recruitment in urban settings. Our findings may be most meaningfully implemented when paired with structured management scenarios that test shifts in urban forest ecosystem function and the outcomes of silvicultural strategies. We suggest continued research within multiple forest community types, the extension of long-term regeneration monitoring, and the introduction of urban-adapted silvicultural experiments to test novel regeneration management approaches.

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Data Availability

Data are available in Figshare: https://doi.org/10.6084/m9.figshare.13129529

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