DOI: 10.1111/avsc.12534

RESEARCH ARTICLE

Applied Vegetation Science



Forest patch size predicts seed bank composition in urban areas

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Funding information This project was funded through grants from Yale Institute of Biospheric Studies (2019) and the Hixon Center for Urban Ecology (2018).

Co-ordinating Editor: Vigdis Vandvik

Abstract

Questions: As urban areas expand around the world, understanding how to restore and maintain forests within the urban environment becomes increasingly important. Given that a comprehensive understanding of regeneration dynamics is critical to designating appropriate management interventions we ask the following: how does regeneration, vis-à-vis the buried seed bank, vary in heterogenous urban forests? And, can forest patch size be used to predict regeneration and consequent management interventions?

Location: Vacant lots and public parks throughout New Haven, CT, USA.

Methods: We sampled buried seed banks in 131 plots distributed across three forest patch sizes ranging from large intact parks (95-126 ha), to small parks (1-19 ha), and vacant lots (0.05-0.65 ha). We collected soil samples from the surface mineral soil and stratified them over sand in a greenhouse over a period of five months to record germination.

Results: By examining seed bank floristics in a range of forest patch sizes we found that species composition, nativity, and dominance of specific functional groups shifted with patch size representing a spectrum of urbanization within just one city. Seed bank floristics in large parks more closely resembled results from seed bank studies in rural forests with over 85% native germinants on average. In contrast, vacant lots were dominated by non-native germinants and more ruderal species indicative of earlier successional stages. Seed banks in small parks were variable and in some cases were more similar to large parks or vacant lots.

Conclusions: Our findings suggest that large parks in urban areas may be largely selfsustaining whereas smaller parks may require more intensive management for site rehabilitation, especially in early states of succession. Furthermore, our results confirm the highly heterogenous nature of urban forest patches and call for more systematic sampling of urban areas to capture this variation and improve management prescriptions and outcomes.

KEYWORDS

invasive species, life history traits, management, native species, recruitment, regeneration, restoration, seed bank floristics, urbanization, vacant lots

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1 | INTRODUCTION

Urbanization is rapidly increasing around the world (Seto et al., 2012). As cities expand their footprint through urban development, intact natural areas are converted to a patchy matrix of built structures, impervious surface, and remnant natural areas (Luck and Wu, 2002). These fragmented natural areas have the potential to provide valuable ecosystem services and to help regionally mitigate the impacts of global climate change (Pataki et al., 2011). As such, there is interest in managing and restoring undeveloped and park lands in cities to establish closed-canopy, native-dominated forests that can provide these services. While the need to manage urban forests is well documented (Tyrväinen et al., 2003; Oldfield et al., 2013) the best approach to doing so is still unknown (MacKay et al., 2011).

Buried-seed-bank studies have been utilized in a variety of community types (grasslands, forests, marshes, heathlands) and across a range of environments (mediterranean, tropical, temperate) to help predict restoration success and inform restoration programs (Bossuyt and Honnay, 2009). Buried seed banks serve as species reservoirs consisting of transient, short-term persistent, and persistent seeds (Gioria et al., 2012). These seeds remain dormant until they are exposed to favorable germination conditions such as increased light, temperature or moisture -conditions often associated with disturbances and ecosystem perturbations (Weerasinghe et al., 2019). Therefore, these seed banks represent both the "ecological memory" of the site as well as the future composition if in situ disturbance creates favorable germination conditions (Leck et al., 1989). As such, the buried seed bank serves as a crucial stepping stone in understanding the successional trajectory of a site and consequently the management interventions - if any - that are best suited to that site (Bossuyt and Honnay, 2009).

While this approach has been successfully employed in non-urban settings (Bossuyt et al., 2002) few studies to date have examined buried seed banks in urban areas. Given that the availability of native seed sources has been identified as one of the most significant bottlenecks to restoration in urban settings, this represents a critical research gap (Labatore et al., 2017; Doroski et al., 2018). The few urban buried-seed-bank studies that have been done, used either an urban-rural gradient (Pellissier et al., 2008; Hahs and McDonnell, 2013) or urban vs. rural dichotomy sampling design (Kleyer, 2002; Overdyck and Clarkson, 2012). While these studies have elucidated important findings regarding the presence of native and invasive species (Kostel-Hughes et al., 1998; King and Buckney, 2001; Overdyck and Clarkson, 2012; Hahs and McDonnell, 2013), they have limited applications to urban forest management because they focus on discerning differences between urban as compared with suburban and rural forests rather than capturing the range of conditions that exist within the urban forest matrix.

For example, Kostel-Hughes et al. (1998) and Overdyck and Clarkson (2012) both found higher densities of non-native invasive species in urban compared with rural buried seed banks. As increasing the presence and abundance of native species is the main target of most urban forest restoration projects (Oldfield et al., 2013), this suggests that urban forested areas will require more intensive management than their rural counterparts. Consistent with this notion, many restoration projects invest in the removal of invasive species and planting of native species (with a particular emphasis on native tree species) in an effort to lower invasivespecies abundances and establish structurally complex forests (Johnson and Handel, 2016). However, there may be situations in the urban forest where native species do dominate the seed bank making these time-and labor-intensive interventions poorly suited to the site slated for restoration.

In order to redress this management conundrum, we took a patch size approach to our buried-seed-bank study. There is a wealth of theoretical papers advocating for a patch approach to urban land management (Zipperer et al., 1997; Zipperer et al., 2000). This is because urban development fragments forest patches at several critical scales ranging from large parks to small vacant lots. This fragmentation has profound impacts on ecological processes and structure in urban forest patches. For example, depending on patch size, forest fragments will have varying degrees of edge effect (Murcia, 1995), limited seed sources (Chazdon, 2008), and unique disturbance regimes (Pickett et al., 2001). The extent to which these urban stressors impact a given forested area will then have major implications on the buried seed bank and, ultimately, on the direction and intensity of our restoration efforts.

Previous research in urban areas has applied the theory of island biogeography to show how patch size can predict the distribution of existing invasive plant species (Vidra and Shear, 2008), species composition (Zipperer, 2002; Honnay et al., 2005), plant species richness/diversity (Hobbs, 1988; Godefroid and Koedam, 2003), and faunal communities (Gibbs, 1988; Renjifo, 2001) in urban forest patches. These findings confirm differences between patch sizes but do not report key information essential to restoration especially regarding seed stocks that may remain latent in the soil. This poses a significant limitation to our ability to predict what treatments are needed to rehabilitate a forest patch or whether urban forest patches can naturally recover without human intervention.

In order to fill this information gap, we examined buried seed banks in 26 urban forest patches throughout New Haven, CT, USA. Our patches ranged in size from large forested parks (126 ha) to small vacant lots (0.05 ha). Because native forest cover is the primary goal of urban forest restoration projects, we wanted to examine if and how the nativity and life form (i.e., presence of trees as opposed to herbs or vines) of germinants in the buried seed bank shifted between different patch sizes. We also sought to examine trade-offs in other life history traits to better understand how dispersal limitations could impact restoration success and how life-cycle strategies could illuminate successional stages in different forest patches. Ultimately, by exploring the relationship between patch size, connectivity, and the buried seed bank, we highlight the inherent heterogeneity within the urban environment and use this framework

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to provide managers the basis for the construction of more refined guidelines regarding urban forest restoration.

2 | METHODS

2.1 | Site description

We conducted this study in 17 parks and nine forested vacant lots throughout New Haven, CT, USA (41.3083° N, 72.9279° W). New Haven is a small city located on Long Island Sound in southern Connecticut (Figure 1). Average temperatures in July and January are 24.0°C and -0.8°C respectively; mean annual rainfall is 112.0 cm (NOAA, 2018). Soils in the region are classified as well-drained cambisols (FAO/UNESCO, 2019); the city itself is dominated by anthropogenic soil types including the Udorthents and Penwood urban complexes (NRCS, 2019) (see Appendix S1 for a complete list of study sites and soil types). Oak-hickory is the dominant forest type and includes a forest canopy comprised primarily of *Quercus, Carya, Acer,* and *Betula* species (Wharton et al., 2004).

2.2 | Experimental design

In order to capture a representative sample across our study sites, we employed a proportionate stratified sampling design. We stratified sites by patch size — this included large parks (95–126 ha, n = 4), small parks (1–19 ha, n = 13), and vacant lots (0.05–0.65 ha, n = 9). We used a sampling fraction of 1/10 in each stratum so that the number of plots in each park/lot was proportional to the overall

FIGURE 1 Location of parks and vacant lots in New Haven, CT, USA. New Haven city center is starred, all parks and lots fell within 8 km of this point. Blue polygons designate large parks, green designates small parks, and orange points are vacant lots

park/lot area. This approach allowed us to sample a proportionally similar area of each stratum while still accounting for large discrepancies in overall patch size (126 ha vs. 0.05 ha) (see Appendix S1 for patch sizes and the corresponding number of plots). We selected our parks from the State of Connecticut Department of Energy & Environmental Protection's Municipal and Federal Open Space Layer (Department of Energy & Environmental Protection, 2018) and New Haven Land Trust land holdings (New Haven Land Trust, 2018) using Global Information Systems (ArcGIS 10.4). We limited our site selection to parks that fell within 8 km of the geographical center of New Haven (Figure 1). All of our sites fell within an urban developed landscape. Because we were only interested in forested systems, we removed areas within parks that were classified as "hydric" or paved road (Department of Energy & Environmental Protection, 2018) using the erase feature in GIS. From this subset of polygons, we visually inspected each area using satellite imagery (Esri, 2018) and created new park polygons that encompassed forested areas only. The city of New Haven keeps records of vacant lots (Livable City Initiative, 2018) and we used this database to identify forested vacant lots within the city bounds. All of the parks and lots in this study would be considered second-growth forests with established canopies (see Appendix S2 for examples of typical forest cover in large parks, small parks, and vacant lots). These forests established post-development or agricultural abandonment in the last 150 years (see Appendix S1 for the approximate age of each forest). Given the large size of many of our parks we anticipated spatial variation in vegetation so we utilized a systematic sampling method to capture heterogeneity within our study sites. Using a random starting point, we laid a grid over each park or lot with the fishnet feature in ArcGIS to identify plot centers for each site. We adjusted the grid



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size depending on patch stratum. To measure connectivity between forest patches we used satellite imagery in ArcGIS to measure the distance (in meters) from plot center to the closest forest patch, hereafter referred to as "distance to nearest forest patch." Before sampling, we ground-truthed all of our study sites to make sure that they fell within forested areas and did not have evidence of recent management (i.e., mowing).

2.3 | Field measurements

We collected soil samples and measured the landscape attributes for 131 plots across 26 sites (parks + vacant lots) in June of 2018. We located plots in the field using a handheld GPS unit (Garmin eTrex Vista H, Garmin Ltd., Olathe, KS, USA) and measured 2 m in each cardinal direction. At each of these four points and at the plot center we took one soil sample which we later combined into one composite seed bank sample per plot. We took all samples with a 7-cm diameter soil core to a depth of 7 cm. This method insured that we collected equal volume across all plots and sites. Before sampling, we removed any surface litter layer or gravel but included the fine component of the organic layer. We sealed composite samples in plastic bags and refrigerated them at 4°C for up to five days prior to processing at the greenhouse.

2.4 | Greenhouse analyses

After a five-day refrigeration period, we processed soils at the greenhouse to remove any litter, large roots, rocks, or other debris. We filled 131 plastic germination trays with 1 cm of sterilized sand and 2 cm of sterilized potting soil (Sun Gro Metro-Mix®, Sun Gro Horticulture, Agawam, MA). We then spread our field-collected soil samples (one composite sample per plot amounting to 450 cm³ of soil) evenly over the sand/potting soil mixture at 0.5 cm thickness to ensure complete germination. We filled five additional trays with the sand/potting soil mixture only and randomly dispersed them throughout the greenhouse to serve as control trays to track any weed seeds or potential contaminants. We watered trays with an overhead misting system twice a day for four minutes total (two minutes in the morning and two in the evening). Every five days we checked trays for new germinants and either identified them to species or repotted samples and grew them on until they could be identified. We randomly reassigned the location of each tray once per week inside the greenhouse to reduce the effect of any spatial variations in temperature and light intensity. We monitored germination over a period of five months (June 2018-November 2018). After the fourth month, we removed all germinants, scarified the soil and monitored trays for one additional month until no new germination occurred. While previous buried-seed-bank studies suggest that six months to two years is required to capture all potential germinants, we were primarily interested in the species that germinated first and most abundantly as these have a competitive advantage

in establishment and therefore the greatest restoration implications (Warr et al., 1993). Most germination in buried seed bank studies has been found to occur within the first two months (Graber and Thompson, 1978) and therefore we felt that our timeframe was appropriate given our research objectives. By the fifth month, we were recording no new seedlings germinating on a weekly basis. In the limited cases when we were not able to identify a seedling to species without reproductive material, or when a seedling succumbed to mortality before a species level identity was confirmed, we used congeneric or confamilial classification in the analyses (see Appendix S3 for a complete list of germinants). These cases collectively amounted to <3% of all germinants in our study. We had three individual seedlings that we were unable to identify to the genus or family level due to damping off mortality so we removed them from our analysis.

2.5 | Statistical analyses

We created a series of generalized linear mixed-effect models (GLMMs) to test for differences in the number and composition of seed bank germinants in our three patch size classes (large parks n = 48, small parks n = 60, and vacant lots n = 23) and with varying distances to the nearest forest patch. We used R version 3.5.1 software (R Core Team, 2019) to complete all statistical analyses and the "glmer" function in the "*Ime4*" package for GLMMs (Bates et al., 2015).

To determine how patch size impacted the total number of germinants we created a GLMM with the number of germinants in each plot as a response variable, size class (large park, small park, vacant lot) as our predictor variable, and park as a random effect assuming a negative binomial error distribution. We used a negative binomial distribution because the total number of germinants was rightskewed and overdispersed. We included park as a random effect in our model to incorporate park-to-park variability and improve our ability to describe how our fixed effects relate to seed bank floristics. We used the "glm.nb" function in the "MASS" package (Venables and Ripley, 2002) to build our negative binomial GLMM.

To determine how patch size impacted the species richness of germinants we built a GLMM with species richness as our response variable, size class as our predictor variable and park as a random effect assuming a Poisson error distribution. Because our sample size was uneven between size classes, we also included the log of our sample effort (i.e., number of plots in each size class) as an offset function to ensure that our smallest size class (vacant lots, n = 23) was equally represented in terms of species richness (Geyer et al., 2003). We then used species accumulation curves to compare species richness between size classes using the "rarefaction" method. We selected this method because it rarefies richness to both the number of plots and the number of individuals, therefore accounting for both our uneven sample design as well as the fact that vacant lots in our study had significantly more germinants than small and large parks overall. This allowed us to discern whether patterns in species richness were best explained by differences between size classes or by differences in the number of germinants in each size class. We used the "specaccum" function in the "vegan" package for species accumulation curves (Oksanen et al., 2019). To determine how distance to nearest forest patch impacted species richness we built a separate GLMM using data from small parks and vacant lots only. We excluded plots from large parks in this model because the size and shape of our large parks would make dispersal from other areas within the same park more likely than dispersal from adjacent forest patches (Figure 1). We set species richness as our response variable, average distance to nearest forest patch as our predictor variable and park as a random effect assuming a Poisson error distribution. Again, we included the log of our sample effort as an offset term.

Because we were also interested in how patch size could impact species composition, particularly regarding the nativity and life history traits of germinants, we categorized individual species using data from the United States Department of Agriculture (USDA) PLANTS database (USDA NRCS, 2018). We classified individual germinants based on nativity (native, non-native) according to the USDA PLANTS database with one exception. Robinia pseudoacacia, a tree native to the southeastern United States is classified as native by the USDA but is considered invasive throughout the northeastern United States where it is actively managed/removed in natural areas (Black Locust (Robinia pseudoacacia)|Connecticut Invasive Plant Working Group, 2019; Mass Audubon, 2019). As our goal was to frame results for management, we classified Robinia pseudoacacia as a non-native species in our study. We also categorized germinants based on life-cycle strategy (annual, perennial, or biennial), life form (trees, shrubs, herbs, subshrubs (low-growing shrubs typically under 0.5 m tall), graminoids, or vines), and dominant dispersal mode (wind-, gravity-, bird-, insect-, or mammal-dispersed) (USDA NRCS, 2018). While some of these species traits were correlated with each other, each trait was analyzed separately with the aim of informing a specific management prescription (see Appendix S4 for a correlation matrix of these different trait/nativity categories). Nomenclature for all individuals follows the USDA PLANTS database (USDA NRCS, 2018).

We constructed another series of GLMMs to test how patch size class and distance to nearest forest patch impacted nativity and species traits. Because our goal was to evaluate trade-offs in traits and nativity between patch sizes, we built our GLMMs with a binomial error distribution and the proportion of germinants with each species trait as our response variable rather than using raw abundance data. This approach tests for shifts in the proportion of a particular species or species trait in relation to a predictor variable (Clarke et al., 2015; Doroski et al., 2018) and helped standardize data from vacant lots which had significantly more germinants than our large and small parks.

To test for differences in nativity, we built a GLMM with germinant nativity (native vs. non-native) as a response variable, size class as a predictor variable, park as a random effect and a binomial error distribution. To test how size class impacted life form, we built five GLMMs for each of the five categorical life forms (trees + shrubs,

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herbs, subshrubs, graminoids, and vines). We combined trees and shrubs into a single life form category because shrubs were relatively rare in our study representing less than 5% of all germinants and only four species (Kalmia angustifolia, Rhus copallinum, Rhus glabra, and Rhus typhina). For each of these five GLMMs, we set relative germinant life form (i.e., the number of germinants of life form A vs. number of germinants of all other life forms) as our response variable, size class as a predictor variable, park as a random effect and used binomial error distributions. We created three separate GLMMs for the three life-cycle strategies (annual, perennial, biennial) so that our response variable was number of germinants with one life-cycle strategy vs. number of germinants with all other life-cycle strategies, size class was a predictor variable, park was a random effect and used binomial error distribution. Finally, we built five GLMMs for the five dispersal modes (wind-, bird-, gravity-, insect-, or mammal-dispersed) with germinant dispersal mode (number of germinants with a specific dispersal mode vs. number of germinants with all other dispersal modes) as our response variable, size class as our predictor variable, park as a random effect and a binomial error distribution. To test how distance to nearest forest patch impacted germinant traits and nativity, we used the same model structure as above but set distance to nearest forest patch as our predictor variable and used data from small parks and vacant lots only.

Finally, to test for differences in species composition between our patch sizes, we used indicator species analyses and non-metric multidimensional scaling (NMDS). To identify individual species that are characteristic of a group of samples (in our case patch size) we utilized indicator species analyses which use relative species frequency and abundance to distinguish between samples. We used "multipatt" function in the "indicspecies" package (De Caceres and Legendre, 2009) with 999 permutations on relative species abundances. We considered a species a true indicator if it had an indicator value over 0.4 and a p-value < 0.05. To visualize differences in species composition, we constructed ordination diagrams using NMDS with Bray-Curtis distance. We performed NMDS on standardized species data using the Wisconsin double standardization to account for the fact that vacant lots had significantly more germinants overall than large parks and small parks and dropped plots that did not have any regeneration (n = 3). Final stress for the best solution was 0.11 with five dimensions. We used the "metaMDS" function in the "vegan" package for NMDS (Oksanen et al., 2019).

3 | RESULTS

3.1 | Germinant floristics

We recorded a total 2,325 germinants representing 85 species from 63 genera in 40 families (see Appendix S3 for full list). On average, plots had 16.5 germinants (\pm SE 2.1) per 450 cm³ of soil, though the number of germinants ranged from zero (n = 3) to 190. Average species richness was 4.9 (\pm SE 0.3) with the most species-rich plot having 14 different species.





FIGURE 2 Species accumulation curves for large parks (green), small parks (yellow) and vacant lots (navy). When each size class is rarefied back to the lowest number of plots (n = 23) species richness was significantly higher in vacant lots than in large parks (a). However, when richness is adjusted for the total number of individuals overlap between species accumulation curves suggest that there is no difference in species richness between size classes (b). Vertical lines indicate standard deviation

Across all sites, herbaceous germinants dominated the seed bank accounting for 43% of total germinants followed by trees and shrubs (30%), graminoids (14%), subshrubs (12%), and vines (1%). Herbs also represented the most species-rich life form with 47 herb species recorded, followed by graminoids (17 species), trees and shrubs (15), subshrubs (4), and vines (2). Native species were slightly more abundant than non-native species with 53% of germinants representing native species. Perennial species dominated the seed bank representing nearly 68% of germinants followed by annual (25%) and biennial (7%) species. Most germinants were primarily wind-dispersed (48%) followed by 29% that were bird-dispersed, 20% gravity-dispersed, 2% that were insect-dispersed (primarily by ants), and less than 1% that were mammal-dispersed (namely Galium aparine which has seeds that attach to human clothing and animal fur). The most abundant families included Fabaceae (legumes = 14%) followed by Asteraceae (composites = 14%), Rosaceae (roses = 12%), and Solanaceae (nightshades = 8%).

3.2 | Germinant floristics in relation to patch size

Seed banks in vacant lots had the highest number of germinants of all the size classes sampled (GLMM, coefficients ± standard error, p-value; intercept = 2.175 \pm 0.302, p \leq 0.05; small parks = 0.533 ± 0.358 , p = 0.136; vacant lots = 0.868 ± 0.401 , $p \leq 0.05$). On average, plots in vacant lots had nearly three times more germinants than large parks (large parks = 9.8 ± 1.6 , small parks = 17.9 ± 2.8 , and vacant lots = 26.8 ± 7.9). Species richness was also significantly higher in vacant lots than in large parks (GLMM, coefficients \pm standard error, *p*-value; intercept = -2.673 \pm 0.157, $p \le 0.05$; small parks = 0.226 ± 0.183, p = 0.216; vacant lots = 1.433 ± 0.199 , $p \le 0.05$). When species richness was rarefied back to the smallest sample size (n = 23), vacant lots had over 1.25 times more species than large parks (Figure 2a). However, this trend was largely driven by the higher number of germinants in vacant lots as compared with large parks. When richness was rarefied by the number of individual germinants, there was no difference in species

richness between size classes (Figure 2b). Richness did not shift with distance to nearest forest patch (GLMM, coefficients \pm standard error, *p*-value; intercept = -2.270 \pm 0.245, *p* \leq 0.05; distance to nearest forest patch = 0.0003 \pm 0.0002, *p* = 0.18).

Different patch sizes also exhibited trade-offs in nativity. On average, seed banks in large parks were comprised of over 85% native germinants as compared with 53% and 39% native germinants in small parks and vacant lots, respectively (Table 1a; Figure 3). As parks/lots became more isolated (i.e., as distance to nearest forest patch increased) the proportion of native germinants also decreased (Table 1b).

Dispersal mode was also impacted by patch size. While wind-dispersed species dominated the seed bank across all patch sizes, the proportion of wind-dispersed species was significantly higher in large parks than in small parks and in vacant lots (Table 1a; Figure 4a). On average, over 76% of the germinants in large parks were wind-dispersed species compared with less than 47% in small parks and 48% in vacant lots. In contrast, small parks had two times more bird-dispersed species than large parks and 1.3 times more than vacant lots (Table 1a; Figure 4b). Over 35% of the germinants in small parks were bird-dispersed compared with only 17% in large parks and 27% in vacant lots. Vacant lots and small parks also had higher proportions of gravity-dispersed species with 10.5 and nearly 3.5 times more gravity-dispersed species than large parks, respectively (Table 1a; Figure 4c). As lots and parks became more isolated, the proportion of gravity-dispersed germinants also increased significantly (Table 1b).

Different patch sizes also had trade-offs in dominant life-cycle strategies and life forms of germinants. Large parks had on average half as many annual germinants as small parks and vacant lots (Table 1a). Only 15% of the germinants in large parks were annual species compared with 26% in small parks and 35% in vacant lots. In terms of life form, trees and shrubs were evenly distributed across patch sizes (Table 1a). However, the number of herbaceous germinants was marginally significantly higher in vacant lots than in large parks (Table 1a). Conversely, large parks had significantly more graminoid germinants than vacant lots and small parks (Table 1a).

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(a)	Intercept (large parks)	Small park	Vacant lot
Nativity			
Proportion of natives	2.104 ± 0.427	-2.082 <u>+</u> 0.487	-2.623 <u>+</u> 0.516
Dispersal			
Proportion of wind-dispersed	1.038 <u>+</u> 0.515	-1.431 ± 0.592	-1.119 <u>+</u> 0.625
Proportion of bird-dispersed	-1.624 <u>+</u> 0.406	0.964 <u>+</u> 0.465	0.373 ± 0.496
Proportion of gravity-dispersed	-3.218 <u>+</u> 0.807	$1.258 \pm 0.918^{*}$	1.388 ± 0.967
Life form			
Proportion of trees and shrubs	-0.484 ± 0.576	-0.809 ± 0.225	-0.394 ± 0.703
Proportion of subshrubs	-3.228 <u>+</u> 0.636	$1.281 \pm 0.708^{*}$	-1.059 ± 0.813
Proportion of herbs	$-0.831 \pm 0.480^{*}$	0.523 ± 0.553	$1.027 \pm 0.585^{*}$
Proportion of graminoids	-1.707 <u>+</u> 0.557	-0.526 ± 0.647	-0.948 ± 0.700
Life-cycle strategy			
Proportion of annuals	-1.731 <u>+</u> 0.570	0.563 ± 0.553	0.911 ± 0.583
Proportion of perennials	1.063 <u>+</u> 0.459	-0.286 ± 0.529	-0.815 ± 0.559
Proportion of biennials	1.238 <u>+</u> 0.339	-0.58 ± 0.520	0.04 ± 0.520
(b)	Intercept		Distance to nearest forest patch
Nativity			
Proportion of natives	0.398 ± 0.318		-0.0007 ± 0.0003
Dispersal			
Proportion of wind-dispersed	0.156 ± 0.401		-0.0005 ± 0.0004
Proportion of bird-dispersed	-0.472 ± 0.322		-0.0005 ± 0.0003
Proportion of gravity-dispersed	-2.835 ± 0.001		0.0011 ± 0.0005
Life form			
Proportion of trees and shrubs	-1.092 ± 0.037		0.0001 ± 0.001
Proportion of subshrubs	-1.925 ± 0.485		$-0.0009 \pm 0.0004^{*}$
Proportion of herbs	-0.096 ± 0.406		-0.0000 ± 0.0004
Proportion of graminoids	-2.027 <u>+</u> 0.482		-0.0005 ± 0.0005
Life-cycle strategy			
Proportion of annuals	-1.017 ± 0.383		-0.0001 ± 0.0002
Proportion of perennials	0.244 ± 0.3812		0.0004 ± 0.0004
Proportion of biennials	-1.757 ± 0.320		-0.001 ± 0.0003

TABLE 1 Results from generalized linear mixed-effects models exploring the effects of (a) patch size and (b) distance to nearest forest patch on nativity and species traits of germinants in the buried seed bank in New Haven, CT, USA

Note: Model coefficients \pm standard error significant at p < 0.05 are bolded, marginally significant results at p < 0.10 are marked with *. See *Methods* for model construction.

3.3 | Species composition in relation to patch size

While the distribution of trees and shrubs was even across all patch sizes, the distribution of individual tree species differed. Given that the presence of trees is critical to achieving management goals to establish forest cover, we examined how different tree species were distributed across our forest patch sizes. In our study, three tree species accounted for 81% of all the tree/shrubs recorded (*Robinia pseudoacacia* = 46%, *Betula lenta* = 23%, *Ailanthus altissima* = 12%). These species, however, were not evenly distributed across patch size classes. The native *Betula lenta* was associated primarily with large parks (Indicator Value (*IV*) = 0.677; $p \le 0.05$) and was over 8.75

times more abundant in large parks as compared with vacant lots. The non-native *Robinia pseudoacacia* was associated with vacant lots (IV = 0.659; $p \le 0.05$) and was 200 times more abundant in vacant lots than in large parks and over fourtimes more than in small parks. The non-native *Ailanthus altissima* (IV = 0.613; $p \le 0.05$) was associated with both small parks and vacant lots and was over seven times more abundant in vacant lots than in large parks and over fourtimes and over 4.5 times more abundant in small parks than in large parks. In addition to *Robinia pseudoacacia*, vacant lots were also characterized by nonnative annual herbs including *Mollugo verticillata*, *Verbascum thapsus*, *and Chenopodium album*. For a complete list of indicator species see Table 2.





FIGURE 3 The proportion of native to non-native species decreased significantly with decreasing patch size. Green, yellow, and navy points represent the native to non-native ratio for germinants at each plot in large parks, small parks, and vacant lots respectively. Violin plot outlines illustrate kernel probability density; wider sections represent a higher probability of observations taking a given value whereas thinner sections correspond to a lower probability. Black points represent mean values for each size class, black lines are standard error

Overall plant composition also shifted between patch sizes (Figure 5). Vacant lots and large parks had minimal overlapping along axis 1 and 2 whereas plots in small parks were more spread out and indistinguishable from vacant-lot and large-park plots.

4 | DISCUSSION

Our study finds that the floristics of the buried seed bank — and consequently the management interventions required — represent a spectrum of urbanization within just one city. Our results show that forest patch size and connectivity can help predict trends in species composition and assemblages — as such we recommend that land managers consider forest patch size and proximity to nearby forest when designing management interventions.

One of the most frequently cited urban restoration goals is to steer species composition toward a "native-dominated" forest system (Oldfield et al., 2013; Pregitzer et al., 2018). In order to achieve this, many cities invest significant resources in planting projects aimed at increasing the number of native species in the urban forest (Moro and Castro, 2015; PlaNYC, 2019). This is based on the expectation that natural regeneration of native species will not occur without human intervention. While other buriedseed-bank studies have found that non-native species dominate the seed bank in urban areas (Overdyck and Clarkson, 2012; Hahs and McDonnell, 2013; Londe et al., 2017), we found this to only be the case for vacant lots in our study. Rather, large parks in our study were comprised of over 85% native species - a result that is more consistent with findings from buried-seed-bank studies in temperate rural forests rather than urban ones (Ashton et al., 1998; Leckie et al., 2000). Large parks in our study were also more similar to rural forests having a relatively higher proportion of graminoids than the smaller patch sizes (Ashton et al., 1998; Leckie et al., 2000). Additionally, in our large parks, one native tree species, Betula lenta, comprised 84% of all tree germinants. This is similar to seed bank studies by Ashton et al. (1998), Leckie et al. (2000), and Tiebel et al. (2018) who also found that Betula species dominate the seed bank in non-urban forests. While plant communities dominated by native species are the primary goal of most urban forest restoration efforts, the similarity in species composition of our large parks to non-urban parks suggests that these parks are more similar to a target ecosystem and not as degraded as previously thought (Shochat et al., 2010). Consequently, these large forest patches may not require the same intensity of management as smaller patches because an intact seed bank of native species for regeneration is already present.

Large parks also had the highest proportion of wind-dispersed germinants as compared with small parks and vacant lots. While wind-dispersed species typically dominate buried seed banks (Bakker et al., 1996), we found that the abundance of these species diminished with patch size reflecting the physical and biotic limitations to dispersal in urban areas (Schleicher et al., 2011). Instead, small parks were largely dominated by bird-dispersed and vacant lots with gravity-dispersed species. This was even more pronounced for lots/parks that were located further from nearby forest patches. Because seed banks are reflective of the species available for recruitment at a given site before habitat filtering takes place (Török et al., 2018), these distinct communities make a case for dispersal as a primary structuring mechanism of future urban forests. Thus, in smaller more spatially isolated patches, target broadcast seeding of desirable wind-dispersed native tree species (e.g., Betula spp.) may offer an inexpensive way to increase native tree species diversity in these sites.

Small parks in our study exhibited the most variation across patch sizes; in some cases, resembling large parks and in other cases vacant lots in terms of species composition, nativity, and species traits. While patch size does play a role in shaping the buried seed bank, our small parks also highlight the importance of landscape connectivity in appropriately prescribing management interventions. In our study, small parks and vacant lots that were further from nearby forest had



FIGURE 4 The proportion of wind-dispersed (a), bird-dispersed (b), and gravity-dispersed (c) germinants in each patch size. Winddispersed species were significantly less abundant in vacant lots and small parks as compared with large parks whereas bird-dispersed species were highest in the small park size class and gravity-dispersed species were highest in small parks and vacant lots. Green, yellow, and navy points represent the proportion of wind-dispersed, bird-dispersed, and gravity-dispersed species for germinants at each plot in large parks, small parks, and vacant lots, respectively. Violin plot outlines illustrate kernel probability density; wider sections represent a higher probability of observations taking a given value whereas thinner sections correspond to a lower probability. Black points represent mean values for each size class, black lines are standard error

higher proportions of non-native species. Consequently, land managers aiming to increase native species cover in small parks may want to evaluate the proximity of a given park to nearby forest patches as a second tier to their decision-making.

Our smallest patch size, vacant lots, consistently represented the earliest successional stage and most degraded habitat in terms of species composition. Seed bank analyses for the vacant lots in our study corroborate results from other urban seed bank studies being non-native dominated (Overdyck and Clarkson, 2012; Hahs and McDonnell, 2013; Londe, et al., 2017). The abundance of non-native species may be attributed to relatively higher edge-to-interior ratios in vacant lots as compared with large parks. While some of our vacant lots were large enough (0.65 ha) to have plots situated in what would be considered "interior forest," in most cases (70% of plots), they fell within 15 m of either a road or residential area. King and Buckney similarly conducted a seed bank study in an urban bushland and found that the proportion of invasive species was greatest in seed banks 10–20 m from forest edge (King and Buckney, 2001). Given that roads are known corridors for invasive species (Hulme, 2009) we suspect some of the trade-offs in nativity observed in our study are reflective of exacerbated edge effects and unique landscape structures in vacant lots.

Vacant lots in our study were also similar to other urban buried-seed-bank studies in being dominated by herbaceous species (Pellissier et al., 2008; Overdyck and Clarkson, 2012; Londe et al., 2017). The abundance of herbaceous germinants suggests an earlier successional stage and has implication for restoration projects aimed at establishing forest cover as these herbs could slow forest succession by competing with tree species. The one tree species that

 TABLE 2
 List of indicator species for each patch size in order of highest indicator value per size class

	Species	Indicator value	p- Value
Large Parks	Betula lenta	0.677	0.001
Small Parks	Muhlenbergia frondosa	0.459	0.016
Vacant Lots	Robinia pseudoacacia*	0.659	0.001
	Mollugo verticillata*	0.504	0.003
	Verbascum thapsus*	0.452	0.003
	Chenopodium album*	0.437	0.004
Vacant Lots + Small Parks	Solanum physalifolium*	0.652	0.001
	Ailanthus altissima*	0.613	0.001
	Phytolacca americana	0.489	0.007
	Rubus occidentalis	0.411	0.033

Note: Non-native species are marked with *. Indicator species analysis was run on relative species abundances with 999 permutations. Statistically significant results are reported with indicator values and *p*-values.

was strongly associated with vacant lots was *Robinia pseudoacacia*, an early-successional nitrogen-fixing species (Phillips and Shure, 1990). Kim and Lee (2005) examined seed bank composition in urban landfills and similarly found that woody recruitment was dominated by *Robinia pseudoacacia*. Their study sites, much like our vacant lots, are consistent with patterns of primary succession in rural forests where lethal disturbances remove existing substrate and fast-growing nitrogen-fixing species are among the first to re-colonize (Vitousek et al., 1993). Interestingly, Robinia pseudoacacia is specifically targeted in many restoration projects as an invasive to be removed (Black Locust (Robinia pseudoacacia)|Connecticut Invasive Plant Working Group, 2019; Mass Audubon, 2019) but in our study, we found it was almost completely restricted to vacant lots. This suggests that this species is unlikely to invade surrounding larger forests following disturbance. Rather, Robinia pseudoacacia may play a critical role in recapturing sites that have recently been abandoned and rebuilding soil and organic matter in a primary succession scenario for urban areas; similar to its role as an old-field successional dominant in its native range further south (Phillips and Shure, 1990). As such, current management that actively removes this species may want to shift objectives away from removal of Robinia pseudoacacia and instead allocate resources to the removal of other invasive tree species (such as Ailanthus altissima) that appear to dominate seed banks in small parks as well (Table 2).

As our investment in urban forested areas increases, so too should our understanding of the unique dynamics and conditions within these stands. As a nascent field, urban forestry is quickly becoming recognized as a complex and nuanced system that can be better understood by leveraging tools and methods from rural forestry and other fields. Our seed bank study adds another layer of complexity and comprehension of urban forest stand dynamics. By highlighting the range of regeneration that exists in urban forest patches, findings from our study can help inform urban forest management and make a case for a patch approach to sampling forests within the urban matrix.



FIGURE 5 Compositional shifts between large parks, small parks, and vacant lots. The first two dimensions of five are displayed to show maximum variance. Minimal overlap between plots in large parks (green points) and vacant lots (navy points) suggests species composition is more unique in these two size classes. In contrast, plots in small parks (open yellow points) are indistinguishable from large parks and vacant lots

ACKNOWLEDGEMENTS

This study took place on the territorial homeland of the Quinnipiac peoples. We thank the Livable City Initiative, New Haven Department of Parks and Recreation, and New Haven Land Trust for information on and access to our field sites; the New Haven Promise Program and Hixon Center for Urban Ecology for logistical support; the Ashton and Duguid Labs at Yale University and Rich Hallett for feedback on the study design and analysis.

AUTHOR CONTRIBUTIONS

DAD and MPA conceived and designed the study. DAD collected the data, DAD and MCD performed statistical analyses. DAD wrote the paper and all authors contributed to the final manuscript.

DATA AVAILABILITY STATEMENT

All data supporting our results is archived in Dryad, a public repository at https://doi.org/10.5061/dryad.8w9ghx3hs.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

Appendix S1. Study sites in New Haven, CT, USA

Appendix S2. Photos with examples of the large parks, small parks, and vacant lots sampled in New Haven, CT, USA

Appendix S3. Family, nativity, life-cycle strategy, life form, dispersal mechanisms, relative abundance (% of all germinants), and distribution (% of plots present in) of all species recorded in New Haven plots

Appendix S4. Correlation matrix outlining the relative abundance of life history traits and nativity to each other

How to cite this article: Doroski DA, Duguid MC, Ashton MP. Forest patch size predicts seed bank composition in urban areas. *Appl Veg Sci*. 2020;00:1–13. <u>https://doi.org/10.1111/</u> avsc.12534