

PLANT RECRUITMENT DYNAMICS IN URBAN FORESTS: CONSEQUENCES FOR SEED  
AND SEEDLING ESTABLISHMENT

By

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## ABSTRACT OF THE DISSERTATION

### PLANT RECRUITMENT DYNAMICS IN URBAN FORESTS: CONSEQUENCES FOR SEED AND SEEDLING ESTABLISHMENT

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Plant recruitment dynamics in urban ecosystems can be influenced by multiple co-occurring and often exacerbated conditions and stressors common to most cities. Urban associated habitat fragmentation and land transformation, altered climate and microclimates, biotic invasion, pollution (e.g. elevated atmospheric carbon and nitrogen), and human activity, both direct and indirect, are all observed to have species-specific effects that may limit or facilitate recruitment success. A core question is whether urban ecosystems are functionally different, and if so, what that means for management and restoration practice. This dissertation investigates the application of plant life history frameworks and analyses in the context of urban forest populations. Chapter 1 presents a review of recent literature and a modified recruitment limitation framework for understanding plant recruitment dynamics within urban ecosystems. In the subsequent chapters (2-5) I present a series of related studies that examine seed and site limitation in urban and rural oak-hickory forests located in the New York City metropolitan area. Chapter 2 compares the advance regeneration of native tree species in these sites and the implications for urban forest management. I found urban forests to be seedling limited, however advance regeneration stages were not different from rural forests. Chapter 3 uses the recruitment limitation framework to investigate the relative contribution of seed and site as limiting factors for seedling establishment. Urban and rural forests were both strongly site limited. The native canopy in urban forests is limited by site factors, not seed availability. Chapter 4 presents findings from a seed addition experiment that tested the influence of seed predation and herbivory on early seedling

establishment in urban and rural forests. This experiment confirms that seed predation and herbivory pressure is greater in urban forests and contributes to the observed differences in urban and rural forest seedling recruitment. Finally, Chapter 5 presents a multi-year experiment of seed predation dynamics that identifies differences in the temporal pattern of seed removal in urban and rural forests; a potentially critical shift in forest function. Collectively, this dissertation identifies ecological mechanisms that limit plant recruitment in urban forests. A comprehensive understanding of urban recruitment limitation, as a scientific foundation with respect to plant abundance and distribution, will allow us to successfully conserve, manage, and restore plant communities to enhance the human experience of nature in cities.

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## Introduction

As urban ecology has matured there has been a recognized need to advance the field from descriptive research towards studies that develop a mechanistic understanding of urban ecological patterns and processes (Schochat et al. 2006, Hahs and Evans 2015). Now, more than a decade since this original call, mechanistic driven research is more common, although many key processes are still lacking data.

The study of urban plant recruitment dynamics is one important emerging research topic. In plant ecology, recruitment is the process whereby new individuals found a population or are added to established population (Eriksson and Ehrlén 2008). While recruitment results from processes throughout the life history of a plant species, early life stage dynamics, such as propagule availability and seedling establishment, are considered critical for determining future plant community composition and structure (Chambers and MacMahon 1994, Hurt and Pacala 1995). A mechanistic understanding of these life stages will provide critical information for conservation, restoration, and management of urban vegetation.

In urban habitats, altered recruitment dynamics is evidenced by reduced native plant seedling diversity and abundance, shifts in community composition, and the filtering of species by functional traits (e.g. Aronson et al. 2015, Williams et al. 2015, Zeeman et al. 2017). Urban hierarchical and functional trait filter models identify how urban plant community assembly may be impacted at multiple scales. These models are useful for identifying functional traits which may relate to specific recruitment processes (e.g. seed size and vagility) (e.g. Williams et al. 2009, Williams et al. 2015, Aronson et al. 2016). However, the specific ecological mechanisms driving these observed changes in plant recruitment remain vague (Williams et al. 2015).

In this dissertation, I investigate how urban ecosystem conditions influence plant recruitment dynamics in urban forested natural areas. Urban forested natural areas are an important component of the total urban tree canopy (UTC) and of sustainable cities. These greenspaces provide valuable ecosystem services for residents (e.g. Hasse et al. 2014), and habitat

for local, and even regional, biodiversity (e.g. Ives et al. 2016, Lepzyck et al. 2017). They are also common in many of the world's largest and densest cities (e.g. Lawrence et al. 2013) and given their scale, often contain the majority of all trees found in temperate cities. For example, in New York City (NYC), more than 75% of all trees are found in forested natural areas (Pregitzer et al. 2018). Consequently, these forests provide a disproportionate amount of the ecosystem services generated for the city and, as a result, should be a priority for environmental managers.

The sustainability of urban forested natural areas is dependent upon the ability for native trees to naturally regenerate. However, there is evidence that urban forests may be more recruitment limited. Comparing plant communities between urban and rural plots and across an urban-rural gradient, researchers report greater non-native seedling species richness in urban forests (Airola, 1984; Guntenspergen et al., 1997; Zipperer et al., 2002; Cadenasso et al. 2007) and reduced native seedling abundance (Burton et al., 2005; Cadenasso et al., 2007; Pennington et al., 2010; Trammell & Carreiro, 2011; Overdyck & Clarkson, 2012). However, a recent city-scale assessment of urban forested natural areas found these habitats to be dominated by native canopy and midstory trees, with decreasing relative abundance of native species among seedlings (Pregitzer et al. 2019). Assessments at this resolution highlight the range of forest condition and community types present in cities. By continuing to refine our understanding of urban forests with specific attention to changes in recruitment dynamics, we can advance sustainable management solutions for both urban and rural forests.

This dissertation is divided into five chapters which are briefly introduced below. Chapter 1 presents a review and conceptual framework. Chapters 2-5 present field a series of concurrent studies conducted in the same urban and rural forest plots. Co-authors for each chapter are specified in their summaries below.

Chapter 1: *Plants in the city: understanding recruitment dynamics in urban landscapes*

From grasslands to forests, and from natural to constructed habitats, multiple urban drivers – including climate, land-cover change, pollution, and biotic invasions – affect plant recruitment. In chapter 1, I review emerging research on urban plant recruitment dynamics through the context of recruitment limitation. Recruitment limitation is defined as the failure of a species to recruit in all suitable places (Muller-Landau 2002, Schupp et al. 2002) and may be decomposed into different stages of limitation that occur throughout plant life history. Recruitment limitation can be divided into six stages, including: source, production, dispersal, early-establishment, establishment, and maturation (Nathan and Muller-Landau 2000). These categories are typically simplified further to compare seed (source, production, dispersal) and site (early-establishment, establishment, maturation) limitation. Seed limitation, the failure of seeds to arrive, may result from either source and production limitation (not enough seeds produced) or dispersal limitation (not enough seeds reach recruitment sites) (Crawley 1990, Schupp et al. 2002). Site limitation identifies instances where plant populations are constrained by the quality and/or quantity of available sites including all potential barriers, abiotic and biotic, following seed dispersal (Eriksson and Ehrlén 1992, Clark et al. 1998, Nathan & Muller-Landau 2000).

The concept of recruitment limitation provides a framework through which emerging research in urban plant dynamics may be synthesized, future research agendas organized, and basic science applied. The conceptual framework presented in Chapter 1 is used to guide subsequent field-based research presented in Chapters 2-5.

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Chapter 2: *Natural regeneration in urban forests is limited by early-establishment dynamics: implications for management*

In rural forests, land managers often rely on natural regeneration, leveraging early recruitment processes from seed dispersal, seed banking, and early-establishment as a means of forest management. These approaches are fundamental to ecological forest management and silviculture (Ashton et al. 2018). Rural forestry is guided by data common to forest management science, such as advance regeneration and stocking indices which account not just for seedling or sapling abundance, but the size class. In urban forests, managers more typically rely on artificial regeneration and planting. Such approaches are resource intensive (DiCicco 2014, Pregitzer et al. 2018). A fundamental question for applied ecologists is: what is the potential for natural regeneration in our urban forested natural areas? Or more simply: is planting the only option? As urban ecosystem assessments increase in resolution (Forgione et al. 2016, Pregitzer et al. 2019) so can research grounded in function and process, and we may begin to answer such questions.

In Chapter 2, I compare urban and rural oak-hickory forest composition and structure, and the capacity for natural regeneration in the New York metropolitan area. I use seed rain, seed bank, and vegetation data from the canopy, midstory, and understory to compare community composition across multiple strata. Additionally, I apply metrics of advance regeneration to compute stocking indices and the relative dominance of sapling and canopy species. Stocking indices provide an understanding of seedling limitation through the lens of management, quantifying the potential for natural regeneration. The comparison between sapling and canopy forecasts potential in community composition. Integrating traditional metrics of forest management science and plant ecology are not common in urban habitat, and together inform whether alternatives to planting and traditional forest management treatments for natural regeneration are a viable option.

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Chapter 3: *Native tree recruitment in urban and rural forests: differences in seed and site limitation as barriers to natural regeneration*

In Chapter 2 I found evidence that urban forests are more seedling limited when compared to rural forests. However, the ecological processes driving these differences, as well as the stage at which populations are most limited, is not well understood. Plant ecologists use the recruitment limitation framework to compare the relative contribution of seed and site limiting factors to recruitment limitation. In urban forests, there is evidence that both categories of plant life history stages may be disrupted and increase overall recruitment limitation. Urban fragmentation, land use change, and historic management regimes may alter seed dispersal and availability, increasing seed limitation (Cutway & Ehrenfeld, 2010; Ettinger et al., 2017). Alternatively, abiotic and biotic changes to the environment, including but not limited to climate, soil biochemistry, reduction in leaf litter, biotic invasion and increased competition, as well as, altered herbivory and disturbance regimes may result in altered recruitment dynamics and establishment limitation (e.g. Kostel-Hughes et al., 1998; Pregitzer et al., 2016; O'Brien et al., 2016; Labatore et al., 2017; Ettinger et al., 2017).

In Chapter 3, I use three years of seed rain and seedling establishment data to investigate differences in the contribution of seed and establishment limitation to overall recruitment limitation in urban and rural forests. Data from paired seed traps and natural regeneration plots is analyzed to test relative differences in the contribution of source, production, and dispersal to overall seed limitation, as well as rates of seedling emergence and total establishment limitation.



This study focuses on tree species common in the canopy in both urban and rural oak-hickory forests. The careful examination of population dynamics, focused on recruitment limitation, is needed for management of sustainable and resilient urban forest ecosystems. Through this work we identify population bottlenecks and ecological barriers that may be addressed through restoration and management strategies.

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Chapter 4: *Early-establishment limitation in urban and rural forests: seed predation and herbivory limit tree seedling recruitment in urban forested natural areas.*

Chapter 4 continues to build off findings from the previous chapters, where urban forest sites were found to be more seedling limited than rural equivalents, and that establishment, not seed limitation factors (e.g. seed production, dispersal), more strongly limit early recruitment. Increased establishment limitation in urban forested natural areas may result from multiple factors, both biotic (e.g. invasive plants, pests, herbivores) and abiotic (atmospheric pollution, altered disturbance regimes). While speculated as key drivers in urban forests, less studied are post-dispersal seed predation and early herbivory, ecological processes known to exert significant influence on early recruitment dynamics in rural forest systems (Louda, 1989; Hurtt and Pacala, 1995; Clark et al., 1999; Hulme, 1996; Hulme, 1998; Levine & Murrell, 2003; Clark, Poulsen, & Levey, 2012; Larios et al., 2017).

In this Chapter I conducted a two-year seed addition experiment in urban and rural oak-hickory forests and compare the relative strength of site limiting factors in the establishment tree species. Small mammal exclosures were used to compare the importance of seed predation and

seedling herbivory on seedling establishment, seedling survival, and relative establishment limitation for four common native (*Quercus rubra*, *Carya tomentosa*, *Acer rubrum*, *Prunus serotina*) and two common non-native (*A. platanoides*, *Ailanthus altissima*) tree species. I quantify cumulative survival from seed germination through 18 months of seedling survival.

This chapter was formatted for *Journal of Applied Ecology*, and will be submitted:

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#### Chapter 5: *Evidence of functional shifts in urban ecology: temporal dynamics of post-dispersal seed removal in urban and rural forests*

In non-urban systems, post-dispersal seed predation is known to significantly alter plant recruitment and community composition (Louda 1989, Hulme 1998, Levine and Murrell 2003, Larios et al. 2017). Elevated seed predation has been hypothesized to limit native plant recruitment in urban forests (Rudnicki and McDonnell 1989, Labatore et al. 2016), but there is little empirical research that supports this contention or that directly compares rural and urban sites. Also, those experiments that do compare seed predation have been conducted for a single year, missing potential temporal dynamics (Bowers et al. 1996, Pufal et al. 2015).

In Chapter 5, I address this research gap and present findings from a cafeteria study design, replicated over three years to test the patterns of seed removal of native and non-native species in urban and rural oak-hickory forests. The experiment investigates seed removal in five native species (*C. tomentosa*, *Q. rubra*, *P. serotina*, *S. albidum*, *A. rubrum*) and two common non-native species (*A. platanoides*, *A. altissima*). To our knowledge, this is the first multi-year study comparing urban and rural seed removal dynamics. The results from this study improve our understanding of the contribution of post-dispersal seed removal and predation to recruitment

limitation in urban forests, and advance our knowledge of the influence of urbanization on plant community assembly.

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Collectively the research presented in this dissertation advances a mechanistic framework for urban plant ecology and begins to identify the potential for natural regeneration in urban forests relative to rural forests, as well as the ecological processes and life history stages where recruitment may be limited. In Chapter 2, I report significant differences in early regeneration for tree species in urban forests compared to rural forests. However, later stages of advance regeneration, including established seedlings and saplings, were not different in urban and rural forests. These findings suggest that early recruitment limitation may be greater in urban forests, but once established, urban tree seedlings may successfully recruit to adult stages. In Chapter 3, I use the recruitment limitation framework to compare the strength of seed and establishment limiting factors in urban and rural native tree populations. Both urban and rural sites are recruitment limited and for all species, establishment limitation was the most important barrier to natural regeneration. Early establishment limitation was greater in urban forests compared to rural forests for all species, except *Prunus serotina*. Unlike studies from other disturbed sites, such as forest fragments, we did not find the magnitude of seed limiting factors to increase. In Chapter 4, the seed addition experimental design reinforced findings from Chapter 3 that urban forests are more establishment limited than rural forests. Furthermore, seed predation and seedling herbivory were found to more strongly limit recruitment in urban forests. In Chapter 5 I found additional support that seed predation may be greater in urban forests, however these differences may not be

constant across time. Specifically, I found interannual patterns of seed removal to differ between urban and rural sites, a finding that may suggest a broader functional shift in early plant and granivore population dynamics.

This research also highlights the potential for life-history frameworks, such as recruitment limitation, to inform management. For example, we can determine life stages or ecological processes that either inhibit or facilitate plant recruitment in urban habitats. Managers can then leverage this knowledge to prescribe targeted treatments that are more time and cost-effective. For urban oak-hickory forests, early recruitment is limited, but once established seedlings are more likely to advance to juvenile and adult stages. Chapters 3-5 determine that the canopy dominant species of these forests are not seed limited. Instead, it is processes following dispersal, including seed predation and early-herbivory, that contribute to decreased early recruitment in urban forests. As a result, managers should consider augmenting seed in urban sites to over-satiate granivore populations and encourage seedling establishment, or bypass this stage and plant seedlings. The latter may be most appropriate for species with large-sized seeds, such as *Quercus* and *Carya*. These species were found to experience the highest rates of seed predation. Future urban forest research should determine the size that seedlings are more likely to survive in urban forests. In doing so, we can inform nursery practice and determine cost-saving measures for planting stock size.

In each of the chapters presented here I identify multiple future directions for urban plant ecology and forest research. Most broadly, there is a need to extend population studies of urban plants across multiple life-history stages. There is also a need for urban ecologists to begin testing explicit ecological processes across different urban gradients and site types, as well as for multiple species and functional groups. In doing so, we may broaden the generalizations that can be made about the influence of urban ecosystems on plants and consider these findings in the context of global change ecology and anthropogenic forces outside of cities. With respect to urban forested natural areas, this work should be extended across different community types as

well as forest conditions which may shift in response to human disturbance, biotic invasion, edge effect, among others. The impact of urban ecosystems on temporal dynamics is compelling and warrants future research. In particular, the results from Chapter 5 highlight several new lines of investigation into the response of mast dynamics of oak species across urban-rural gradients and how this may alter pre- and post-dispersal seed predation dynamics. Finally, from a management perspective, there is a clear opportunity to integrate process-based urban ecology in active management scenarios. In doing so we will not only learn about the basic ecology of these habitats, but inform strategies for sustaining natural systems in our cities.

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**Chapter 1: Plants in the city: understanding recruitment dynamics in urban landscapes**

## **Abstract**

In cities, naturally regenerating plant populations are critical in sustaining both ecological function and ecosystem services. However, scientists have a limited understanding of the urban ecosystem conditions and stressors that influence basic life-history processes and constraints for plant populations. Here, we synthesize current research on the recruitment dynamics of urban plants (processes associated with adding individuals to populations) and present a conceptual framework for urban recruitment limitation. From grasslands to forests, and from natural to constructed habitats, multiple urban drivers – including climate, land-cover change, pollution, and biotic invasions – affect plant recruitment. These drivers often interact, and their effects are frequently species-, habitat-, or region-specific. Furthering a “mechanistic” understanding (one that focuses on the underlying ecological mechanisms of observed phenomena) of how these drivers alter plant population dynamics will improve the conservation, management, and restoration of urban greenspaces.

### **In a nutshell:**

- A key challenge for urban ecologists is to understand the compositional and functional differences between urban and non-urban habitats
- For naturally regenerating populations of plants in cities, reproduction, establishment, and survival are influenced by multiple urban stressors and conditions
- The effects that urban conditions and stressors have on plant recruitment are often species-specific, and they can either facilitate or limit plant establishment
- Plant life history analyses can be adapted to urban environments to identify barriers to plant establishment and develop effective management strategies to sustain urban populations and communities.

## Introduction

As urban ecology has matured, there has been a growing recognition that the discipline must progress from research that is descriptive to research that develops a mechanistic understanding of urban ecological patterns and processes (Shochat *et al.* 2006). Now, more than a decade since the first calls for such advancements, process-based research is emerging, which has both improved knowledge and highlighted key processes for which data are lacking. Such pursuits in urban ecology may benefit from the application of mechanistic frameworks to interpret and guide future studies.

Because of the importance of managing urban greenspaces for enhanced ecosystem services, research on plant recruitment – that is, the addition of individuals to a new or existing population by births or immigration – in city habitats is attracting attention. While recruitment is the net result of processes throughout the life history of a plant species, early life-stage dynamics (such as propagule availability and seedling establishment) are particularly important for determining future plant community composition and structure, especially in altered or disturbed environments (e.g. Clark *et al.* 2007; McConkey *et al.* 2012). A mechanistic understanding of these life stages will provide critical information for the conservation, management, and restoration of urban habitats.

Reductions in native plant seedling diversity and abundance are often observed in urban greenspaces, as are shifts in community composition and diversity, both taxonomic and functional (e.g. Williams *et al.* 2015; Zeeman *et al.* 2017), all of which are products of altered recruitment dynamics. The use of urban hierarchical and functional trait filter models aid in identifying how urban plant community assembly may be affected at multiple scales. Filter models can be used to identify key functional traits that relate to specific recruitment processes, such as seed size or dispersal distance, and predict species establishment success (Williams *et al.* 2009, 2015;

Aronson *et al.* 2016). However, the specific ecological mechanisms driving the observed changes in plant recruitment remain poorly understood (Williams *et al.* 2015). The concept of “recruitment limitation” has long been a research focus for ecologists seeking to explain plant species abundance, distribution, rarity, and coexistence (e.g. Crawley 1990; Nathan and Muller-Landau 2000; Beckman and Rogers 2013). Generally defined as the failure of a species to recruit in all suitable places, recruitment limitation can be analyzed by different stages of limitation that occur throughout a plant’s life history, including source, production, dispersal, early-establishment, establishment, and adult limitation. Notably, recruitment limitation is an index, and as such can reference conditions that may either positively or negatively affect the chances of plant establishment.

Recruitment limitation is frequently separated into two subcategories: *seed limitation* and *site limitation* (Eriksson and Ehrlén 1992). Seed limitation, or the failure of seeds to arrive, may result from either source and production limitation or dispersal limitation (i.e. inadequate numbers of seeds reach recruitment sites). Site limitation occurs when plant populations are constrained by the quality and/or quantity of available sites, and includes all potential ecological barriers, abiotic and biotic, following seed dispersal through the establishment of adult plants (Nathan and Muller-Landau 2000; Muller-Landau *et al.* 2002).

Here, we present an urban recruitment limitation framework (Figure 1) that references the role of common urban stressors and conditions (e.g. Pickett *et al.* 2011; Aronson *et al.* 2016) in the life-history stages of plants. Although each of these categories of drivers are not unique to cities and all have been the subject of investigation in non-urban but still human-impacted contexts (e.g. Hobbs and Yates 2003), we argue that these drivers often co-occur within cities, and that their magnitude and associated impacts are exacerbated in urban environments. Urban-specific research is therefore required for a more comprehensive understanding. Previous frameworks applied to the urban context have focused on plant community and succession

dynamics (e.g. Pickett *et al.* 1987; Zipperer 2010). Our urban-centric framework addresses the need for mechanistic detail and completeness at the population level, which fits within and informs community frameworks. Through our framework, we synthesize recent research, conducted across the range of existing urban greenspaces and plant community types (Aronson *et al.* 2017), that explicitly measures a given process related to recruitment limitation (Table 1). This review is the product of an exhaustive Web of Science search (WebPanel 1). Finally, we identify critical research needs and how advances in a mechanistic approach to urban ecology can be applied to and improve the management of urban greenspaces.

## **Evidence of urban plant recruitment limitation**

### ***Source and production limitation***

Source and production limitation are the combined result of reduced population-level seed availability and individual seed production (Muller-Landau *et al.* 2002). For urban plants, source limitation may fundamentally increase as a result of urban fragmentation and land transformation, which directly reduces habitat area and lowers the number of reproducing individuals. Source limitation may also shift as a result of direct human activity, which may selectively introduce or remove individuals in a landscape. For example, in urban forested natural areas in Seattle, Washington, logging and the selective removal of old-growth trees, which contribute a disproportionate amount of total seed within populations, have been hypothesized to drive local source limitation and limit natural regeneration of conifer species (O'Brien *et al.* 2012; Ettinger *et al.* 2017). Despite the inherent effects of urban drivers on adult plant abundance and distribution, there are few studies that have quantified the effects on relative seed availability in the landscape.

Urban production limitation can be affected at multiple stages, from the number of flowers produced to pre-dispersal seed predation (e.g. Bode and Gilbert 2016), but research has

mainly focused on the impact of urban drivers on pollen limitation. Pollen limitation may be due to changes in pollen quality and quantity, resulting in unfertilized flowers or self-fertilization, which increases the risk of inbreeding depression. For wind-pollinated species in urban areas, habitat fragmentation and land-use change are critical drivers, and may result in greater pollen limitation and lower seed production (Wang *et al.* 2010). Such findings contradict what has been reported for forests embedded in agricultural landscapes, where fragmentation increases the dispersal distances for wind-pollinated species and enhances pollen flow (e.g. Nielsen and Kjær 2010). This may reflect the role of buildings acting as barriers to pollen dispersal.

Although the effect of urban drivers on plant–pollinator interactions has received the attention of researchers (Harrison and Winfree 2015), only a few studies have directly quantified outcomes for production limitation (i.e. viable seed set). As with research on abiotic pollination, studies of biotic-pollinated species spanning multiple habitat types, from upland forests to mangroves, have shown that urban fragmentation and land-use change increase pollen limitation, reduce seed set, and, at times, produce strong Allee effects (e.g. Hermansen *et al.* 2017). Conversely, several studies have demonstrated that pollination can persist across urban landscapes and conditions, including isolated spaces like green roofs (e.g. Ksiazek *et al.* 2012; Theodorou *et al.* 2016). Other urban drivers – such as invasive plants, light and noise pollution, and phenological shifts associated with the urban heat island effect – have been linked to changes in pollinator communities and behavior (Harrison and Winfree 2015). However, how these changes affect pollen limitation varies, and the strength of plant–pollinator associations (e.g. generalist versus specialist species) might leave certain plants more vulnerable to urban drivers.

In addition to pollen limitation, global change research has identified multiple conditions that are inherently related to urban drivers – such as climate change and land-use change – that may influence plant reproductive output (e.g. Selwood *et al.* 2015). Other drivers, such as atmospheric nitrogen deposition, may extend across multiple regeneration processes that

influence seed production and other life stages. The effect of such drivers on overall seed production and recruitment limitation may be complex. For example, in a non-urban study of northern red oak (*Quercus rubra*), a temperate deciduous tree, Bogdziewicz *et al.* (2017) found that nitrogen addition increased growth and allocation of resources for reproduction, including seed set, but simultaneously promoted pre-dispersal seed predation by weevils (*Curculio* spp.). The net result was a reduction in the total amount of viable seed despite greater plant productivity. There is a need for future studies of urban plants to examine the combined effects of multiple ecological processes associated with production limitation.

### ***Dispersal limitation***

Dispersal limitation is the failure of a species' propagules to arrive at a site even though sufficient numbers of seeds are produced to saturate sites (Muller-Landau *et al.* 2002). While the abundance and identity of biotic dispersal vectors in cities have been shown to change over the course of urbanization (e.g. Corlett 2011), relatively few studies have examined the impacts of such changes on effective dispersal and recruitment outcomes. Urban plant research would benefit from using traditional dispersal and recruitment experimental methods (Figure 2). In cities, frugivore visitation and fruit removal behavior have been a focus of scientific interest. Although research has pointed to the potential for frugivores to act as "mobile links" and sustain dispersal within cities (e.g. Lundberg *et al.* 2008), many studies have reported decreased or delayed fruit removal events in urban plant populations. In one experiment conducted across a gradient of urban fragmentation, researchers found that the most isolated populations of a barrel cactus (*Ferocactus wislizeni*) experienced less fruit removal and later fruit removal events (Ness *et al.* 2016). In this case, the negative implications of delayed fruit removal were considerable, because longer fruit presentation on cacti resulted in higher levels of pre-dispersal frugivory; moreover, models suggested that later dispersal events for isolated patches increase the probability that the

dispersed seeds will miss seasonal rain events critical for successful germination and seedling establishment. Other drivers, such as noise and light pollution, are known to affect nocturnal dispersers and reduce visitation rates (Francis *et al.* 2012; Lewanzik and Voigt 2014). In addition, invasive plants or introduced cultivars may act as competitors and promote frugivore diet switching (Møller *et al.* 2012), although invasive plants may also attract frugivores and increase fruit removal rates for nearby species that would otherwise remain dispersal limited (Gleditsch and Carlo 2011).

Although urban conditions alter abiotic dispersal vectors, such as wind and water, only a handful of studies have investigated the associated consequences for dispersal and recruitment outcomes, and an expansion of research efforts is greatly needed. In a graph-theory-based model, fragmentation was determined to drive dispersal limitation in urban grassland patches (Hejkal *et al.* 2017). However, the model parameters referenced non-urban dispersal distances, and given changes in urban microclimate patterns, the spatial distribution of seed dispersal may shift. Furthermore, different land-use types may impede or promote dispersal. For example, in a study focusing on tree-of-heaven (*Ailanthus altissima*), a wind-dispersed species, Kowarik and von der Lippe (2011) demonstrated that secondary dispersal along hardscape (artificial [and often impervious] surfaces incorporated into landscape architecture, such as sidewalks) and urban land cover may extend long-distance dispersal events by as much as 400 m. Other secondary dispersal vectors directly related to human activity (e.g. cars, railways, transfer of fill and soil material) may facilitate dispersal in and out of cities, especially for species with favorable seed traits or that are highly abundant (von der Lippe and Kowarik 2012). In such instances, human activity might be expected to increase the probability of long-distance dispersal events, which are critical to recruitment. Finally, while dispersal may be limited by factors such as urban fragmentation and land-use change, these forces may result in rapid microevolution that increases effective dispersal



rates (e.g. Cheptou *et al.* 2008). Such research highlights the potential role that barriers in each life-history stage (not just dispersal) may play in the evolution of urban plant species.

### ***Early-establishment limitation***

Early-establishment limitation is defined as conditions where, despite arriving, a seed fails to establish a seedling due to site unsuitability (Nathan and Muller-Landau 2000; Muller-Landau *et al.* 2002). In urban plant populations, transitions into and persistence within the seed bank may shift and increase early-establishment limitation. Urban seed banks have been characterized by a greater abundance of exotic plant species and are frequently dissimilar in composition when compared to existing vegetation (e.g. Pellissier *et al.* 2008). One mechanism driving such compositional change may be increased seed predation, which could increase establishment limitation in urban forested natural areas (Overdyck *et al.* 2013; Labatore *et al.* 2016). Seed removal and predation rates are reported to be higher in urban plant communities than in rural sites (Bowers and Breland 1996), though such trends may be species dependent (Pufal and Klein 2015). What drives these changes is less clear, but there is evidence that light pollution, fragmentation and patch size, and biotic invasion may alter the intensity and spatial patterns of seed predation (e.g. Bode and Gilbert 2016; Guiden and Orrock 2017). Other urban drivers, including pollutants such as nitrate and ammonium, may also modify seed bank dynamics and drive compositional shifts in seed bank populations (Pellissier *et al.* 2008).

Findings from seed addition studies suggest that multiple urban drivers can impact seed germination. Invasive flora and fauna may alter early-establishment, although invasive plant removal experiments reveal both positive and neutral effects on native plant seed germination success (e.g. Bauer and Reynolds 2016; Ettinger *et al.* 2017). For example, Bauer and Reynolds (2016) found that while the presence of an invasive shrub reduced native plant establishment

success, it did not affect seedling survival or growth. Human activity and management also limit germination. In urban forested natural areas and parks, removal of coarse woody debris, a common management activity in deciduous forest regions, shifts microclimate conditions and limits seed germination and early-establishment (Ettinger *et al.* 2017). Moreover, suppression of natural disturbance regimes may limit germination; for instance, Labatore *et al.* (2016) found the introduction of burning treatments to increase recruitment success for early-successional tree species in an urban forest. To date, no experiments have been conducted across urban–rural gradients to determine functional shifts in early-establishment limitation for urban plant populations.

### ***Juvenile and adult establishment limitation***

Juvenile and adult establishment limitation are defined here as the probability of a transition from seedling to juvenile stages and from juveniles to reproducing individuals (adults), respectively. While numerous studies have involved the transplanting of urban seedlings, few of these have been long-term experiments and there is limited demographic understanding of urban plant populations (Kowarik and von der Lippe 2018).

As in other life stages, the effects of urban conditions are species-specific, and can both facilitate and limit plant establishment and growth. Edge effects, human activity, and soil contamination are just a few of the many urban drivers that may limit plant growth and survival (e.g. O’Brien *et al.* 2012; Pregitzer *et al.* 2016). Other factors in urban sites, such as elevated tropospheric ozone, temperature, and nitrogen deposition, have been shown to promote the establishment and growth of urban plants (e.g. Gregg *et al.* 2003; O’Brien *et al.* 2012; Zhao *et al.* 2016). In addition to being species-specific, these impacts may be region-specific; in grasslands, for instance, high levels of nitrogen facilitate the growth of only a few species, especially more

common ones, which alters not only interspecific competition dynamics but also community composition (Zeeman and Morgan 2018). Although relatively scarce, tropical urban studies have reported that increased local temperature due to the urban heat island effect may constrict plant ranges along elevation gradients and exacerbate climate stress (Valle-Díaz *et al.* 2009). Such research highlights the need to extend urban ecological research to different geographic regions and contexts to identify generalizable trends.

Urban drivers may also affect these later stages of establishment by changing the diversity, abundance, and behavior of other species that act as competitors, consumers, or facilitators. The effects of invasive plant species on native seedling establishment and growth in urban areas have been thoroughly examined, and generally mirror findings from research conducted in non-urban settings. Most studies have shown that seedling survival and growth are negatively affected by competition with invasive plant species (e.g. Wallace *et al.* 2017). Research has further revealed that highly degraded sites may reduce mycorrhizal abundance and community diversity, although the benefits from these symbioses for seedlings, in terms of growth and survival, may also be species-specific, making generalizations difficult (Tonn and Ibáñez 2017).

Likewise, overabundant herbivore populations can greatly reduce recruitment into juvenile and adult stages, although from a community perspective the potential outcomes are complex (Raupp *et al.* 2010). For example, foliage losses to insects were lower in urban sites than in rural habitats despite urban plant populations having higher quality leaf material (Kozlov *et al.* 2017). Furthermore, insect herbivory decreased with increasing city size. Kozlov *et al.* (2017) proposed that this shift is due to predation of herbivorous arthropods by ants and birds and constitutes evidence of top-down control mediating plant–herbivore interactions. Their experiment represents one of the few studies that have tested urban trophic interactions and highlights a critical knowledge gap.

### **Recruitment limitation, from theory to practice**

Applying the recruitment limitation framework to urban contexts not only informs basic science but can also engage urban ecologists in broader debates on ecological theory, such as the relative contribution of seed versus site limitation (Panel 1) and metapopulation dynamics (e.g. Cheptou and Dornier 2012). In addition, recruitment limitation research may improve other conceptual frameworks, such as urban trait filter models. To determine specific mechanisms, researchers investigating recruitment limitation can test plant traits hypothesized to drive community shifts; for example, does dispersal limitation drive community shifts toward species with smaller seeds or is the success of small-seeded species due to changes in site conditions? Mechanistic research may also identify and measure new traits critical to plant regeneration to advance filter-based models. In a recent review, Larson and Funk (2016) highlighted the importance of early regeneration dynamics and the need to expand the traits used in filter analyses related to these stages in plant life history. Ecologists studying urban plant recruitment may begin to collect these trait measures, informing future models, while at the same time testing current trait-filter-generated hypotheses. In so doing, scientists may gain a better understanding of how species respond to different urban conditions.

From an applied perspective, recruitment limitation is a fundamental concept that quantifies site potentials and thresholds – which species can establish, persist, and regenerate – and may aid in developing appropriate management strategies and restoration activities. Restoration practitioners are attuned to such questions and often monitor early demographic patterns as a means of measuring project success and failure, or predicting future outcomes.

Urban restoration studies, conducted on a range of greenspace types from constructed to natural areas, have helped to advance knowledge of the ecological barriers and mechanisms influencing recruitment dynamics in cities (Figure 4). For example, urban forest restoration

studies have determined the potential for planting strategies to reduce dispersal limitation and facilitate native plant recruitment (Robinson and Handel 2000), while broadcast seeding experiments have demonstrated not only the potential for seed predation to limit native species recruitment but also the viability of passive restoration strategies (Overdyck *et al.* 2013). In urban grassland restoration projects, management intensity, human activity, and site context have been found to alter plant recruitment and community diversity (Fischer *et al.* 2013; Rudolph *et al.* 2017), while investigations of urban green roof systems have demonstrated the persistence of pollination services, despite shifts in pollinator communities (Ksiazek *et al.* 2012). Likewise, urban afforestation studies have tested the potential for site manipulations (e.g. invasive species removals, soil treatments, plantings) to promote native plant establishment, growth, and natural regeneration (e.g. Doroski *et al.* 2018), whereas long-term restoration studies have provided insights into the potential successional trajectories of urban plant communities (e.g. Wallace *et al.* 2017).

Collectively, urban restoration research has demonstrated its value in part by identifying ecological processes that may act as barriers to native plant species, as well as establishing the drivers responsible for shifting plant community dynamics. There is the potential to embed research in restoration projects that evaluates management strategies to better ensure successful outcomes and improve our conceptual understanding of plant establishment mechanisms (Frances *et al.* 2010).

### **Panel 1. Are urban plant populations more seed or site limited?**

The relative contributions of seed and site limitation to total recruitment are the subject of a fundamental debate in plant ecology (Clark *et al.* 2007) and can inform appropriate management actions (Frances *et al.* 2010). While most species are seed limited, the effects of site limitation are

likely stronger than the effects of seed limitation (Clark *et al.* 2007), but the role of seed limitation may be more important for certain species (e.g. those that produce large seeds) and for some populations (e.g. those in disturbed sites). Urban plant communities provide a new context to consider the role of seed and site limitation: for instance, how does the importance of seed and site limitation change in response to urban drivers (Figure 3)? And more specifically, which species or types of species (e.g. functional groups, spring ephemerals, etc) experience greater limitation or facilitation by urban conditions?

Seed addition experiments, modeling, and demographic studies – including Caughlin *et al.* (2012), Overdyck *et al.* (2013), Labatore *et al.* (2016), Ettinger *et al.* (2017), and Hermansen *et al.* (2017) – have been deployed across different urban habitat types to begin testing these questions. Of these studies, only two – Caughlin *et al.* (2012) and Hermansen *et al.* (2017) – compared recruitment limitation across multiple urban sites, and both identified seed limitation to be a major driver of overall recruitment limitation. No direct comparison of seed versus site limitation has been conducted between urban and rural sites, but indirect comparisons suggest that seed limitation may be more important in urban greenspaces such as forested natural areas (Ettinger *et al.* 2017). Long-term seed addition and demographic studies across gradients of different urban drivers may expand upon this experimental work and integrate findings into more comprehensive plant population models.

## Conclusions

Evidence accumulated to date suggests that the recruitment dynamics of many native plant species are modified in urban systems. Despite the emerging body of research supporting this framework, many basic questions remain. Our review of the current literature revealed five overarching needs and opportunities that will improve future research in recruitment limitation.

First, urban ecologists should follow recruitment processes across multiple life-history stages; this will allow comparison of the contribution of different processes to recruitment limitation and may highlight the complexity of opposing forces of some urban drivers. For example, for both noise pollution and nitrogen deposition, studies have demonstrated competing forces that may both decrease or increase limitation at different stages (Francis *et al.* 2012; Bogdziewicz *et al.* 2017). Given the many urban drivers acting on urban plant communities, multiple opposing forces are likely at play. Urban plant ecology will benefit by bridging the efforts of scientists currently studying the phases of plant recruitment separately.

Second, urban ecologists should also seek to extend experiments over multiple years and establish long-term research projects that record basic demographic data on plant populations. Although such work has begun (e.g. Kowarik and von der Lippe 2018), very little is known about the transition probabilities between life-history stages for urban plants, especially after seedling stages. Collecting basic demographic data on urban plant populations will enable the development of comparative models and generation of new hypotheses on urban plant community dynamics.

Third, research should be precisely designed to test mechanisms across explicit urban drivers and in different urban environments. Determining what forces drive ecological dynamics is a recognized challenge (Williams *et al.* 2009), but with carefully designed and replicated studies, we may begin to refine our understanding of drivers and changes across urban gradients and not simply between urban and non-urban sites. Research should also consider recruitment limitation in different categories of urban environments, from remnant patches to constructed or designed natural areas. Understanding recruitment limitation for a range of sites may inform the potential for cities to support broader conservation goals related to native species and habitat (Kowarik and von der Lippe 2018).

Fourth, the recommendations identified above should be applied to multiple species and functional groups. Clearly, the impact of urban conditions on plants is species-specific; indeed, many species may become less recruitment limited. More generalizable observations may be achieved by establishing an adaptive research program between recruitment and functional trait studies. Collectively, this work may determine groups of species and the specific mechanisms that drive recruitment facilitation or limitation, informing urban ecology theory, management for ecosystem services, and the development of targeted strategies for species conservation.

Finally, an important question is whether urban experiments may serve as model systems for the ecological outcomes of plant communities located outside of cities but confronted by global change and anthropogenic forces (Grimm *et al.* 2008). For example, plant responses to the urban heat island effect could provide insight into the future impacts of increasing global temperature. Testing recruitment processes across gradients of urban drivers will improve our awareness of the functional shifts that occur and potentially enable us to better predict future impacts on global plant communities. A comprehensive understanding of urban recruitment limitation, as a scientific foundation with respect to plant abundance and distribution, may allow us to successfully conserve, manage, and restore vegetation to enhance the human experience of nature.



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## Tables

**Table 1.** Plant recruitment stages, ecological processes, and impacts of urban drivers on plant recruitment processes

<b>Recruitment limitation stage</b>	<b>Commonly associated ecological processes and causes</b>
Source <i>and</i> production	Adult plant rarity and distribution; pollen, flower, fruit, and seed production; pollination; pre-dispersal seed predation
Dispersal	Frugivore diet choice, visitation, removal, handling, seed passage time; disperser and hoarder behavior; abiotic dispersal vector speed or direction
Early-establishment	Seed predation, dormancy, decay, and germination; resource availability; soil mutualist availability; pathogens
Juvenile <i>and</i> adult establishment	Density-dependent mortality; inter- and intra-specific competition; herbivory; resource availability; soil mutualist availability; pathogens

## Figures

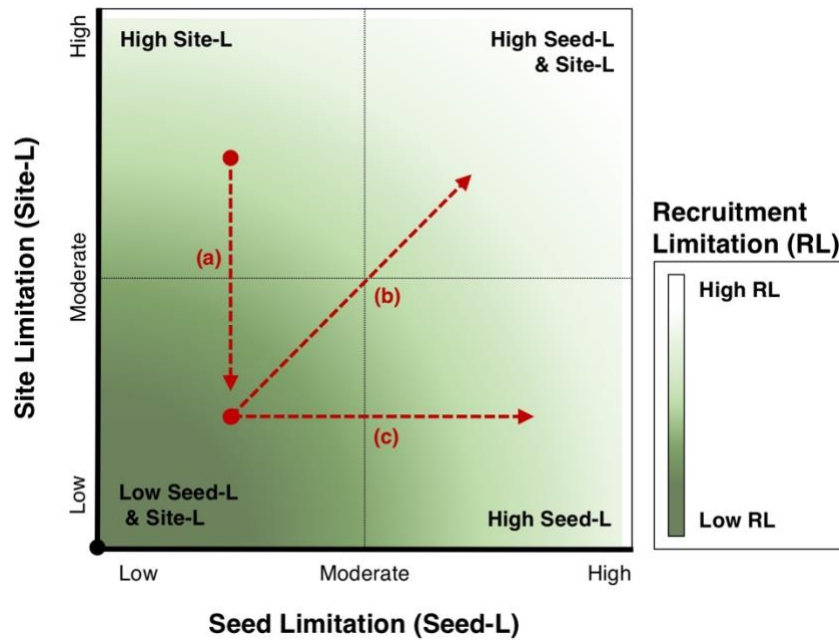


**Figure 1.** The urban recruitment limitation framework. Sub-categories of recruitment limitation (black text) can be organized by transitions in plant life history (gray text). We identify five categories of urban drivers (red text) that may impact plant recruitment processes (clockwise from top): climate (e.g. urban heat island); biotic invasions (e.g. flora, fauna, pests, pathogens); pollution and environmental contamination (e.g. carbon dioxide, nitrogen deposition, volatile organic compounds, heavy metals, light); land-cover change (e.g. habitat loss or conversion, fragmentation); and human activity, both direct and indirect (e.g. planting, recreation, chemical treatment).



**Figure 2.** Urban seed trap, seed addition, and exclosure experiments can elucidate the role of different ecological mechanisms throughout the life history of plants in limiting or facilitating recruitment. Image credit: MH Helmer.





**Figure 3.** The range of response options for plant recruitment in urban contexts. Urban drivers may shift seed limitation (Seed-L) or site limitation (Site-L), and therefore overall recruitment limitation (RL). These shifts are species-specific and can vary in magnitude and direction, potentially reducing or increasing the probability of recruitment. For example, urban-based research has shown that (red dashed lines): (a) nitrogen pollution reduces Site-L for nitrophilic-species in grasslands (e.g. Zeeman and Morgan 2018), (b) fragmentation increases both Seed-L and Site-L in populations of cacti (e.g. Ness *et al.* 2016), and (c) habitat loss increases Seed-L in mangrove populations (Hermansen *et al.* 2017).





**Figure 4.** Ecological design and restoration projects provide opportunities to study the impact of urban drivers on plant recruitment across a range of site types, such as (a) pollen limitation on green roofs (e.g.Ksiazek *et al.*2012), (b) seed dispersal and early-establishment limitation in urban afforestation sites (e.g.Robinson and Handel 2000), and establishment limitation from human activity and management regimes in (c) grasslands (e.g.Rudolph *et al.* 2017) and (d) wetlands. Image “C” photo credit: J. Epiphan.

## **Supplemental Material**

**WebPanel 1:** Summary of literature review search terms.

## WebPanel 1

**Literature review.** A comprehensive review of urban plant recruitment research was conducted through Web of Science (WoS), all databases, on February 1, 2018. The initial search returned 891 records (all years) and 462 records from January 2010 through January 2018. Supplementary reviews were conducted through Google Scholar.

**Search terms used in WoS:** TS=((“urban” OR “urbanization” OR urban–rural OR periurban OR peri-urban) AND (“seed” OR “seeds” OR “seedling” OR “seedlings” OR “fruit” OR “fruits” OR “flower” OR “flowers”) AND (“seed set” OR “seed production” OR “pollen limitation” OR “dispersal limitation” OR “seed dispersal” OR “removal rate\*” OR “visitation rate\*” OR “recruitment limitation” OR “establishment limitation” OR “microsite limitation” OR “micro-site limitation” OR “seed limitation” OR “post-dispersal limitation” OR “seed predation” OR “germination” OR “seed survival” OR “seedling survival” OR “seed mortality” OR “seedling mortality” OR “seed bank” OR “regeneration”))

**Chapter 2: Natural regeneration in urban forests is limited by early-establishment  
dynamics: implications for management**

## Abstract

Urban forested natural areas are valuable ecological and social resources. However, the long-term sustainability of these habitats is challenged by urban environmental and social conditions. City-scale assessments of natural areas allow for more targeted research and improved understanding of ecological function, such as natural regeneration, within these systems. A fundamental question for urban forest managers is whether or not planting is the only option to maintain native forest. 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. We apply metrics of advance regeneration, the abundance of seedling and sapling, to test whether alternatives to planting, including traditional forest management treatments for natural regeneration are a viable option. We found differences in recruitment dynamics between urban and rural forests which have implications for the sustainability of these forests and could influence management strategies. First, despite controlling for forest community type, species composition in urban and rural sites were significantly different across multiple strata and within the seed bank. The 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 ( $1.9/m^2$ ) compared to rural ( $7.1/m^2$ ) sites, we observed greater abundance of sapling in urban forests, and no significant difference in stocking index between sites. These findings suggest that early-establishment barriers to recruitment may be greater in urban sites. However, once established, seedling transition into advance regeneration stages may not be different, and in fact, advance regeneration may actually be more viable in urban forested natural areas. Collectively, these results highlight functional differences in urban and rural forest recruitment dynamics that may have significant impact on the future community composition of

urban and rural oak-hickory forests. Effective management of urban forest patches will require better understanding of the specific ecological barriers and early recruitment processes limiting regeneration.

**Keywords:** forest management, urban forestry, restoration ecology, urban biodiversity, urban tree canopy, seed rain, seed bank, advance regeneration, plant recruitment dynamics

## Introduction

Urban forested natural areas are an important component of the total urban tree canopy (UTC) and of sustainable cities. These greenspaces provide valuable ecosystem services for residents (e.g. Hasse et al. 2014), and habitat for local, and even regional, biodiversity (e.g. Ives et al. 2016, Lepzyck et al. 2017). Natural areas make up approximately 85% of municipal parkland in the United States (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, New York City (NYC) contains 4,250 hectares of urban forested natural areas, representing 5% of the total land area, nearly 25% of all parkland, and more than 70% of the total natural area in the city. More than 75% of all trees in NYC are found in forested natural areas (Pregitzer et al. 2018). Consequently, these forests provide a disproportionate amount of the ecosystem services generated for the city and are a priority for environmental managers.

Despite providing many ecological and cultural services, urban forests often connote degradation, perceived as sites dominated by exotic and invasive species, and different from non-urban forests, both in composition and structure. However, recent research reveals this may not be the case, and these perceptions may result from sampling approaches (Pregitzer et al. 2019). In fact, urban forested natural areas are characterized by primarily native tree species in the canopy

and forest community types commonly identified in non-urban landscapes (Fig. 1; Forgione et al. 2016, Pregitzer et al. 2019). While native canopies may dominate our urban forest now, the long-term fate of these forests is not certain. 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 non-native seedling species richness in urban forests (Airola 1984, Guntenspergen et al. 1997, Zipperer et al. 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). Furthermore, in a recent NYC city-scale assessment, native tree seedlings were found to represent 53% of total understory cover (Pregitzer et al. 2019).

Early life-stages in plants, from seed dispersal to seed banking and seedling establishment, are important in determining future forest composition and structure (Hurt and Pacala 1995, McConkey et al. 2012). This a rapidly expanding line of urban plant ecology research, and there is a need for more research focused on these stages and processes (Piana et al. 2019). Seed rain and dispersal studies, still limited in number and scope, identify potential shifts in the dispersal of native canopy species and the introduction of exotic species (e.g. Cutway and Ehrenfield 2010, Overdyck et al. 2013, Labatore et al. 2016). Other urban forest systems are seed limited due to management activity and land use history (Ettinger et al. 2017). Likewise, while rural forest seed banks have been extensively studied, there is limited research on urban seed banks. Findings from these studies suggest that urban forest seed banks contain more non-native species when compared to rural forests (Kostel-Hughes and Young 1998, Pysek et al. 2002, Overdyck et al. 2012, Beauchamp 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 (Kostel-Hughes and Young 1998, Beauchamp et al. 2013).

As urban ecosystem assessments increase in resolution (Forgione et al. 2016) so can research grounded in function and process. This focus will advance urban ecological theory in areas like the influence of anthropogenic forces on recruitment limitation which, in turn, can inform management strategies. In rural sites, foresters and land managers often rely on natural regeneration, leveraging early recruitment processes from seed dispersal, seed banking, and early-establishment as a means of forest management. These approaches are fundamental to ecological forest management and silviculture (Ashton et al. 2018a). Rural forestry is guided by data, common to forest management science, such as advance regeneration and stocking indices which account not just for seedling or sapling abundance, but size class. Advance regeneration is defined as tree seedlings that are established in the understory, often for more than one year (Ashton et al. 2018b). In urban forests, managers more typically rely on artificial regeneration and planting; such approaches are resource intensive (DiCicco 2014, Pregitzer et al. 2018). A fundamental question for applied ecologists is: what is the potential for natural regeneration in our urban forested natural areas? Or more simply, is planting the only option? To advance such understanding requires mechanistic urban ecological research grounded in understanding early recruitment processes. Such studies match the science and knowledge associated with our rural forest equivalents.

In this study we investigate whether urban forested natural areas can sustain themselves through natural regeneration processes, utilizing common ecological and forestry metrics. In addition, we examine the potential for seed rain and seed banks to play a role in urban natural area restoration. To explore these processes, we compare oak-hickory forests in urban and rural sites of the NYC region and ask: (1) Do urban and rural forests differ in composition and abundance of tree species in forest strata, seed rain, and seed bank? (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 ecoregion of the northeastern United States and are the most common forest community type in NYC natural areas (Forgione et al. 2016).

Furthermore, the New York metropolitan area is one of the most densely developed areas in the United States with a population of approximately 20 million (Short 2007, Auch et al. 2012: US Census 2018). By refining our understanding of urban forests with specific attention to changes in recruitment dynamics, we can advance sustainable management solutions for both urban and rural forests in one of the most densely populated regions of the United States.

## **Methods**

### ***Study Location***

The study was conducted in six mature oak-hickory forests located in NYC and the NYC metropolitan area (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. Rural sites (n=3) were in the New York Highlands region at Sterling Forest State Park, Blue Lake Park, and Black Rock Forest. All sites were located more than 15 km apart and within the southernmost region of the Northeastern Upland Province (Broughton et al. 1966). Sites were classified as either urban or rural using percent population density and percent impervious surface in two buffer classes (500 m, 2 km), where rural sites were characterized by <1% impervious cover and zero human residents within 500 m and <5% impervious cover and <500 human residents within the 2 km buffer (Appendix S1: Fig. S1 and Table S1). To take into account the likelihood of vandalism on the urban plots, six plots were installed in each of the three urban sites (n=18), while three plots were installed in each of the

rural sites (n=9). Three urban plots experienced significant disturbance related to human activity and were not included in the final analysis.

All plots were randomly located in stands classified as the oak-hickory forest community type and located more than 200 m from the next nearest plot. Urban site selection was informed by a recent city-scale ecological assessment and urban-specific classification system (Forgione et al. 2016, Pregitzer et al. 2019). Plots were located in closed canopy (80-95% canopy cover) stands of mature trees 60-100 years 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. 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, Cote et al. 2004). The rural sites in this study have a history of deer management and hunting which appears to have minimized herbivory pressure and allow an understory and midstory to establish. In the urban sites, deer were not present in two (IHP and VCP) of the three sites, but were common in Pelham Bay Park.

### ***Field methods***

Tree species were sampled within three classifications of forest strata: canopy, saplings, and understory. Canopy trees were sampled in 35 m fixed radius plot. 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 to 10 cm dbh and sampled in 10 m fixed radius plots. Additionally, we followed standardized methods for calculating a stocking index by sampling all saplings 1 to 2.5 cm dbh in three 3 m radius sub-plots within each plot (McWilliams et al. 2011). Canopy trees and saplings were sampled in July 2016. Seedlings were sampled in ten

1x1 m semi-permanent 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 less than 100 cm tall and 1 cm caliper. For the stocking index, we sampled all seedling that were less than 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 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<sup>2</sup>) (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. 1998). 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 to August, and bi-weekly, August to January, 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<sup>3</sup>) 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 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 and homogenized. Pooled samples were planted into one greenhouse tray (50.8 cm x 28.0 cm). The soil core samples were mixed with sterilized greenhouse potting mix in order to obtain equal volume of soil per tray. Control flats (n=5) which contained only sterilized greenhouse potting soil were placed among the experimental trays in order 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. *Carya* seedlings were identified to 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). Data were 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 were identified to species level. 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 (Okansen et al. 2013). Two-dimensional solutions were chosen and final ordinations were generated from 200 random starts.

PERMANOVA analyses were used to test whether community composition varied between forest strata in both 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 between each strata and site type 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 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. The critical  $\alpha$  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>38.0cm) 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. Additionally, we calculated a regeneration stocking index (RSI) following methods developed by the U.S. Forest Service and applied regionally in the northeast United States (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, >150cm = 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<sup>2</sup>, 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 compare 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<sup>2</sup>. Seed rain and seedling abundances are reported as average abundances from 2016-2018. For each comparison we tested for normality, using non-parametric tests (Mann-Whitney U test) when our data failed to fit a normal distribution.

## Results

### *Forest Strata Community Composition*

Despite selecting plots located in forest stands identified as oak-hickory forests, there were significant differences in urban and rural forest communities. Nonmetric multidimensional scaling (NMDS) ordination plots (stress=0.159) indicated that the composition of tree species in all forest strata and seed stages differs 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 (PERMANOVA;  $F=7.60$ ,  $df=9$ ,  $P=0.001$ ).

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). There was, however, 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. Additionally, 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, as well as between sapling and both seed rain and seedlings. All other strata comparisons were significantly different.

The permdisp analysis (Appendix S1: Table S2), a measure of betadiversity, 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 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. 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 seed stages.

### ***Forest Strata and Seed Richness and Abundance***

In total, 55 tree species were recorded. Of these, 24 species were identified in all forest strata and only 6 were observed in all forest strata and seed stages. Of the 55 total species, 7 were identified as non-native to the region (*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 reported in the supplemental material (Appendix S1: Table S3).

Urban forest canopy was characterized by greater basal area (30.8 m<sup>2</sup>/ha) than rural sites (25.8 m<sup>2</sup>/ha) (Table 1). Within the canopy, 48 species were identified, 6 of which were non-native. There were no significant differences in canopy species richness between urban and rural sites. However, there were significantly more non-native tree species in urban canopies. Despite

systematically selecting sites for 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 canopy. Non-native species were not present in rural canopies, while six of the seven non-native species identified in this study were present in urban forest canopies.

Urban forests had significantly greater average basal area of saplings (2.0 m<sup>2</sup>/ha) than rural forest sites (1.0m<sup>2</sup>/ha) (Fig. 3). There were 23 species identified in the sapling layer, of which *Morus alba* was the only non-native 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*. Like the canopy, there were no observed differences in overall or native species richness among sapling strata. Non-native species were only observed among urban forest saplings.

The average annual density of seedlings was much greater in rural forests (7.1 seedlings/m<sup>2</sup>) compared to urban forests (1.9 seedlings/m<sup>2</sup>) (Fig. 3). Thirty-one species of tree seedlings were identified in the understory. There was on average greater seedling species richness in rural forests (10.4 species) than urban sites (4.4 species). Again, there were no non-native 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* were by far the most abundant seedlings (1.2 seedlings/m<sup>2</sup>). There



were significantly fewer total oak seedlings in urban sites (0.1 seedling/m<sup>2</sup>) compared to rural sites (0.9/m<sup>2</sup>). These differences were observed across all oak species.

Seed rain was the only life stage that did not differ when comparing total and native species abundances in urban (603.9 seeds/m<sup>2</sup>) and rural (239.1 seeds/m<sup>2</sup>) sites (differences explained by high variation) (Table 1). There were, however, significantly more non-native seeds present in urban seed rain (Urban= 4.5 seeds/m<sup>2</sup>, Rural= 0.03 seeds/m<sup>2</sup>). 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. At a species-specific focus, seed rain corresponded with canopy 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*, the seeds of which are wind dispersed, was the most common non-native species in both urban and rural sites.

Urban forests had significantly greater total and non-native 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 non-native species. As observed in the NMDS ordination, there were strong differences in canopy and seed bank species composition. Despite the low abundance of non-native species in canopy and sapling strata, urban seed banks were dominated by these species, including *Paulownia tomentosa* (princess tree) and *Morus alba* (white mulberry), 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 high average seedling density in rural sites, but no significant difference in the RSI between sites ( $t = -0.26246$ ,  $p=0.796$ ) (Fig. 3). In fact, urban sites (RSI=82.0) were on average

greater compared to rural (RSI=75.9) forests. The RSI was variable across all rural sites 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 deer, Van Cortlandt Park and Inwood Hill Park, RSI exceeded baseline thresholds. The other urban site Pelham Bay, 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 advanced sapling stages. Across all regeneration stages, native species were dominant and there were few, if any, non-native tree species identified.

## Discussion

Our findings identify differences in recruitment dynamics between urban and rural forests which have implications for the sustainability of these forests and could influence management strategies. Early-establishment barriers to recruitment appear to be greater in urban sites. However once established, transition into advanced regeneration stages may not be different, and, in fact, advance regeneration may actually be more viable in urban forested natural areas. Collectively, these results highlight potential functional differences in urban and rural forest recruitment dynamics that may have a significant impact on the future community composition of these forests. Furthermore, managing for natural regeneration may be a viable option for intact native forest in urban forested natural areas. The dominance of native vegetation across all strata, as well as greater potential for advance regeneration, contradicts generalized conceptions of urban

forests as invaded and not self-sustaining. As such, we argue that more nuanced understanding of forest structure, composition, and function is required for sustainable management in urban forested natural areas.

***The fate of oak-dominant forests: similarities and differences in urban and rural response***

Oak forests across the eastern United States are undergoing shifts in community composition (McEwan et al. 2011). Although red oaks are dominant in the canopy, smaller size classes are not as well represented, indicating recruitment limitation (Lorimer 1984, Loftis et al. 1993). This loss of oaks has been associated with increases in maple species, particularly *A. rubrum* (Abrams et al. 1998). 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). We also found maple species dominating the seedling stages in rural forests. However, in urban forests, *P. serotina*, not maple, is the most dominant among younger strata, including both saplings and seedlings. This evidence suggests that successional trajectories in urban and rural forests may differ, with rural sites transitioning to maple dominated forests and urban forests dominated by *P. serotina*.

Our results suggest that the mechanisms behind these successional shifts are different between urban and rural forests. While changes in disturbance regimes, specifically the reduction of fire and burn events, are often cited as the drivers of these community changes (e.g. Crow 1998, Abrams 1992, Nowacki and Abrams 2008), recognition of multiple interlocked drivers has established the “multiple interaction ecosystem drivers hypothesis” (McEwan et al. 2011). In addition to suppressed fire regimes, these factors include, but are not limited to, changes in regional temperature, moisture and nitrogen dynamics, the loss of keystone tree species such as the American Chestnut (*Castanea dentata*), and changing animal population dynamics altering herbivory pressure.

Notably, the over-abundance of white-tailed deer causing severe herbivory pressure 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 our study support the conclusion that all rural sites were below sustainable thresholds of advance regeneration for areas with high deer abundance ( $>8$  individuals/km). Urban sites were on average below this threshold, but several plots exceeded high deer density thresholds for regeneration. Two of the three urban sites are without, or with minimal, deer abundance. In these sites, RSI values are well above recommend thresholds for adequate natural regeneration. However, even with more herbivory pressure from deer, the abundance of *Quercus* sp. seedlings still was much greater in rural sites. Consequently, while advanced regeneration may be greater in urban sites, there appear to be additional ecological barriers resulting in greater site limitation for oak species, as well as sub-dominant canopy species. Such factors may include pre-dispersal and/or post-dispersal seed predation, changes in soil structure and chemistry, leaf litter depth, or microclimate, and competition with non-native plants (Aronson and Handel 2011, Piana et al. 2019).

Regardless of the mechanism driving these changes, the findings from our study emphasize the need to move away from dichotomous perceptions of urban and rural forests. There are certainly instances where urban forests may have high levels of deer and therefore increased recruitment limitation, as well as multiple disturbances from direct human activity often associated with urban forests. Alternatively, urban forested natural areas embedded within cities, essentially “green islands” buffered from deer populations, may actually exceed non-urban sites with respect to advanced regeneration. There is also evidence that while deer may be key drivers of these differences, if herbivory pressure is reduced, recruitment dynamics in urban and rural sites may still differ.

***Alternatives to planting: Managing for natural regeneration***

Despite lower annual seedling abundance, the RSI of urban forests was slightly greater than rural forests. Furthermore, sapling abundance was greater in urban sites, although the identity of these trees was different than current canopy dominants. To our knowledge this is the first application of advance regeneration and stocking indices to urban forested natural areas and it identifies a potentially overlooked difference in urban forest ecosystems. Many forest restoration studies have been conducted in degraded sites or former canopy gaps, highlighting long-term success and the need for planting and intense management (Johnson and Handel 2016, Simmons et al. 2016).

There are however a range of forest conditions present in urban forested natural areas, from invaded gaps to intact native canopy. In the latter, which may be the dominant forest condition in eastern U.S. cities, advance regeneration could be adequate to accommodate alternatives to planting. Traditional forestry approaches for natural regeneration may indeed be a viable management option for some urban forests.

One passive restoration strategy is to rely on seed banks to replenish native plant stock. While seed banks are considered important determinants of succession and gap dynamics in North American eastern deciduous forests (Mladenoff 1990, Hyatt and Casper 2000), the role of seed banks in regenerating forests may be limited (Pickett and McDonnell 1989, Hopfensperger 2007). That said, 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 et al. 1992, Hille Ris Lambers et al. 2005, Hille Ris Lambers and Clark 2005). Some studies indicate that canopy dominant species have low abundance and importance value in urban forest seed banks (Wang et al. 2015, Beauchamp et al. 2013). 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). We observed low abundances of woody species in both urban and rural seed

banks. In particular, there were few dominant canopy species present in seed banks. Urban seed banks were characterized by non-native and invasive species that were not present in the canopy. These findings support existing research that suggests seed banks are not a viable option for passive restoration in urban forests. Not only were few species present among any of the strata represented in urban seed banks, the majority of these species were exotic invasive species. Large seeded species such as *Quercus* sp. and *Carya* sp. were not found in soil seed bank despite their abundance in the canopy. Clearly, relying on the seed bank for passive restoration is not a viable management option for urban forest regeneration.

While the seed bank may not be relied upon, we have shown here that seed rain is a significant source of propagules for natural regeneration management treatments. Urban forest seed rain has been quantified in just four studies (Cutway and Ehrenfeld 2010, Overdyck et al. 2013, Martinez-Garcia et al. 2014, Labatore et al. 2016). In the only study to compare urban and rural seed rain, the authors report greater non-native seed dispersed in urban forests when compared to rural forests (Overdyck et al. 2013). Landscape context may matter for seed rain, as Cutway and Ehrenfeld (2010) identify residential and industrial land use agencies to influence the abundance of non-native species in urban forest seed rain. While we found greater non-native seed abundance in urban sites, we also found no difference in native seed abundance between sites, suggesting that urban sites were no more seed limited than rural sites and thus these sites are not source limited.

The urban forested natural areas in our study are characterized by advance regeneration sufficient to support natural regeneration methods. However, our findings also indicate significant early-establishment barriers in urban sites. There are multiple examples of urban-specific studies that have identified potential limiting factors to natural regeneration (for review see Piana et al. 2019), but there are few studies that directly compare mechanisms limiting recruitment in urban and rural sites. More research is needed to examine these early-establishment phases and compare

the magnitude of potential drivers and ecological barriers through existing ecological frameworks (e.g. Piana et al. 2019, Kowarik et al. 2018). Furthermore, such research should be integrated within traditional management frameworks to both test the viability of traditional silvicultural treatments for natural regeneration and support the development of urban-adapted silviculture programs. In addition to informing application, such research may also contribute to broader ecological theory such as understanding what determines plant abundance and distribution in urban landscapes.

Our findings challenge the notion that urban forested natural areas are inherently recruitment limited, and highlight the potential to adapt traditional forest management approaches that may be more cost effective and sustainable than current practice. With improved understanding of stand dynamics in urban forested natural areas, we may be able to structure comprehensive management plans that include both restoration planting treatments and more traditional silvicultural approaches. We advocate for 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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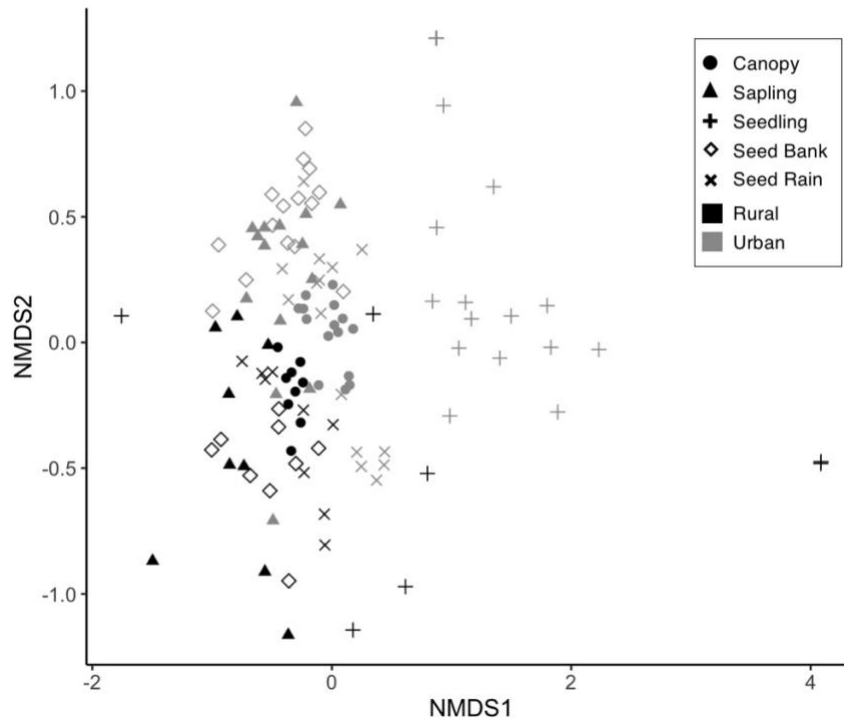
## Tables

**Table 1** Mean ( $\pm$  standard error) species richness and density of forest canopy (all stems  $\geq 10$  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 ( $n=9$ ). The densities for canopy (basal area,  $m^2/hectare$ ), sapling (basal area,  $m^2/hectare$ ), and seed bank (seeds/ $m^2$ ) were determined from a single sample collected in 2018. The density of seedlings (stems/ $m^2$ ) and seed rain (seeds/ $m^2$ ) was the average abundance from 2016-2018. Abundances were standardized from plot measures. Bold text 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).

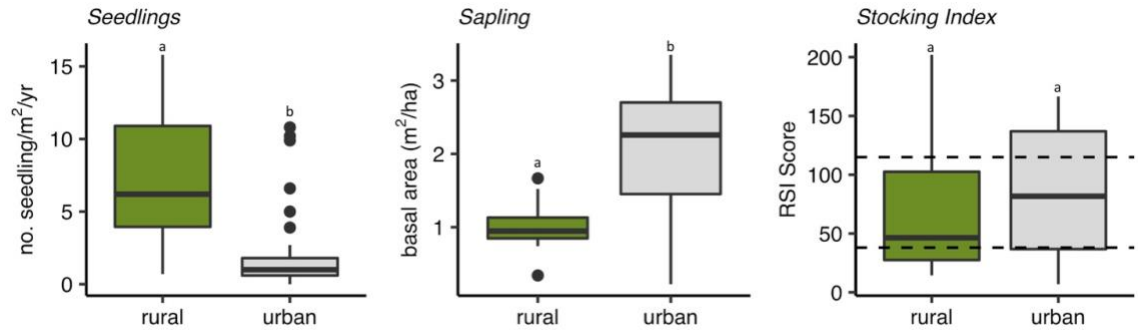
Strata and Seed Stage	Site Type	All Species		Native		Exotic	
		Richness	Density	Richness	Density	Richness	Density
Canopy	Urban	12.9 $\pm$ 0.8	<b>30.8 <math>\pm</math> 0.9</b>	11.8 $\pm$ 0.8	<b>30.3 <math>\pm</math> 1.0</b>	<b>1.3 <math>\pm</math> 0.2</b>	<b>0.5 <math>\pm</math> 0.2</b>
	Rural	13.8 $\pm$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

**Figures**

**Figure 1** Urban forested natural areas (left, Van Cortlandt Park, Bronx, NY) are greenspaces that are characterized by ecological function and processes, such as natural regeneration, commonly associated with rural forest systems (right, Blue Lake Forest Park, NY) (Photo credit: Max R. Piana).

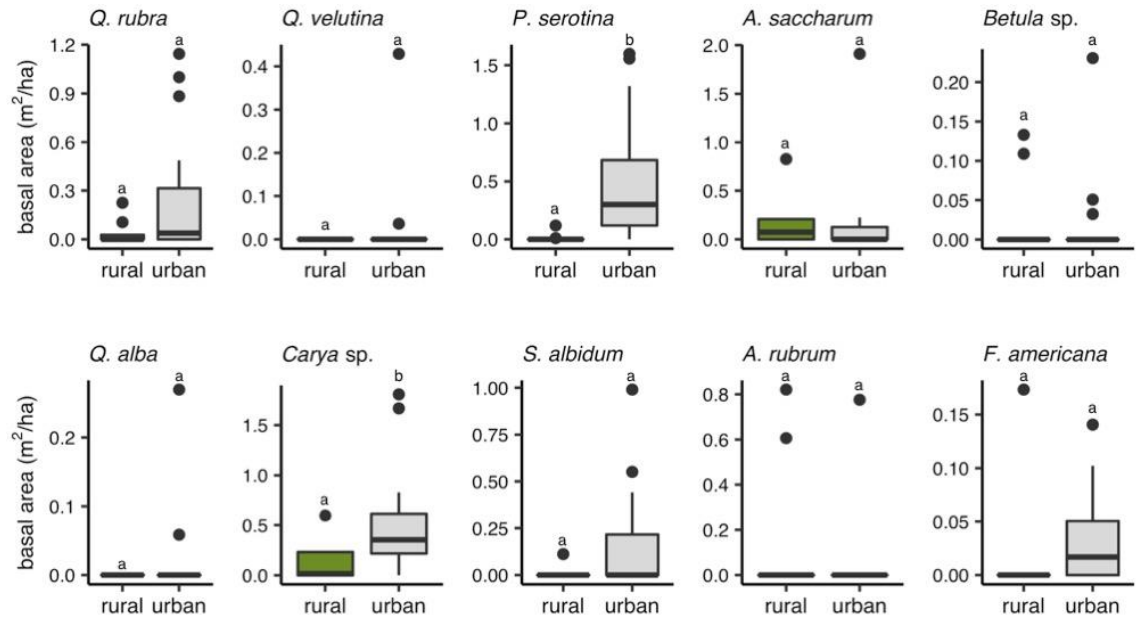


**Figure 2** NMDS ordination plots based on Bray-Curtis dissimilarities (stress=0.159) of forest tree community composition among forest strata (canopy, sapling, and seedling), seed rain and seed bank for all urban (n=15) and rural (n=9) forest plots. All data were converted to relative abundance prior to analysis. *Carya* was reported to genus.

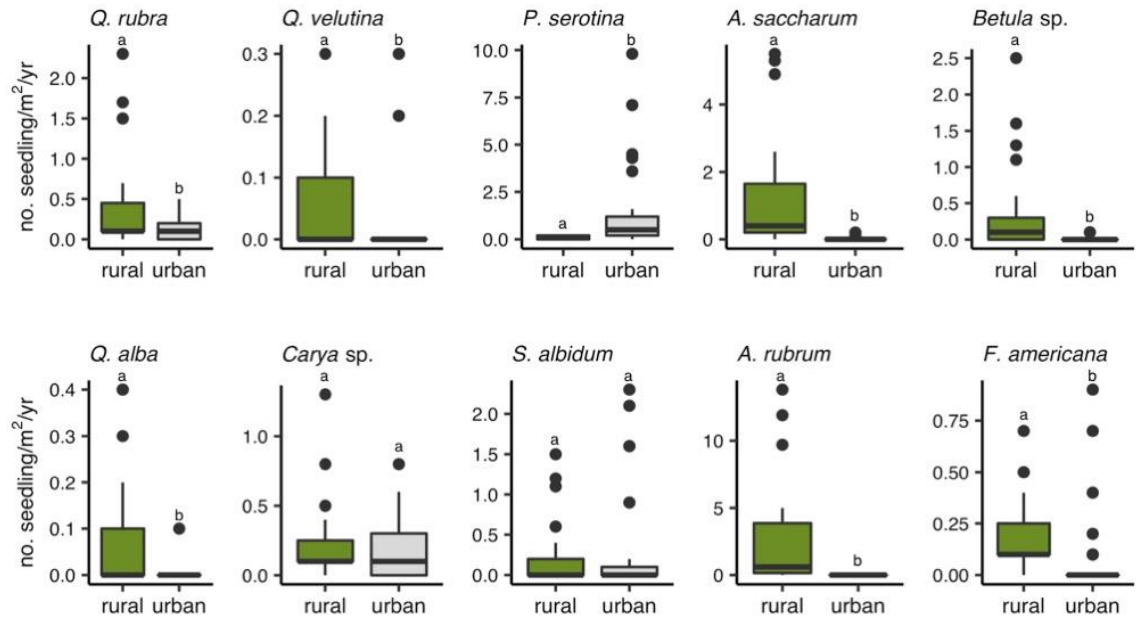


**Figure 3** Mean annual seedling abundance, total sapling abundance, and the natural regeneration stocking index (RSI) for urban (grey) and rural (green) forests. Seedling density was greater in rural forests ( $W=117.5$ ,  $p<0.010$ ), sapling density was greater in urban forests ( $W=29.0$ ,  $p<0.050$ ), and there was no difference in RSI ( $t=-0.26$ ,  $p=0.796$ ). 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<sup>2</sup>) 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  $\pm 1.5$  times the interquartile range to the 25th and 75th percentiles. Outlier points are beyond 1.5 times the interquartile range.

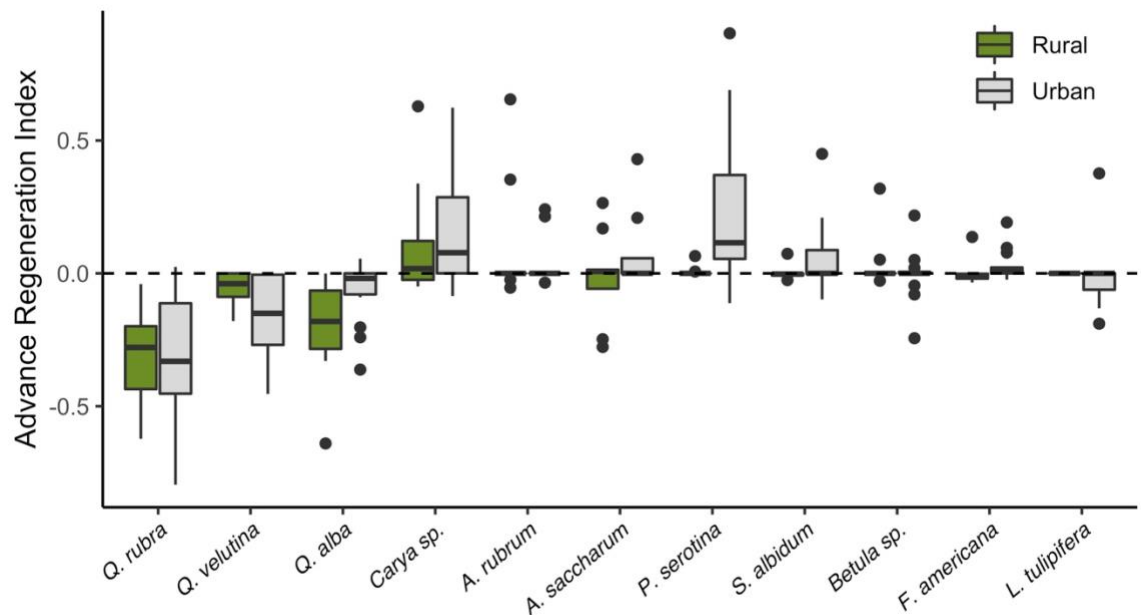




**Figure 4** Sapling abundance (seedling/m<sup>2</sup>) for canopy dominant species in urban and rural forests. Sapling abundances are the average of total seedling observed over three sampling years (2016-2018). We found greater density of *P. serotina* ( $W=8.5$ ,  $p<0.001$ ) and *Carya sp.* ( $W=27.0$ ,  $p<0.050$ ) 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.



**Figure 5** Seedling abundance (seedling/m<sup>2</sup>) 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* (W=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 *L. tulipifera* in 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.



**Figure 6** Advance regeneration index for canopy dominant species in urban (grey) 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 10m 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. The transition from oak to maple species corresponds with trends observed throughout oak forests on the east coast of the US (McEwan et al. 2011).

## **Supplemental Material**

### **Appendix S1**

**Table S1:** Study site descriptions.

**Table S2:** PERMANOVA and PERMDISP results.

**Table S3:** Complete list of species and abundance for all strata and seed stages.

**Figure S1:** Map of study sites, impervious cover, and human population density.

**Figures S2:** Seed trap design.

**Appendix S1: Table S1** Study Site Descriptions. Urban conditions were defined by population density (U.S. Census Bureau 2012) and percent impervious cover (USGS 2011). Each of these conditions was assessed at two buffer distances from each study site.

Site	Type	Human Population		% Impervious	
		0.5 km	2.0 km	0.5 km	2.0 km
Van Cortlandt Park	Urban	257.6	77541.7	10.1	27.7
Pelham Bay Park	Urban	246.8	3508.1	7.2	35.6
Inwood Hill Park	Urban	1073.6	121354.2	15.9	33.1
Black Rock Forest	Rural	0.0	486.0	0.8	3.6
Sterling Forest Park	Rural	0.0	167.0	0.1	0.3
Blue Lake Park	Rural	0.0	65.0	0.2	0.4

**Appendix S1: Table S2** PERMANOVA and PERMDISP analyses comparing differences

between strata within sites and the differences between the same strata in urban and rural sites.

Bold text indicates significant difference between urban and rural sites ( $p < 0.05$ ).

		PERMANOVA			PERMDISP	
Site	Pairwise Comparison	F	R <sub>2</sub>	P-adj.	t	P-adjust
Urban Only	Canopy-Sapling	<b>8.314</b>	<b>0.229</b>	<b>0.045</b>	<b>-2.329</b>	<b>0.022</b>
	Canopy-Seedling	<b>12.952</b>	<b>0.316</b>	<b>0.045</b>	-0.718	0.478
	Canopy-Seed Rain	<b>6.643</b>	<b>0.192</b>	<b>0.045</b>	<b>-3.323</b>	<b>0.003</b>
	Canopy Seed-Bank	<b>19.615</b>	<b>0.412</b>	<b>0.045</b>	-1.217	0.233
	Sapling-Seedling	1.337	0.046	1.000	0.880	0.369
	Sapling-Seed Rain	4.184	0.130	0.090	-0.395	0.699
	Sapling-Seed Bank	<b>13.829</b>	<b>0.331</b>	<b>0.045</b>	0.183	0.864
	Seedling-Seed Rain	5.845	0.173	0.090	-1.216	0.242
	Seedling-Seed Bank	<b>15.562</b>	<b>0.357</b>	<b>0.045</b>	0.499	0.631
	Seed Rain- Seed Bank	<b>12.021</b>	<b>0.300</b>	<b>0.045</b>	-0.412	0.682
Rural Only	Canopy-Sapling	<b>5.587</b>	<b>0.259</b>	<b>0.045</b>	<b>-9.051</b>	<b>0.001</b>
	Canopy-Seedling	<b>6.658</b>	<b>0.294</b>	<b>0.045</b>	<b>-4.761</b>	<b>0.001</b>
	Canopy-Seed Rain	<b>7.199</b>	<b>0.310</b>	<b>0.045</b>	<b>-3.773</b>	<b>0.002</b>
	Canopy Seed-Bank	<b>7.179</b>	<b>0.310</b>	<b>0.045</b>	<b>-10.777</b>	<b>0.001</b>
	Sapling-Seedling	0.910	0.054	1.000	2.135	0.053
	Sapling-Seed Rain	1.884	0.105	1.000	<b>2.738</b>	<b>0.014</b>
	Sapling-Seed Bank	2.410	0.131	0.135	-1.047	0.301
	Seedling-Seed Rain	2.457	0.133	1.000	0.611	0.548
	Seedling-Seed Bank	<b>3.528</b>	<b>0.181</b>	<b>0.045</b>	<b>3.028</b>	<b>0.014</b>
	Seed Rain- Seed Bank	<b>4.511</b>	<b>0.220</b>	<b>0.045</b>	<b>3.600</b>	<b>0.004</b>
Urban-Rural	Canopy-Canopy	<b>7.447</b>	<b>0.253</b>	<b>0.045</b>	<b>-2.719</b>	<b>0.011</b>
	Sapling-Sapling	3.539	0.139	<b>0.045</b>	<b>2.135</b>	<b>0.047</b>
	Seedling-Seedling	<b>9.020</b>	<b>0.291</b>	<b>0.045</b>	0.714	0.487
	Seed Rain – Seed Rain	3.817	0.148	0.450	-1.241	0.237
	Seed Bank – Seed Bank	<b>5.237</b>	<b>0.192</b>	<b>0.045</b>	1.718	0.101

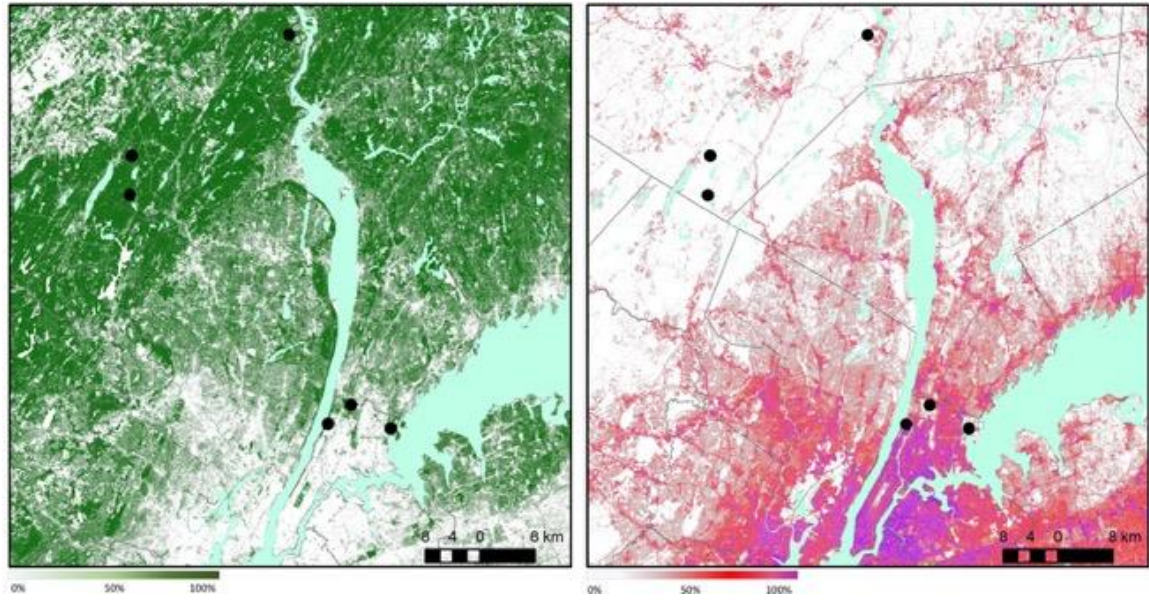
**Appendix S1: Table S3** Mean ( $\pm$  standard error) abundance of dominant tree species in urban and rural forest canopy (all stems  $\geq 10$  cm DBH), sapling, (all stems  $> 2$  and  $< 10$  cm DBH), and seedling strata (all stems  $< 2$  cm DBH and  $< 100$  cm height). The abundance for canopy (basal area/ha), sapling (basal area/ha), and seed bank (seeds/m<sup>2</sup>) was determined from a single sample collected in 2018. The abundance of seedlings (stems/m<sup>2</sup>) and seed rain (seeds//m<sup>2</sup>) is the average abundance from 2016-2018. See Supplemental Table S1 for complete species list.

Species	Site Type	Canopy (ba/ha)	Sapling (ba/ha)	Seedling (stems/m <sup>2</sup> )	Seed Rain (seeds/m <sup>2</sup> )	Seed Bank (seeds/m <sup>2</sup> )
<i>Acer negundo</i>	Urban	0.00 +/- 0.00	-	-	-	-
	Rural	-	-	-	-	-
<i>Acer pennsylvanica</i>	Urban	-	-	-	-	-
	Rural	-	-	0.00 +/- 0.00	-	-
<i>Acer platanoides</i>	Urban	-	-	-	0.10 +/- 0.06	-
	Rural	-	-	-	-	-
<i>Acer rubrum</i>	Urban	0.26 +/- 0.11	0.05 +/- 0.05	--	7.61 +/- 2.71	--
	Rural	1.37 +/- 0.65	0.16 +/- 0.11	2.61 +/- 0.72	48.32 +/- 21.59	2.12 +/- 1.50
<i>Acer saccharum</i>	Urban	0.29 +/- 0.22	0.17 +/- 0.13	0.01 +/- 0.01	0.34 +/- 0.25	-
	Rural	3.97 +/- 0.73	0.17 +/- 0.09	1.23 +/- 0.72	32.62 +/- 18.62	-
<i>Aesculus hippocastanum</i>	Urban	0.05 +/- 0.05	-	-	-	-
	Rural	-	-	-	-	-
<i>Ailanthus altissima</i>	Urban	0.02 +/- 0.02	-	0.01 +/- 0.00	1.14 +/- 0.31	-
	Rural	-	-	-	0.03 +/- 0.03	-
<i>Amelanchier</i> sp.	Urban	-	-	-	0.09 +/- 0.07	-
	Rural	0.09 +/- 0.05	0.10 +/- 0.07	0.06 +/- 0.02	0.00 +/- 0.00	-
<i>Betula</i> sp.	Urban	1.37 +/- 0.59	0.02 +/- 0.02	0.00 +/- 0.00	341.91 +/- 103.32	-
	Rural	0.49 +/- 0.19	0.03 +/- 0.02	0.35 +/- 0.12	105.68 +/- 46.68	-
<i>Carpinus carolina</i>	Urban	-	-	-	-	-
	Rural	0.02 +/- 0.02	0.00 +/- 0.00	-	-	-
<i>Carya</i> sp.	Urban	3.59 +/- 0.72	0.51 +/- 0.14	0.15 +/- 0.03	17.76 +/- 3.87	0.42 +/- 0.42
	Rural	2.31 +/- 0.43	0.12 +/- 0.07	0.23 +/- 0.06	25.61 +/- 7.48	-
<i>Carya cordiformis</i>	Urban	1.07 +/- 0.32	0.29 +/- 0.10	0.11 +/- 0.03	6.55 +/- 2.24	-
	Rural	-	-	-	-	-
<i>Carya glabra</i>	Urban	0.74 +/- 0.32	0.06 +/- 0.03	0.00 +/- 0.00	6.94 +/- 3.15	-
	Rural	1.51 +/- 0.31	0.09 +/- 0.20	0.16 +/- 0.05	22.48 +/- 7.31	-
<i>Carya ovata</i>	Urban	0.41 +/- 0.21	-	0.00 +/- 0.00	0.34 +/- 0.28	-
	Rural	0.10 +/- 0.06	-	-	0.32 +/- 0.18	-
<i>Carya tomentosa</i>	Urban	1.37 +/- 0.47	0.16 +/- 0.08	0.04 +/- 0.01	3.93 +/- 1.16	-
	Rural	0.69 +/- 0.16	0.03 +/- 0.03	0.07 +/- 0.01	2.81 +/- 1.13	-
<i>Celtis occidentalis</i>	Urban	0.05 +/- 0.02	0.07 +/- 0.05	-	0.21 +/- 0.08	-
	Rural	-	-	0.00 +/- 0.00	0.09 +/- 0.09	-
<i>Cornus florida</i>	Urban	0.01 +/- 0.00	0.02 +/- 0.01	-	0.05 +/- 0.03	-

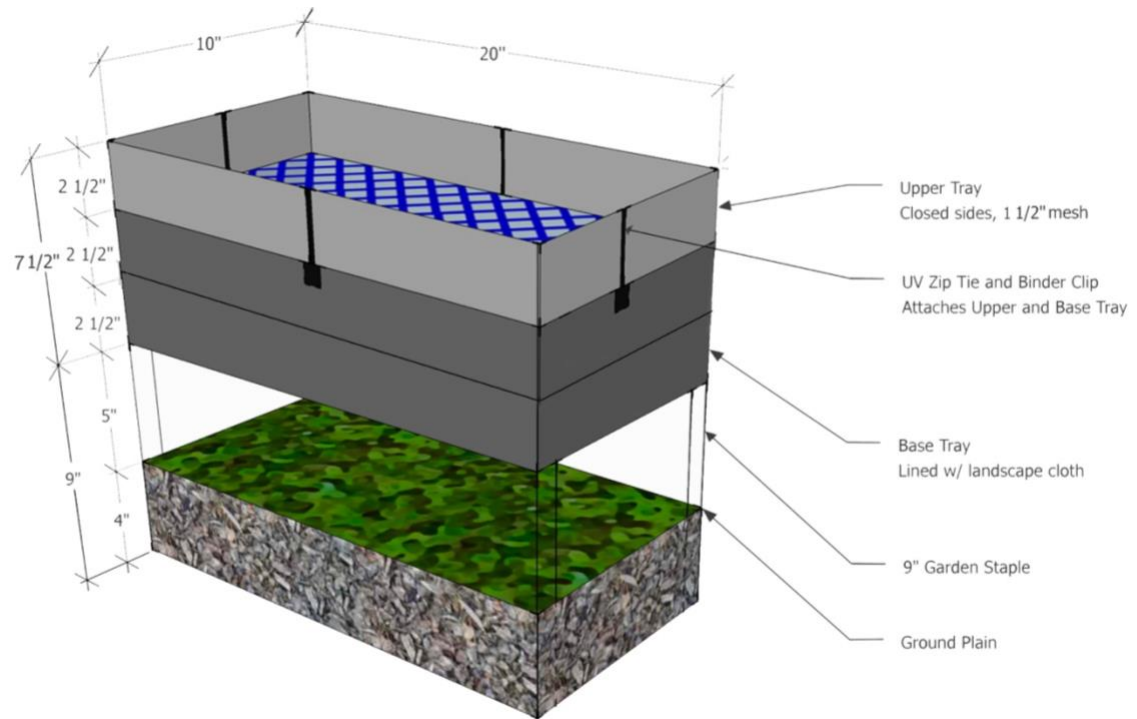
	Rural	0.02 +/- 0.01	0.05 +/- 0.05	-	0.78 +/- 0.46	-
<i>Crataegus sp.</i>	Urban	-	0.00 +/- 0.00	-	0.03 +/- 0.02	-
	Rural	-	-	-	-	-
<i>Diospyros virginiana</i>	Urban	0.03 +/- 0.03	-	-	-	-
	Rural	-	-	-	-	-
<i>Fagus grandifolia</i>	Urban	-	-	-	-	-
	Rural	0.08 +/- 0.05	0.02 +/- 0.02	0.01 +/- 0.00	-	-
<i>Fraxinus americana</i>	Urban	0.06 +/- 0.5	0.03 +/- 0.01	0.06 +/- 0.03	0.40 +/- 0.25	-
	Rural	0.48 +/- 0.13	0.02 +/- 0.02	0.18 +/- 0.03	4.05 +/- 3.14	-
<i>Fraxinus pennsylvanica</i>	Urban	-	-	0.01 +/- 0.00	-	-
	Rural	0.04 +/- 0.04	-	-	-	-
<i>Hamenalis virginia</i>	Urban	-	-	0.02 +/- 0.01	0.02 +/- 0.02	-
	Rural	0.03 +/- 0.03	0.11 +/- 0.06	0.41 +/- 0.10	0.63 +/- 0.53	-
<i>Juglans cinerea</i>	Urban	0.00 +/- 0.00	-	-	-	-
	Rural	0.06 +/- 0.06	-	-	-	-
<i>Juglans nigra</i>	Urban	-	-	-	-	-
	Rural	-	-	-	-	-
<i>Juniperus virginiana</i>	Urban	-	-	-	-	-
	Rural	0.03 +/- 0.03	-	-	-	-
<i>Liquidambar syrica</i>	Urban	0.60 +/- 0.54	0.00 +/- 0.00	-	52.39 +/- 30.45	2.55 +/- 1.84
	Rural	-	-	-	-	-
<i>Liriodendron tulipifera</i>	Urban	1.49 +/- 0.73	0.02 +/- 0.01	0.00 +/- 0.00	100.09 +/- 27.89	7.6 +/- 3.30
	Rural	--	--	-	0.43 +/- 0.13	-
<i>Maclura pomifera</i>	Urban	0.01 +/- 0.01	-	-	2.20 +/- 2.20	-
	Rural	-	-	-	-	-
<i>Malus sp.</i>	Urban	0.03 +/- 0.02	0.01 +/- 0.01	0.01 +/- 0.01	0.21 +/- 0.19	-
	Rural	-	0.00 +/- 0.00	-	-	-
<i>Morus alba</i>	Urban	0.16 +/- 0.14	0.00 +/- 0.00	-	0.43 +/- 0.35	7.64 +/- 2.50
	Rural	--	--	-	-	-
<i>Nyssa sylvatica</i>	Urban	-	-	0.04 +/- 0.02	7.17 +/- 5.10	-
	Rural	0.17 +/- 0.10	-	0.07 +/- 0.04	0.86 +/- 0.63	0.71 +/- 0.71
<i>Ostrya virginiana</i>	Urban	0.00 +/- 0.00	0.03 +/- 0.03	-	0.17 +/- 0.16	-
	Rural	0.50 +/- 0.44	0.15 +/- 0.10	0.63 +/- 0.25	7.90 +/- 5.78	-
<i>Paulownia tomentosa</i>	Urban	0.00 +/- 0.00	--	-	-	120.59 +/- 57.40
	Rural	--	--	-	-	-
<i>Phellodendron amurense</i>	Urban	0.01 +/- 0.01	-	-	-	-
	Rural	-	-	-	-	-
<i>Pinus strobus</i>	Urban	0.01 +/- 0.01	-	-	-	-
	Rural	-	-	-	-	-
<i>Platanus occidentalis</i>	Urban	-	-	-	0.43 +/- 0.36	-
	Rural	-	-	-	-	-
<i>Populus sp.</i>	Urban	0.00 +/- 0.00	-	-	0.26 +/- 0.13	-
	Rural	-	-	-	5.48 +/- 1.34	-
<i>Prunus avium</i>	Urban	0.05 +/- 0.02	0.00 +/- 0.00	0.04 +/- 0.02	0.91 +/- 0.43	-
	Rural	-	-	-	0.03 +/- 0.03	-
<i>Prunus serotina</i>	Urban	1.45 +/- 0.38	0.52 +/- 0.14	1.22 +/- 0.32	27.53 +/- 6.49	-
	Rural	0.01 +/- 0.01	0.01 +/- 0.01	0.09 +/- 0.02	0.49 +/- 0.19	-
<i>Quercus alba</i>	Urban	2.03 +/- 0.85	0.02 +/- 0.02	0.00 +/- 0.00	3.08 +/- 1.73	-
	Rural	3.21 +/- 0.65	--	0.07 +/- 0.02	3.59 +/- 1.93	-



<i>Quercus bicolor</i>	Urban	0.13 +/- 0.13 <sup>*</sup>	-	-	-	-
	Rural	0.02 +/- 0.02	-	-	-	-
<i>Quercus coccinea</i>	Urban	0.04 +/- 0.03	-	-	-	-
	Rural	0.02 +/- 0.02	-	-	-	-
<i>Quercus montana</i>	Urban	--	0.01 +/- 0.01	-	-	-
	Rural	3.01 +/- 0.36	0.02 +/- 0.02	0.38 +/- 0.13	1.38 +/- 0.67	-
<i>Quercus palustris</i>	Urban	0.32 +/- 0.20	-	-	3.41 +/- 1.68	-
	Rural	0.03 +/- 0.03	-	-	0.34 +/- 0.34	-
<i>Quercus rubra</i>	Urban	12.28 +/- 1.75	0.26 +/- 0.11	0.12 +/- 0.02	21.53 +/- 4.94	-
	Rural	8.40 +/- 1.34	0.04 +/- 0.03	0.40 +/- 0.11	16.74 +/- 4.50	-
<i>Quercus velutina</i>	Urban	5.32 +/- 1.36	0.03 +/- 0.03	0.02 +/- 0.01	10.53 +/- 3.08	-
	Rural	0.96 +/- 0.93	--	0.06 +/- 0.01	3.53 +/- 1.31	0.71 +/- 0.71
<i>Rhus glabra</i>	Urban	-	-	0.00 +/- 0.00	-	2.55 +/- 1.50
	Rural	-	-	-	-	1.42 +/- 0.94
<i>Rhus typhina</i>	Urban	-	0.00 +/- 0.00	0.00 +/- 0.00	-	1.27 +/- 0.68
	Rural	-	-	-	-	2.83 +/- 1.54
<i>Robinia pseudoacacia</i>	Urban	0.26 +/- 0.18	0.01 +/- 0.01	0.01 +/- 0.00	0.59 +/- 0.32	3.82 +/- 1.50
	Rural	-	-	-	-	-
<i>Sassafras albidum</i>	Urban	0.47 +/- 0.22	0.16 +/- 0.08	0.21 +/- 0.08	0.10 +/- 0.10	-
	Rural	0.14 +/- 0.07	0.01 +/- 0.01	0.22 +/- 0.08	0.03 +/- 0.03	-
<i>Tilia americana</i>	Urban	0.24 +/- 0.20	-	-	0.28 +/- 0.20	-
	Rural	0.28 +/- 0.19	-	0.09 +/- 0.04	2.56 +/- 1.72	-
<i>Tilia cordata</i>	Urban	0.00 +/- 0.00	-	-	-	-
	Rural	-	-	-	-	-
<i>Tsuga canadensis</i>	Urban	-	-	-	-	-
	Rural	0.05 +/- 0.05	-	-	-	-
<i>Ulmus americana</i>	Urban	-	0.03 +/- 0.03	-	-	-
	Rural	-	-	-	-	-
<i>Ulmus rubra</i>	Urban	0.08 +/- 0.05	0.03 +/- 0.03	0.00 +/- 0.00	0.26 +/- 0.15	-
	Rural	-	-	-	-	-



**Appendix S1: Figure S1** Urban and rural forest site locations in relation to (A) percent regional forest canopy cover and (B) percent impervious cover (National Land Cover Database 2016).



**Appendix S1: Figure S2** Seed trap design. Each trap consists of three 52.0 x 26.5 cm plastic trays, stacked and attached with a combination of binder clips and utility ties. Traps are elevated 15 cm off the ground with garden staples. Weed barrier cloth is secured to the base tray to capture seeds. The upper tray limits granivore access to captured seeds.

**Chapter 3: Native tree recruitment in urban and rural forests: differences in seed and establishment limitation as barriers to natural regeneration**

## ABSTRACT

1. Anthropogenic disturbances affect plant recruitment and for some species may increase the magnitude of seed and establishment limitation. There is evidence that natural regeneration, especially early seedling establishment, may be more limited in urban compared to rural forested natural areas. However, there are few process-based studies that examine recruitment dynamics in urban plant communities.
2. We apply the recruitment limitation framework to urban forested natural areas to advance a mechanistic understanding of observed differences in tree recruitment. We report findings from a three-year study comparing seed source limitation, seed production (fecundity) limitation, and early seedling establishment limitation in urban and rural forested natural areas in the northeast United States.
3. Our findings show that early recruitment limitation is greater in urban forests than rural forests. Differences in seed availability in urban and rural forests were driven by adult abundance and source limitation, not changes in fecundity. However, we do find evidence that interannual patterns of seed availability in some species may be different between urban and rural forests. Total seedling abundance and mean annual seedling establishment were both greater in rural forests. In both site types, we observed limited oak regeneration and successful recruitment of subdominant species. In rural forests, maple species are successfully regenerating, following regional trends in oak forests. *Acer rubrum* (red maple) was not seed limited in urban forests, however no recruits were found over the 36 months of this study. Instead, *Prunus serotina* (black cherry) was commonly observed, but primarily absent from rural forest sites. Both urban and rural oak-hickory forests may be experiencing a shift in community composition; however, our results suggest that they are on divergent successional trajectories.

4. *Synthesis.* There are fewer total and first-year native tree seedlings in urban than rural forests. Establishment factors, not differences in seed availability, drive this change. Early-establishment is a significant barrier for seedling recruitment in both urban and rural forests, but the magnitude of this stage is greater in urban forests. Improved understanding of urban-driven changes to recruitment dynamics will advance sustainable land management in cities and provide insight into how our rural forests may respond to continued global change and anthropogenic forces.

**Keywords:** natural regeneration dynamics, oak decline, plant recruitment, seed dispersal, seed production, seed fecundity, site limitation, seedlings, urban ecology

## 1. Introduction

In an increasingly human-impacted planet, ecologists seek to determine the effect of multiple anthropogenic forces, such as climate change, fragmentation and land use change, nitrogen deposition, and invasive species on plant biodiversity and community dynamics (Sala et al., 2000; Vitousek et al., 1997; McEuen & Curran, 2004; McConkey et al. 2012). With respect to plant recruitment, there is strong evidence that global change factors may limit recruitment, especially early-recruitment stages and process (e.g. Clark et al. 2007; Ibanez et al. 2007; McConkey et al., 2012; Uriate et al., 2012). Urban ecosystems are characterized by multiple, co-occurring, and often exacerbated anthropogenic forces (Picket et al., 2011). By directing urban research toward forest function and processes, such as recruitment dynamics, we may engage urban plant ecology in a broader conversation, advancing both theory and application (Piana et al., 2019).

Recruitment limitation provides a framework for quantifying the contribution of different plant life history stages to recruitment success. Recruitment limitation is defined as the failure of a species to establish in all suitable places (Muller-Landau, 2002). The three mechanisms commonly cited as drivers in recruitment limitation research include: (1) source limitation, defined as low seed availability at the population scale which may be the result of low adult population abundance or fecundity, also referred to as production limitation (Clark et al., 1998); (2) dispersal limitation, the failure of seeds to arrive to all potential recruitment sites (Crawley, 1990; Schupp et al., 2002); and (3) site limitation, also referred to as establishment limitation, defined as conditions where plant populations are constrained by the number and quality of favorable sites (Clark et al., 1998; Nathan & Muller-Landau, 2000). The relative strength and importance of seed (source, production, and dispersal) and site (post-dispersal through adult establishment stages) limiting factors has been a longstanding debate in plant ecology (e.g. Harper, 1977; Clark et al., 2007).

This study tests urban-driven changes to plant recruitment limitation in the context of urban forested natural areas. Urban forested natural areas are an important component of the total

urban tree canopy and sustainable cities. These urban habitats are more akin to rural forests than they are to street trees and landscape trees, supporting the natural regeneration of plants and basic forest ecosystem functions. Urban forested natural areas provide critical ecosystem services for residents (e.g. Hasse et al., 2014) and habitat for local, and even regional, biodiversity (e.g. Ives et al. 2016, Lepzyck et al., 2017). These sites are also common and substantial, making up approximately 85% of municipal parkland in the United States (Trust for Public Land, 2017). Forested natural areas are common in many of the world's largest and densest cities located with forested biomes (e.g. Lawrence et al., 2013).

The sustainability of urban forested natural areas is dependent upon their ability to naturally regenerate. However, there is evidence that urban forests may be more recruitment limited than their rural counterparts. When comparing plant communities between urban and rural plots and across an urban-rural gradient, researchers report greater non-native seedling species richness in urban forests (Airola, 1984; Guntenspergen et al., 1997; Zipperer et al., 2002; Cadenasso et al. 2007) and reduced native seedling abundance (Burton et al., 2005; Cadenasso et al., 2007; Pennington et al., 2010; Trammell & Carreiro, 2011; Overdyck & Clarkson, 2012). Other research has found urban forests to be seedling limited, but not sapling limited, meaning that urban sites may experience greater seed and/or establishment limitation (Chapter2).

The ecological processes driving this response in urban plant populations, as well as the stage at which populations are most limited, is not well understood. Urban fragmentation, land use change, and historic management regimes may alter seed dispersal and availability, increasing seed limitation (Cutway & Ehrenfeld, 2010; Ettinger et al., 2017). Alternatively, abiotic and biotic changes to the environment, including but not limited to climate, soil biochemistry, reduction in leaf litter, and altered herbivory, competition, and disturbance regimes may result in altered recruitment dynamics and establishment limitation (e.g. Kostel-Hughes et al., 1998; Pregitzer et al., 2016; O'Brien et al., 2016; Labatore et al., 2017; Ettinger et al., 2017). Despite



these barriers to early-establishment, there is evidence of similar, or even greater, sapling recruitment and advance regeneration in urban forested natural areas (Chapter 2). From a management perspective, determining the recruitment processes limiting early-establishment in urban forests may help direct effective strategies to promote regeneration of native species and the sustainability of urban forests.

We conducted a three-year study in urban and rural oak-hickory forested natural areas located in the New York City metropolitan area, and asked (1) Are urban forests more seed and/or establishment-limited than rural forest equivalents? (2) What is the magnitude of multiple components of recruitment limitation, including, source limitation, seed availability and fecundity, dispersal limitation, and seedling limitation in urban and rural forests? This careful examination of population dynamics, focused on recruitment limitation, is needed for management of sustainable and resilient urban forest ecosystems.

## **2. Materials and methods**

### **2.1 Study Location**

The study was conducted in six oak-hickory forests sites in New York City (NYC) and the NYC metropolitan area. Urban sites (n=3) were located in forested natural areas in Van Cortlandt Park (VCP) and Pelham Bay Park (PBP) in the Bronx, and Inwood Hill Park (IHP) in Manhattan. Rural forests sites (n=3) were located in the New York Hudson Highlands region at Sterling Forest State Park, Blue Lake Park, and Black Rock Forest. We selected sites in the Hudson Highlands and selected regions of Manhattan and the Bronx, which are all located in the southernmost region of the Northeast Upland Province (Fennemen & Johnson, 1946; Broughton et al., 1966), to maintain similar geophysical histories while minimizing climatic differences

amongst sites. Sites were classified as either urban or rural by both the relative percent human population density and percent impervious surface. All sites were located more than 15km apart.

To minimize risk of loss to vandalism, six plots were installed in each of the three urban sites (n=18) and three plots were installed in each of the rural sites (n=9). Three urban plots experienced significant disturbance related to human activity and were not included in the final analyses. All plots were randomly located in oak-hickory forest stands and located more than 200 m from the next nearest plot. Oak-hickory is a common forest community type in NYC natural areas (Forgione et al., 2016) and throughout the northeast corridor, one of the most densely developed regions in the United States (Short 2010). Urban forest community type was defined by a recent city-wide ecological assessment, which includes the development of urban-specific classification system (Forgione et al., 2016; Pregitzer et al., 2019). In addition to these selection criteria, we controlled for forest structure, relative age (60-100 years), and canopy cover, avoiding gap conditions. We used spherical densiometers to estimate canopy density in each plot and assure similar light regimes in among plots (Supplemental Figure S1). All plots were installed >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. All plots were located where there was minimal evidence of restoration plantings or other active management techniques (e.g. invasive plant removal) to avoid artifact of human management on regeneration dynamics.

## **2.2 Field methods**

Canopy trees were sampled in 20 m fixed radius derived from plot center. Canopy trees were defined as all single- and multi-stemmed individuals greater than 7.5 cm dbh (1.30 m above ground). Trees were sampled in July 2018. Seedlings were sampled in 1x1 m semi-permanent quadrats installed in two parallel transects adjacent to each seed rain trap. Naturally regenerating seedlings were mapped and tagged to record emergence and survival over time. *Carya* seedlings

were identified to genus only. All other species were identified to species. Seedlings were sampled in July each year (2016-2018).

Seed rain was monitored from March 2016 to March 2019 using a custom designed seed trap (0.125 m<sup>2</sup>). Seed traps were elevated from the ground and included a screen to minimize seed predation within the trap. The seed trap design was tested for seed loss due to bouncing for a range of seed types and sizes (Clark et al., 1998). 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 (e.g. Clark et al., 1998). Ten seed traps were installed at each plot in two parallel 20 m transects, 5 meters apart, with traps installed at 5 m intervals. Sampling intensity and trap spacing was modified from protocol established in eastern U.S. deciduous forests and review of seed rain studies (Clark et al., 1998; Clark et al., 1999). Seeds were collected from each trap monthly from January to August, and bi-weekly August to January to minimize seed predation risk during peak dispersal. All captured seeds were identified to the species level. Only mature and intact diaspores were considered in our analyses.

Soil samples were collected in December 2016 at ten randomly selected locations within each plot, using a 2.5 cm diameter soil probe and sampling to 10 cm depth. Samples were processed by the Rutgers University Soil Testing Laboratory and analyzed for nutrient availability (P, K, Ca, Mg, Fe, Mn, Zn, Cu, B, S), lead (Pb), and aluminum (Al), cation exchange capacity, soil organic matter, pH, and total Nitrogen. All samples were processed by the Rutgers University Soil Testing Laboratory. We used principal component analysis (PCA) to compare differences between urban and rural sites, as well as among urban plots only (Supplemental Figure S2).

## 2.3 Data Analysis

Data analysis was limited to species that were dominant and subdominant in both urban and rural forest canopy and seedling banks. This included: *Quercus rubra*, *Q. alba*, *Q. velutina*, *Acer saccharum*, *A. rubrum*, *Carya* sp., *Prunus serotina*, *Betula* sp., *Fraxinus americana*, and *Sassafras albidum*. *Sassafras albidum* was the only species not dominant in the canopy but prevalent in the seedling bank in both urban and rural sites. For *Betula* sp. we did not distinguish between species within seed rain and report only to genera. In our analysis and subsequent discussion, we use “site type” to refer to urban and rural designations. All data were analyzed at the plot-scale and therefore represent stand average.

### **2.3.1 Seed source and production limitation**

Seed limitation (low seed availability at the population level) can result from low adult population (source limitation) and/or low per-capita production (fecundity). Multiple models were used to understand these two components of seed limitation. We used generalized linear models (GLMs) to test how seed density was related to conspecific adult-tree abundance and whether this relationship was annually variable and related to site type (urban or rural). We modeled mean seed density for each plot following a negative binomial distribution with log link. Multiple models were fitted with the effects of adult tree basal area, year, and site type, and the interaction between basal area and year, and year and site type. We report only the most parsimonious model (See Supplemental Table 2 for model equations). The predictive strength of these models must be approached with caution. Stand level basal area measurements are an imprecise measure of adult trees that disperse into seed traps, which may contribute to poor model fit. Second, the log-linear relationship may not be the most appropriate, although there is precedent for this modeling approach (e.g. Krois & HillRisLambers, 2015). The negative binomial distribution was used to account for overdispersion. All GLM models were fit using glmmTMB package in R programming language (version 3.6.0, R Development Core Team 2019; Brooks et al.2017).

To determine whether seed limitation for each of the dominant canopy species was a product of source or production limitation, we directly compared seed density, adult conspecific basal area, and fecundity between urban and rural forests. Analyses included only plots where adult con-specifics were present. Each measure was conducted at the plot (stand) scale. Mean seed density was modeled at the plot-scale, for each year, using GLMs with a negative binomial distribution and log link. Fecundity was measured at the plot scales as the ratio of average seed rain and stand basal area (Clark et al., 1998). Here, fecundity represents the “stand average” or the constancy of fecundity among plots. We did not calculate among-stand fecundity for two reasons. First, agreement has been observed between these two measures in similar forest types as our study. Second, model fit at the level of the individual seed trap is less strong for dispersed populations and species with relatively long dispersal curves (Clark et al., 1998). Urban forest composition in our sites was spatially heterogeneous and many species in our system are gravity or wind dispersed. Fecundity and basal area were modeled following a normal distribution, with site type included as a fixed effect. We observed differences in seed availability among sample years but did not include year as a random effect in mixed-models due to the limited number of total observation levels.

### ***2.3.2 Seedling regeneration and establishment***

We compared site differences in total seedling abundance and the abundance of first-year recruits using GLM. Total seedling abundance includes seedlings of all age and size classes and analysis was only conducted for all observed tree seedling species, including species other than focal species. For emergent seedlings, we fit models for all species pooled and for each individual species. All models were fit using GLM with a negative binomial distribution and log link, where site type was included as a fixed effect and basal area as covariates. Adult con-specific basal area was included as a covariate to account for potential source limitation.

### ***2.3.3 Components of Recruitment Limitation***

Seed trap data were used to quantify the relative magnitude of source limitation, dispersal limitation, and fundamental seed limitation, following Clark et al. (1998) and Muller-Landau et al. (2002). Source limitation was calculated as the proportion of traps at which no seeds arrive if the observed seed rain was randomly (Poisson) distributed. Dispersal limitation was the proportion of traps reached by seeds compared to the proportion expected if dispersal had been randomly distributed; and seed limitation was the proportion of traps not receiving seeds (Muller-Landau et al., 2002). Fundamental seedling limitation and establishment limitation were calculated from the recruitment data collected from 2016-2019 for all newly emerged seedlings quadrats adjacent to each seed trap. Fundamental seedling limitation was equal to the proportion of quadrats where seedlings established as a function of all seedling quadrats. Establishment limitation was equal to the proportion of sites where seeds arrived but seedlings did not recruit, accounting for differences in seed trap and seedling quadrat area. The values of the components of recruitment limitation range from 0 (no limitation) to 1 (maximum limitation). For each category of limitation, we used data collected from across the 36-month duration of this study (April 2016 to April 2019).

### **3. Results**

#### **3.1 Interannual variance in seed availability**

For each of the focal species, stand-specific seed densities were positively related to conspecific tree basal area (Fig. 1, Supporting Information Table 1 and Table 2). These findings support the conclusion that in both urban and rural forests the average seed density is constrained by parent-tree abundance at the stand scale. For all species, except *Q. alba* and *Q. velutina*, seed density also varied by year. The relationship between interannual patterns of seed density in urban and rural forests was species dependent. For *Q. rubra*, *P. serotina*, *A. rubrum*, and *A. saccharum*, best fitting models included site type (urban or rural), year, and their interaction (Supporting

Information Table 1 and Table 2). For example, *Q. rubra* seed density varied by year for both urban and rural forest sites, but years of high and low seed density (mast years) were not synchronized between site types. In the absence of the influence of site type and year (*Carya* sp., *Betula* sp., *F. americana*), interannual patterns of seed availability were similar in urban and rural forests.

### 3.2 Seed source and production limitation

Over the 36 months of this study, seed density was significantly different between urban and rural sites for four species (Fig. 2). Both *A. rubrum* and *A. saccharum* had greater seed density in rural forests. *Betula* sp., *Q. velutina* and *P. serotina* were captured at greater densities in urban forests. For all other species the average seed density at the stand-scale did not differ between site types. Differences in urban and rural seed density for *P. serotina*, *A. rubrum*, *Betula* sp., and *Q. velutina* were driven by the abundance of adult conspecifics, not differences in the fecundity of individual in urban and rural forests. In other words, these species are characterized by source limitation and not production limitation. *A. saccharum* and *Carya* sp. were more fecund in rural forests when compared to urban forests. However, given the observed differences in adult basal area for *A. saccharum*, these differences may be driven by the distribution of adult species in plots. A single or small group of trees located directly above a seed trap could skew results and overestimate seed production. Interestingly, the abundance of adult *Carya* sp. was greater in urban forests, yet the density of seed captured was lower than rural forests. This finding suggests that urban conditions may negatively affect the fecundity of this species.

### 3.3 Seedling establishment and recruitment

Seedling establishment and total seedling abundance was significantly greater in rural forests (Fig. 3). When pooling all species, rural sites had significantly greater average abundance of total seedling recruits (7.1 seedlings/m<sup>2</sup>) and emergent seedlings (3.7 seedlings/m<sup>2</sup>), than urban forests (total recruits = 1.9 seedlings/m<sup>2</sup>; first year seedling recruits = 0.9/m<sup>2</sup>). In our species-specific

models we accounted for adult-conspecific basal area (potential source limitation between site types). Seedling establishment (emergent seedlings only) was low for all species in both urban and rural sites (Fig. 4). Over the 36 months of study, greater seedling establishment was observed in rural sites for *Carya* sp., *Betula* sp., *F. Americana*, *A. rubrum*, and *A. saccharum*. *P. serotina* was the only species with greater first year recruits in urban forests. We did not find a single first year recruit for either *Acer* species in urban forests during the study.

### 3.4 Components of recruitment limitation

Fundamental seed limitation was variable among species and site type, but it confirms many of the observations from the previous analyses (Table 1). We measured seed limitation as the percentage of traps that did not receive seed. In urban forests, seed limitation was weakest (< 30% of traps) for *Carya* sp., *P. serotina*, and *Q. rubra*. Conversely, seed limitation was strongest (>90%) for *F. americana*, *S. albidum*, *Q. alba*, and *A. saccharum*. In rural sites, seed limitation was strongest for *P. serotina* and *S. albidum* (>85%), and to a lesser extent *Q. alba* and *Q. velutina* (>75%). On average in rural sites, seed from *Q. rubra*, *Carya* sp., *A. rubrum*, *A. saccharum*, and *Betula* sp. was received in more than 60% of all traps. With the exception of *P. serotina*, *F. americana*, and *S. albidum*, dispersal was a similar or greater limiting factor than adult source in rural forests.

In both urban and rural forests, establishment limitation (the proportion of plots that did not have first year recruits as a function of the adjacent seed traps that received seed) was strong and typically greater than seed limitation. For all species, more than 85% of plots receiving seed did not have first year recruits. All species, except *P. serotina*, were more seedling limited (the proportion of plots where first year recruits were observed) in urban compared to rural forests. Over the 36 months of study, *P. serotina* established in an average of 67% of urban seedling quadrats. In rural forests, *A. rubrum*, was by far the least seedling- (0.38%) and establishment-



(87%) limited species. Other species with first year recruits in more than 20% of rural forest seedling quadrats were *A. saccharum*, and *Carya* sp.

#### 4. Discussion

Our results indicate that early recruitment limitation is greater in urban forests than in rural forests, but that these trends vary interannually and across species. Additionally, for most species in this study, establishment limitation was stronger than seed limitation. These findings begin to identify the mechanisms, throughout multiple plant life-history stages, responsible for different recruitment patterns in urban and rural forests (Fig. 5). By quantifying seed and site limitation, we can integrate our understanding within the context of existing theoretical frameworks that allow for generalizations of urban plant ecology, beyond cities and across gradients of anthropogenic change. From a management perspective, we show that to promote natural regeneration, managers will need to address site limitations that constrain early seedling establishment.

##### 4.1 Interannual seed availability in urban and rural forests: evidence of a functional shift in urban ecology?

There is evidence that anthropogenic forces such as climate change, fragmentation and land use change result in greater seed limitation (e.g. McCuen & Curran, 2005; Clark et al., 2007; McConkey et al., 2012; Kroiss & HilleRisLambers, 2015). In what is, to our knowledge, the only other comparison of urban and rural seed availability, seed limitation was the primary driver of recruitment limitation (Ettinger et al., 2017). However, in our study, we did not find seed limitation to respond strongly to urban conditions. Species-specific responses for seed limitation by site type varied, and some species, such as *P. serotina*, were less limited in urban forests. In general, species were more site than seed limited. However, for species where seed limitation was strong, it was the absence of an adult source population, not seed production or dispersal, that was the primary ecological barrier to recruitment.

While seed limitation did not differ strongly between urban and rural forests, we did observe different patterns of interannual seed availability for some species. In temperate forests, highly variable seed production and seedling recruitment can occur from year to year (Clark et al., 1998). This is particularly true in oak-hickory forests, which are dominated by masting tree species characterized by episodic dispersal and recruitment events (Sork et al., 1993; Sork et al., 1997). Such patterns also appear in our study, where seed production was positively related to the abundance of adult conspecifics but was markedly different among years. For some species, such as *Carya* sp., the interannual variance was relatively similar for urban and rural forests, but for other species we observed strong interactions between annual seed availability and site type. This was particularly true for *Q. rubra*. In rural sites *Q. rubra* was defined by low seed availability in 2016, with mast year production in both 2017 and 2018. In urban sites we observed greater seed availability in both 2016 and 2017, and lower availability in 2018. These findings suggest that mast dynamics are not synchronized between urban and rural sites.

It is important to note that our study was not designed to monitor masting or seed production of a single species and given the limited length of the study, our data are not substantial enough to fully determine seed production trends. Recent studies have found that masting may vary over small areas and cannot be regionally generalizable (Wang et al., 2017). Understanding the drivers of mast dynamics is complex and involves multiple forces (Crone & Rapp, 2014). With this understanding, global change research provides evidence that supports shifts in urban seed production and mast dynamics. For example, anthropogenic forces associated with cities, such as nitrogen deposition and increased temperatures (Pickett et al. 2011), have been found to increase and alter seed production in oaks (Bogdziewicz et al., 2017; Caignard et al. 2017). In one study, nitrogen addition increased red oak fecundity, but decreased overall viable seed production due to concurrent increases in pre-dispersal predation (Bogdziewicz et al., 2017). There is also evidence that masting may be resilient to changing climate, again

demonstrating the complexity of this ecological process (Kelly et al., 2013). That many of these global change factors co-occur and are often exacerbated in cities presents a strong working hypothesis for future research. It is particularly pertinent to understand if mast dynamics are simply desynchronized at small spatial scales or if dynamics are altered due to urban conditions. We advocate for long-term study of urban and rural sites, located across multiple cities and a latitudinal gradient. This will be needed to develop evidence-based management of our extensive urban forest assets during a period of rapid climate change.

#### **4.2 Early recruitment limitation drives urban forest regeneration**

Lower abundance of seedlings in temperate urban forests has been well established in urban ecology (e.g. Burton et al., 2005; Cadenasso et al., 2007; Pennington et al., 2010; Trammell & Carreiro, 2011; Overdyck & Clarkson, 2012). Our study suggests that site and establishment factors, not seed availability, more strongly limit tree recruitment in these urban forests compared to rural forests. While the results from our study, as well as others, show that canopy dominant tree species are both seed and site limited (e.g. Clark et al., 1998; Lepage et al., 2000; McCuen & Curran, 2004), our research here indicates that site limitation is a stronger barrier to forest regeneration and may drive divergent successional trajectories between urban and rural forest patches. Few of the species in our study saturate sites with seed and only a small proportion of the seeds that arrive establish, let alone recruit beyond a single year. Establishment is therefore a strong ecological barrier determining plant abundance and distribution in both rural and urban forest ecosystems. Given the episodic and relatively low proportion of transition from seed to seedling in rural forests, establishment limitation will have important consequences for urban forest community dynamics.

When comparing between urban and rural site types, establishment was significantly different across multiple species. Specifically, seedling establishment and recruitment limitation were significantly greater in urban sites for all species except *P. serotina*. Recent research has

also observed high establishment limitation for tree species in urban forests, although these studies do not provide rural comparisons to help understand any changes in the magnitude of the ecological barriers (Labatore et al., 2017; Massad et al., 2019).

There are multiple factors, both biotic and abiotic, that may drive higher recruitment limitation in urban forests (Zipperer, 1997; Piana et al., 2019). Global change research has found species with small seeds to be less seed limited in disturbed habitats (Clark et al., 2007). These species may benefit from greater dispersal distances and ability to persist longer. In an urban-rural gradient study, the abundance of seedlings of smaller seeded species, such as birch and maple, were positively correlated with proximity to urban centers (Kostel-Hughes et al., 1998). In a follow up lab study, the success of these species was found to be related to decreased leaf litter depth (Kostel-Hughes et al., 2005). In our study sites we also observed lower leaf litter depth in urban forests.

Other microsite conditions, such as soil contamination, abundance of woody debris, and competition with invasive plants may limit seedling establishment (Pregitzer et al., 2016; Ettinger et al., 2017). Despite controlling for soil series during plot selection, there were distinct differences in urban and rural forest soils (Supplemental Figure S2). Specifically, in urban plots we found higher pH and metal concentrations, and lower organic matter. Such factors may act as site filters for seedling establishment. Conversely, some urban conditions increase seedling survival and growth, such as increased temperatures and atmospheric carbon (e.g. Searle et al., 2010). Post-dispersal limiting factors that affect seedling establishment prior to germination, such as seed predation and seed bank persistence are not well studied but could limit populations. Research is needed to isolate these specific mechanisms and identify potential shifts in their functional response to urban conditions.

#### **4.3 Forest community consequences and implications for management**

Greater recruitment limitation and species-specific recruitment response to urban sites may have important consequences for forest succession and future forest composition. In both urban and

rural forests, we observed limited oak seedling recruitment. These findings support observations from regional studies of red oak dominated forests in the eastern United States (McEwan et al., 2011). Specifically, although oaks are the dominant canopy species in these forests, smaller size classes aren't as well represented (Lorimer, 1984; Loftis et al., 1993). There are multiple hypotheses of what might drive recruitment limitation of oak species, including changing climate, increased herbivory from white tailed deer (*Odocoileus virginianus*), and altered disturbance regimes (McEwan et al., 2011).

With lower abundance of *Q. rubra* in seedling and sapling strata, research shows an increase in maple species, especially *A. rubrum* (Abrams et al., 1998). This pattern is consistent among our rural sites. In rural sites, *A. rubrum* occurred in 62% of all seedling quadrats. Despite similar seed availability in urban sites, we found no red maple seedlings or first year recruits. This was surprising and may highlight a divergent response in urban and rural systems as these oak forest communities succeed. Urban ecosystem conditions, such as the abundance of invasive earthworms may be driving these observed differences. Research has found invasive earthworm species to negatively impact the recruitment of maple species (e.g. Hale et al., 2006; Corio et al., 2009; Drouin et al., 2014; Craven et al., 2017). Invasive earthworms are more abundant in urban habitats (Steinberg et al., 1997), and although we did not test earthworm abundance, there was evidence of earthworm presence in our urban plots. Instead of *Acer* sp., it is *P. serotina*, another early successional tree, that is successful in recruiting in urban oak-hickory forests. A bird-dispersed species, *P. serotina* is characterized by low source and dispersal limitation. Given the fragmented character of urban forested natural areas, such species may be better adapted to succeed in urban landscapes and will need special attention by forest managers.

Understanding whether a forest is seed or establishment limited can help guide the management of urban forests. Current methods often rely on direct planting. In our study system, it is clear that native canopy species are not seed limited but do experience strong barriers to

recruitment from post-dispersal to early-establishment. Although seedling establishment is greatly limited in urban forests, comparison of urban and rural stocking indices suggests that overall recruitment to sapling stages may be no different, and in fact greater in urban sites (Chapter 2). Once established, the transition from seedling to juvenile and adult stages may be comparable in urban to rural sites. Indeed, urban tree growth may outperform rural sites, as a result of increased temperatures and atmospheric carbon (e.g. Gregg et al, 2003; Searle et al., 2010; Zhao et al., 2016; Sonti et al., 2019).

More research is needed to determine the specific ecological processes that cause this bottleneck, as well as the urban driver(s) responsible for these changes. By integrating experiments into management regimes, we may elucidate these drivers and identify effective management strategies. For example, we can test whether broadcast seedling is a viable method to overcome establishment limitation. Or, if seed predation is limiting, we can test whether seedlings must be planted to accelerate the establishment of trees in the understory. Rural forestry is based on over a century of applied research of silvicultural techniques (Ashton et al., 2018). Urban forest management will benefit from a similar research framework, adopting and modifying strategies in response to the constraints of urban ecosystems.

## **5. Conclusion**

What determines plant recruitment, and ultimately plant abundance and distribution, is a fundamental question and challenge of plant ecology. Through the lens of traditional plant ecology research, our findings point to potential shifts in urban forest function from seed production through early-establishment. Urban forests are significantly more recruitment limited than rural forests. Specifically, our data suggest that even intact native forest stands in cities demonstrate a fundamental difference in the ability for seedlings to establish when compared to rural forests. We have highlighted potential divergent successional trajectories for urban and rural

oak forests confronted by a declining oak canopy. Oak forests are the most dominant forest community along the eastern North America seaboard, an area also defined by dense urban development (Short et al., 2010; Auch et al., 2012). Understanding what limits recruitment here has important implications for the management and long-term sustainability of urban forested natural areas and the many ecosystem services they provide. Moving forward research can help determine the potential to manage these sites through traditional ecological forest management frameworks, such as silviculture (Ashton et al., 2018; Piana et al., in prep).

It is important to note that in our study system, native woody species were abundant through all forest strata. Urban forests are connoted to be degraded and heavily invaded. However, there is increasing evidence that much of urban forested natural area is dominated by native canopy and saplings. As ecological communities are better defined and delineated, not just as “urban forest,” but by community type we may develop an ecologically more nuanced perspective through which we may study and manage these sites. Our findings suggest that overcoming early-establishment barriers in urban forests may be an operational challenge. In addition to informing management in cities of existing ecological processes, the results may provide the basis for understanding future regionally based rural systems. Cities experience multiple anthropogenic disturbances, such as fragmentation, elevated temperatures, and atmospheric pollution, and are often the epicenter of exotic invasive species. Consequently, urban areas may be appropriate places to develop novel, effective forest management strategies that can be applied to the rural forests of the future as the latter are confronted with the threats of global change. We advocate for greater mechanistic urban research, conducted over multiple years, to determine the role of cities and specific urban drivers on functional change in forest ecosystems to allow this conceptual connection to be established.

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## Tables

**Table 2** Urban and rural recruitment limitation components observed over 36 months of study (plot average). The values of the components of recruitment limitation range from 0 (no limitation) to 1 (maximum limitation). For each category of limitation, we used data collected from across the 36-month duration of this study (April 2016 to April 2019) (See methods for details).

Species	Site Type	Source Limitation <sup>1</sup>	Dispersal Limitation <sup>2</sup>	Seed Limitation <sup>3</sup>	Seedling Limitation <sup>4</sup>	Establishment Limitations <sup>5</sup>
<i>Q. rubra</i>	Urban	0.14	0.16	0.16	0.92	0.99
	Rural	0.14	0.22	0.22	0.87	0.97
<i>Q. velutina</i>	Urban	0.40	0.48	0.49	1.00	1.00
	Rural	0.62	0.69	0.77	0.97	0.99
<i>Q. alba</i>	Urban	0.86	0.85	0.89	0.99	0.99
	Rural	0.65	0.55	0.77	0.98	0.99
<i>Carya sp.</i>	Urban	0.13	0.18	0.23	0.89	0.98
	Rural	0.08	0.17	0.21	0.79	0.94
<i>A. rubrum</i>	Urban	0.56	0.30	0.65	1.00	1.00
	Rural	0.30	0.20	0.37	0.38	0.87
<i>A. saccharum</i>	Urban	0.93	0.93	0.97	1.00	1.00
	Rural	0.11	0.00	0.10	0.67	0.93
<i>P. serotina</i>	Urban	0.04	0.11	0.13	0.67	0.96
	Rural	0.84	0.46	0.88	0.94	0.97
<i>Betula sp.</i>	Urban	0.54	0.59	0.59	0.99	0.99
	Rural	0.38	0.36	0.36	0.81	0.97
<i>S. albidum</i>	Urban	0.97	0.97	0.99	0.92	0.99
	Rural	0.99	0.88	0.99	0.88	0.96
<i>F. americana</i>	Urban	0.90	0.84	0.92	0.94	0.97
	Rural	0.65	0.13	0.68	0.86	0.93

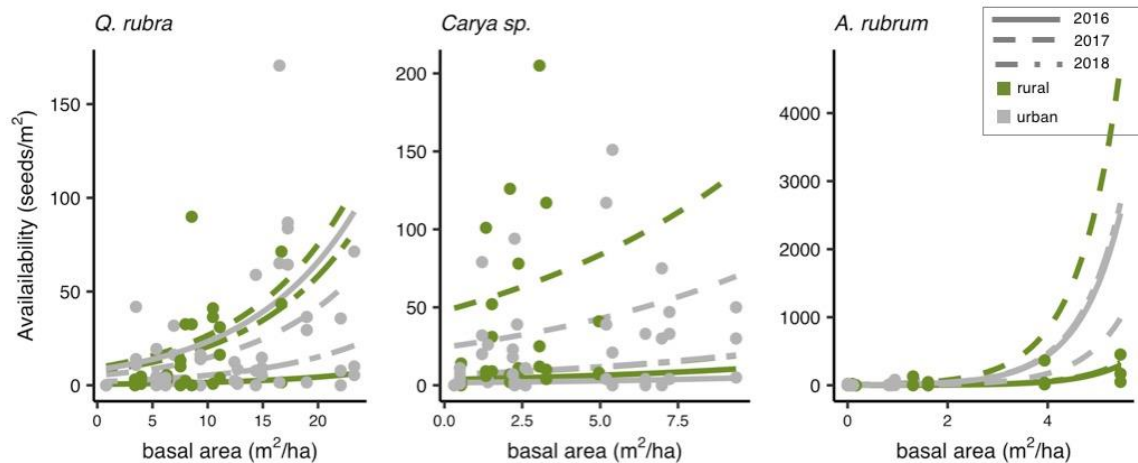
<sup>1</sup>Source limitation is equal to the proportion of traps at which no seeds arrive if the observed seed rain was Poisson (randomly) distributed.

<sup>2</sup>Dispersal limitation is equal to the proportion of traps reached by seeds compared to the proportion expected if dispersal had been Poisson distributed;

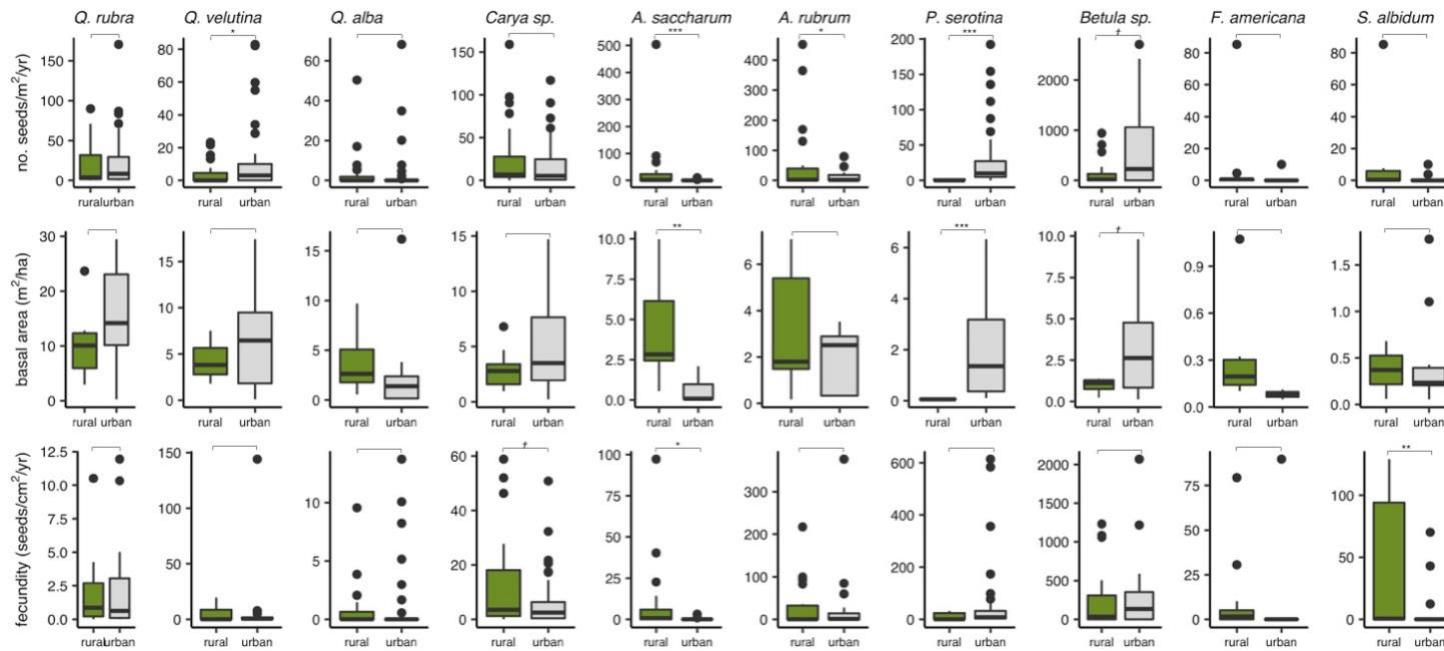
<sup>3</sup>Seed limitation is equal to the proportion of traps not receiving seeds

<sup>4</sup>Fundamental seedling limitation is equal to the proportion of quadrats where seedlings established as a function of all seedling quadrats.

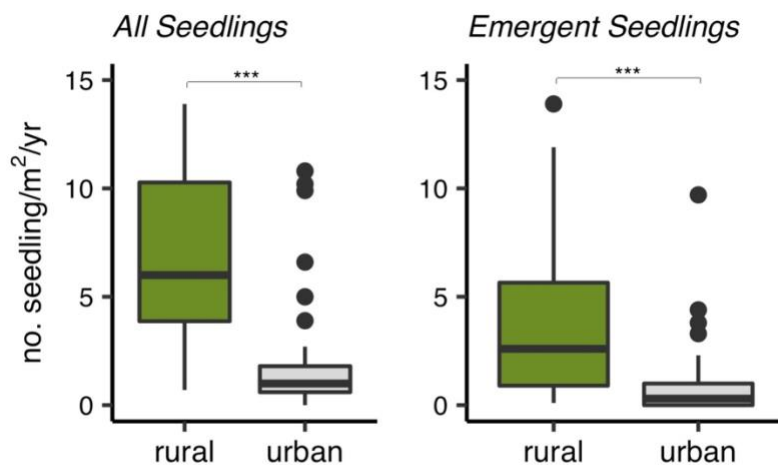
<sup>5</sup>Establishment limitation is equal to the proportion of sites where seeds arrived but seedlings did not recruit, accounting for differences in seed trap and seedling quadrat area.



**Figure 1** Urban (grey) and rural (green) forest seed availability (#seeds/m<sup>2</sup> captured in seed traps) by year (2016-2018) in relationship to adult tree abundance (stand average basal area). For each of the study species seed availability is positively related to adult basal area, but for many species it is also variable between years (See Supplemental Material for model fits). Interannual patterns of seed availability are species-specific and the relationship of these patterns may vary between urban and rural sites.

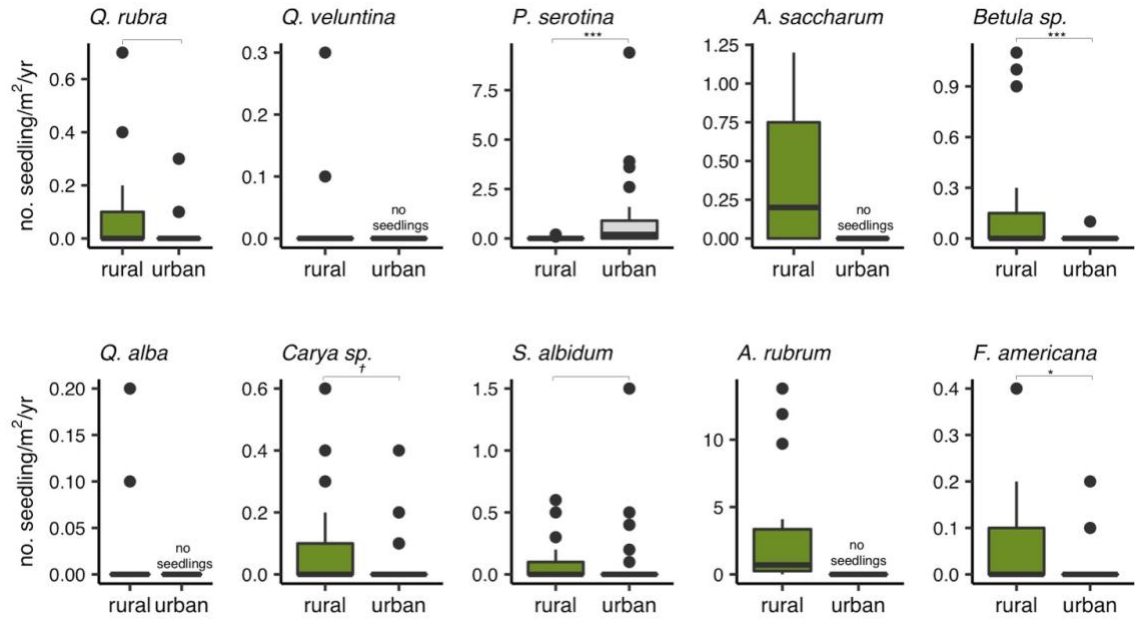


**Figure 2** Plot-scale comparison of urban (grey) and rural (green) seed density (# seeds/m<sup>2</sup>/y captured in seed traps), adult-conspecific abundance (stand average basal area), and fecundity (# seeds/basal area in cm<sup>2</sup>/year averaged at the stand level). Seed density and fecundity were calculated as plot average for each year (2016-2018). Analyses are limited to plots where adult-conspecific trees were present. Boxes indicate the interquartile range (25<sup>th</sup> to 75<sup>th</sup> percentile). Significance levels are reported as: †  $P < 0.10$ ; \*  $P < 0.05$ ; \*\*  $P < 0.01$ ; \*\*\*  $P < 0.001$ .

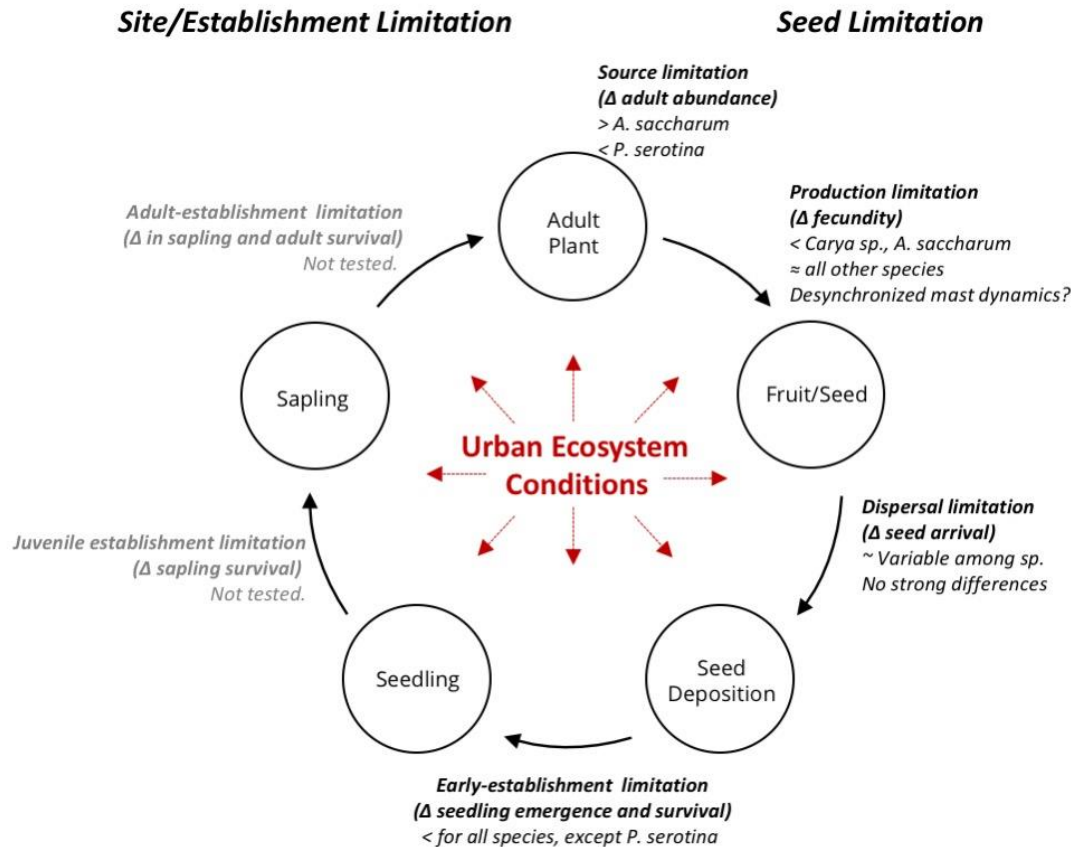


**Figure 3** Total seedling abundance (# seedlings/quadrat/year, including all seedling age classes) (left) and mean annual seedling establishment (# of emergent seedlings/quadrat/year) (right) for all species in urban and rural forests. Total seedling abundance and mean annual establishment is greater in rural forests. Significance levels are reported as: †  $P < 0.10$ ; \*  $P < 0.05$ ; \*\*  $P < 0.001$ ; \*\*\*  $P < 0.001$ .





**Figure 4** Species-specific mean annual seedling establishment (# of emergent seedlings/quadrat/year) for canopy dominant species in urban and rural forests. Significance levels are reported as: †  $P < 0.10$ ; \*  $P < 0.05$ ; \*\*  $P < 0.001$ ; \*\*\*  $P < 0.001$ .



**Figure 5** Conceptual diagram showing plant life history stages, the components of recruitment limitation, and summary of relative difference in urban forests compared to rural sites. Urban-rural differences are often species-specific and can vary within a species across the life history stages. Urban ecosystem conditions and stressors, both abiotic and biotic, can change plant recruitment dynamics and ecological processes associated with each stage of recruitment. Seed limitation includes all process from the source population of adult conspecifics through seed deposition. Establishment limitation, sometimes referred to as site limitation, includes all stages post-dispersal through germination until the plant is reproductive. Note, we did not calculate recruitment limitation in later life stages, including advance seedling and sapling.

**Supplemental Material**

**Table S1** Model selection for seed availability in relation to basal area and years.

**Table S2** Summary of best fit model for seed availability in relation to basal area and years.

**Table S3** Summary of model results from plot-scale comparison of urban and rural seed availability, adult-conspecific abundance (basal area), and fecundity (stand average).

**Table S4** Summary of best fit models for all species total seedling recruitment, seedling establishment, and species-specific seedling establishment (Figure 4).

**Figure S1** Canopy density in urban and rural forest plots.

**Figure S2** Comparison of urban and rural soil and PCA results.

**Table S1** Model selection for seed availability in relation to basal area and years (Figure 3).

Factors influencing seed limitation for canopy dominant species, as determined by AIC model selection of explanatory variables explaining seed availability. We tested how basal area (con-specific adult abundance), year, site type (urban or rural), and the interaction of year and basal area, as well as year and site type influenced seed availability. Most parsimonious models are bolded, with those less than two AIC units considered equally parsimonious.  $\Delta_i$  (AIC) =  $AIC_i - \min(AIC)$ ;  $w_i$  (AIC) = the rounded Akaike weights. Asterisks indicate significance levels (\* =  $P < 0.05$ ; \*\* =  $P < 0.01$ ; \*\*\* =  $P < 0.001$ ).

Species	Model	AIC <sub>i</sub>	$\Delta_i$ (AIC)	$W_i$ (AIC)
<i>Q. rubra</i>	Null (random effects only)	583.9281	20.0	<0.001
	Ba	574.3195	10.4	0.0055
	Year	585.6339	21.7	<0.001
	Ba + Year	576.5490	12.6	0.0018
	Ba x Year	578.5206	14.6	<0.001
	<b>(Ba x Year) + (SiteType x Year)</b>	<b>563.9144</b>	<b>0.0</b>	<b>0.9920</b>
<i>Q. velutina</i>	Null (random effects only)	400.3151	18.3	<0.001
	<b>Ba</b>	<b>382.0018</b>	<b>0.0</b>	<b>0.488</b>
	Year	400.1085	18.1	<0.001
	Ba + Year	383.1842	1.2	0.270
	Ba x Year	385.2978	3.3	0.094
	(Ba x Year) + (SiteType x Year)	384.3965	2.4	0.147
<i>Q. alba</i>	Null (random effects only)	214.9221	10.3	0.0036
	<b>Ba</b>	<b>204.5952</b>	<b>0.0</b>	<b>0.6235</b>
	Year	216.9792	12.4	0.0013
	Ba + Year	206.4483	1.9	0.2469
	Ba x Year	208.0557	3.5	0.1105
	(Ba x Year) + (SiteType x Year)	212.1468	7.6	0.0143
<i>Carya sp.</i>	Null (random effects only)	594.4404	43.3	<0.001
	Ba	594.8369	43.7	<0.001
	Year	551.2499	0.1	0.30
	<b>Ba + Year</b>	<b>551.1366</b>	<b>0.0</b>	<b>0.32</b>
	Ba x Year	551.7045	0.6	0.24
	(Ba x Year) + (SiteType x Year)	552.7056	1.6	0.14
<i>A. rubrum</i>	Null (random effects only)	466.7164	46.0	<0.001
	Ba	428.0310	7.3	0.0246
	Year	463.5342	42.8	<0.001
	Ba + Year	431.6813	11.0	0.0040
	Ba x Year	432.5455	11.9	0.0026
	<b>(Ba x Year) + (SiteType x Year)</b>	<b>420.6846</b>	<b>0.0</b>	<b>0.9689</b>
<i>A. saccharum</i>	Null (random effects only)	284.6352	45.7	<0.001
	Ba	264.6945	25.8	<0.001
	Year	271.8314	32.9	<0.001
	Ba + Year	252.7083	13.8	0.001
	Ba x Year	253.2162	14.3	<0.001
	<b>(Ba x Year) + (SiteType x Year)</b>	<b>238.9225</b>	<b>0.0</b>	<b>0.998</b>
<i>P. serotina</i>	Null (random effects only)	510.1246	54.8	<0.001
	Ba	509.3339	54.0	<0.001
	Year	505.6200	50.3	<0.001
	Ba + Year	503.0096	47.7	<0.001
	Ba x Year	505.2728	49.9	<0.001
	<b>(Ba x Year) + (SiteType x Year)</b>	<b>455.3402</b>	<b>0.0</b>	<b>1</b>
<i>Betula sp.</i>	Null (random effects only)	520.5692	17.7	<0.001
	Ba	512.2440	9.4	0.0073
	Year	522.0931	19.2	<0.001
	<b>Ba + Year</b>	<b>502.8838</b>	<b>0.0</b>	<b>0.7892</b>

	Ba x Year	505.9848	3.1	0.1674
	(Ba x Year) + (SiteType x Year)	509.0660	6.2	0.0359
	Null (random effects only)	166.1797	31.8	<0.001
	Ba	156.1427	21.7	<0.001
	Year	145.0519	10.7	0.0031
<i>F. Americana</i>	<b>Ba + Year</b>	<b>134.3950</b>	<b>0.0</b>	<b>0.6377</b>
	Ba x Year	138.2380	3.8	0.0933
	(Ba x Year) + (SiteType x Year)	136.1445	1.7	0.2659

**Table S2** Summary of best fit model results from Supplemental Table 1. Asterisks indicate significance levels ( $\dagger = P < 0.10$ ;  $* = P < 0.05$ ;  $** = P < 0.01$ ;  $*** = P < 0.001$ ).

Model	Fixed Effect	Estimate	Std. Error	z value
<i>Q. rubra</i>	Intercept	-0.749112	0.644036	-1.163
	Basal Area*	<b>0.121757</b>	<b>0.050991</b>	<b>2.388</b>
	Year.2017***	<b>3.237295</b>	<b>0.894415</b>	<b>3.619</b>
	Year.2018**	<b>2.630428</b>	<b>0.881063</b>	<b>2.986</b>
	Type.Urban***	2.627369	0.610813	4.301
	BasalArea:Year2017	-0.042296	0.068433	-0.618
	BasalArea:Year2018	-0.006607	0.069995	-0.094
	Year2017:Type.Urban***	<b>-3.200728</b>	<b>0.798220</b>	<b>-4.010</b>
	Year2018:Type.Urban***	<b>-4.012497</b>	<b>0.814944</b>	<b>-4.924</b>
<i>Q. velutina</i>	Intercept**	<b>0.77109</b>	<b>0.28117</b>	<b>2.742</b>
	Basal Area***	<b>0.19577</b>	<b>0.04598</b>	<b>4.257</b>
<i>Q. alba</i>	Intercept*	<b>-1.3076</b>	<b>0.5645</b>	<b>-2.316</b>
	Basal Area***	<b>0.6045</b>	<b>0.1604</b>	<b>3.769</b>
<i>Carya sp.</i>	Intercept**	<b>0.94276</b>	<b>0.28663</b>	<b>3.289</b>
	Basal Area	0.08597	0.06021	1.428
	Year.2017***	<b>2.64210</b>	<b>0.32344</b>	<b>8.169</b>
	Year.2018**	<b>1.05984</b>	<b>0.33257</b>	<b>3.187</b>
<i>A. rubrum</i>	Intercept	-0.45173	0.67546	-0.669
	Basal Area**	<b>0.82235</b>	<b>0.26191</b>	<b>3.140</b>
	Year.2017 $\dagger$	<b>1.73762</b>	<b>0.89195</b>	<b>1.948</b>
	Year.2018	-0.20482	0.96018	-0.213
	Type.Urban**	<b>1.94622</b>	<b>0.72920</b>	<b>2.669</b>
	BasalArea:Year2017*	<b>1.22699</b>	<b>0.59533</b>	<b>2.061</b>
	BasalArea:Year2018	0.35952	0.40499	0.888
	Year2017:Type.Urban***	<b>-3.74147</b>	<b>1.00210</b>	<b>-3.734</b>
	Year2018:Type.Urban	0.08389	1.02659	0.082
<i>A. saccharum</i>	Intercept	1.0267	1.1448	0.897
	Basal Area*	<b>0.7968</b>	<b>0.3096</b>	<b>2.574</b>
	Year.2017	0.3597	1.4560	0.247
	Year.2018	-2.4227	2.3628	-1.025
	Type.Urban*	<b>-4.0506</b>	<b>1.0485</b>	<b>-3.863</b>
	BasalArea:Year2017	-0.1920	0.4089	-0.469
	BasalArea:Year2018	-0.8904	0.5765	-1.545
	Year2017:Type.Urban	1.2699	1.3328	0.953
	Year2018:Type.Urban	-15.5790	8476.1777	-0.002
<i>P. serotina</i>	Intercept	-0.84571	0.59171	-1.429
	Basal Area $\dagger$	<b>0.35377</b>	<b>0.19986</b>	<b>1.770</b>
	Year.2017	-1.60487	1.22485	-1.310
	Year.2018	0.79976	0.76889	1.040
	Type.Urban***	<b>2.82698</b>	<b>0.73624</b>	<b>3.840</b>
	BasalArea:Year2017	-0.44575	0.29359	-1.518
	BasalArea:Year2018*	<b>-0.61389</b>	<b>0.28927</b>	<b>-2.122</b>
	Year2017:Type.Urban**	<b>3.76747</b>	<b>1.37467</b>	<b>2.741</b>
	Year2018:Type.Urban	0.09591	0.98548	0.097
<i>Betula sp.</i>	Intercept	1.3860	0.9904	1.399
	Basal Area**	<b>1.5599</b>	<b>0.5656</b>	<b>2.758</b>
	Year.2017**	<b>2.4820</b>	<b>0.9563</b>	<b>2.595</b>
	Year.2018	-1.4539	0.9267	-1.569
<i>F. Americana</i>	Intercept	-22.987	9806.164	- 0.002
	Basal Area**	<b>3.616</b>	<b>1.306</b>	<b>2.770</b>

	Year.2017	23.258	9806.164	0.002
	Year.2018	20.968	9806.164	0.002

**Table S3** Summary of Figure 2 model results from plot-scale comparison of urban and rural seed availability, adult-conspecific abundance (basal area), and fecundity (stand average). Seed availability and fecundity were calculated as plot average for each year (2016-2018). Analyses are limited to plots where adult-conspecific trees were present. Asterisks indicate significance levels († =  $P < 0.10$ ; \* =  $P < 0.05$ ; \*\* =  $P < 0.01$ ; \*\*\* =  $P < 0.001$ ).

Species	Model	Fixed Effect	Estimate	Std. Error	z value
<i>Q. rubra</i>	Seed Density	Intercept***	<b>2.8177</b>	<b>0.2963</b>	<b>9.508</b>
		Type.Urban	0.2519	0.3745	0.673
	Basal Area	Intercept***	<b>10.193</b>	<b>2.682</b>	<b>3.801</b>
		Type.Urban	4.689	3.438	1.364
	Fecundity	Intercept***	<b>1.70975</b>	<b>0.46908</b>	<b>3.645</b>
		Type.Urban	0.08398	0.59334	0.142
<i>Q. velutina</i>	Seed Density	Intercept***	<b>1.5130</b>	<b>0.4250</b>	<b>3.560</b>
		Type.Urban*	<b>1.0524</b>	<b>0.5319</b>	<b>1.978</b>
	Basal Area	Intercept	4.366	2.952	1.479
		Type.Urban	2.448	3.301	0.742
	Fecundity	Intercept	4.159	4.167	0.998
		Type.Urban	1.023	5.243	0.195
<i>Q. alba</i>	Seed Density	Intercept †	<b>1.27783</b>	<b>0.67306</b>	<b>1.899</b>
		Type.Urban	0.07139	0.89014	0.080
	Basal Area	Intercept**	<b>3.6579</b>	<b>1.3162</b>	<b>2.779</b>
		Type.Urban	-0.7155	1.8615	-0.384
	Fecundity	Intercept	0.8216	0.5126	1.603
		Type.Urban	0.3560	0.6781	0.525
<i>Carya sp.</i>	Seed Density	Intercept***	3.2430	0.2859	11.343
		Type.Urban	-0.3660	0.3620	-1.011
	Basal Area	Intercept*	<b>2.876</b>	<b>1.149</b>	<b>2.504</b>
		Type.Urban	1.977	1.453	1.360
	Fecundity	Intercept***	<b>11.949</b>	<b>2.460</b>	<b>4.858</b>
		Type.Urban †	<b>-5.746</b>	<b>3.111</b>	<b>-1.847</b>
<i>A. rubrum</i>	Seed Density	Intercept***	<b>3.9909</b>	<b>0.4344</b>	<b>9.187</b>
		Type.Urban*	<b>-1.3086</b>	<b>0.6373</b>	<b>-2.053</b>
	Basal Area	Intercept***	<b>3.1880</b>	<b>0.9275</b>	<b>3.437</b>
		Type.Urban	-1.2777	1.3117	-0.974
	Fecundity	Intercept*	<b>27.166</b>	<b>13.503</b>	<b>2.012</b>
		Type.Urban	1.178	19.766	0.060
<i>A. saccharum</i>	Seed Density	Intercept***	<b>3.4848</b>	<b>0.4892</b>	<b>7.123</b>
		Type.Urban***	<b>-4.0271</b>	<b>0.7505</b>	<b>-5.366</b>
	Basal Area	Intercept***	<b>4.0371</b>	<b>0.7515</b>	<b>5.372</b>
		Type.Urban**	<b>-3.4314</b>	<b>1.1882</b>	<b>-2.888</b>
	Fecundity	Intercept**	<b>8.367</b>	<b>2.735</b>	<b>3.059</b>
		Type.Urban*	<b>-8.200</b>	<b>3.987</b>	<b>-2.056</b>
<i>P. serotina</i>	Seed Density	Intercept	-0.2546	0.6773	-0.376
		Type.Urban***	<b>3.6231</b>	<b>0.7079</b>	<b>5.118</b>
	Basal Area	Intercept***	<b>3.1880</b>	<b>0.9275</b>	<b>3.437</b>
		Type.Urban	<b>-1.2777</b>	<b>1.3117</b>	<b>-0.974</b>
	Fecundity	Intercept	10.65	51.88	0.205

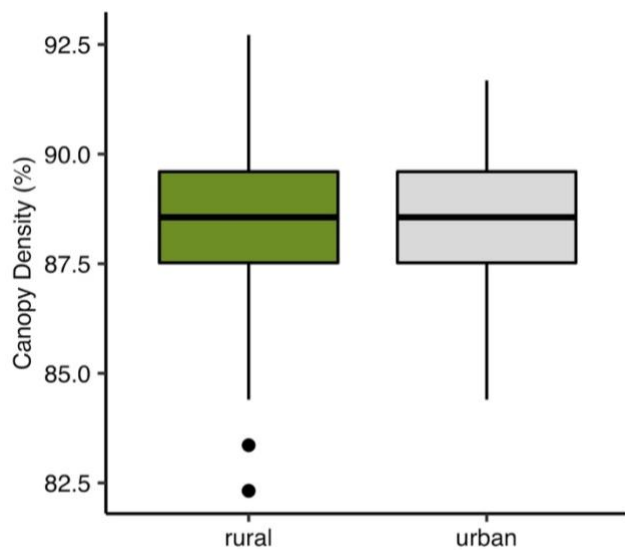


		Type.Urban	45.38	55.46	0.818
<i>Betula sp.</i>	Seed Density	<b>Intercept***</b>	<b>5.0651</b>	<b>0.6195</b>	<b>8.176</b>
		<b>Type.Urban <math>\hat{\tau}</math></b>	<b>1.3981</b>	<b>0.8195</b>	<b>1.706</b>
	Basal Area	Intercept	0.9553	1.1139	0.858
		<b>Type.Urban <math>\hat{\tau}</math></b>	<b>2.5319</b>	<b>1.5082</b>	<b>1.679</b>
	Fecundity	<b>Intercept*</b>	<b>254.6</b>	<b>104.2</b>	<b>2.445</b>
		Type.Urban	26.4	137.8	0.192
<i>S. albidum</i>	Seed Density	Intercept	NA	NA	NA
		Type.Urban	NA	NA	NA
	Basal Area	Intercept	0.37086	0.33544	1.106
		Type.Urban	0.08183	0.36466	0.224
	Fecundity	<b>Intercept***</b>	<b>42.56</b>	<b>10.92</b>	<b>3.897</b>
		<b>Type.Urban**</b>	<b>-38.76</b>	<b>11.87</b>	<b>-3.265</b>
<i>F. Americana</i>	Seed Density	<b>Intercept**</b>	<b>1.6833</b>	<b>0.6245</b>	<b>2.695</b>
		Type.Urban	-1.1648	1.2700	-0.917
	Basal Area	Intercept	0.3377	0.1193	2.832
		Type.Urban	-0.2569	0.2385	-1.077
	Fecundity	Intercept	8.083	5.490	1.472
		Type.Urban	6.884	10.980	0.627

**Table S4** Summary of best fit models for all species total seedling recruitment (Figure 3a) and seedling establishment (Figure 3b), as well as species-specific seedling establishment (Figure 4).

Bold text indicates significant covariates. Asterisks indicate significance levels († =  $P < 0.10$ ; \* =  $P < 0.05$ ; \*\* =  $P < 0.01$ ; \*\*\* =  $P < 0.001$ ).

Model	Fixed Effect	Estimate	Std. Error	z value
<i>All Species – Total Seedling Recruitment</i>	<b>Intercept***</b>	<b>4.2642</b>	<b>0.1717</b>	<b>24.840</b>
	<b>Type.Urban***</b>	<b>-1.3024</b>	<b>0.2191</b>	<b>-5.945</b>
<i>All Species – Seedling Establishment</i>	<b>Intercept***</b>	3.6099	0.2576	14.014
	<b>Type.Urban***</b>	-1.4102	0.3287	-4.291
<i>Q. rubra</i>	Intercept	-0.257617	0.541096	-0.476
	Type.Urban	-0.777202	0.535346	-1.452
	Basal.Area	-0.005174	0.048937	-0.106
<i>Q. velutina</i>	Intercept	-3.255	1.871	-1.740
	Type.Urban	-36.377	29926.177	0.9990
	Basal.Area	1.088	1.434	0.4479
<i>Q. alba</i>	Intercept	-0.8644	1.5510	-0.557
	Type.Urban	-23.4817	37534.2006	-0.557
	Basal.Area	-0.5352	0.5600	-0.557
<i>Carya sp.</i>	Intercept	-0.10426	0.47531	-0.219
	<b>Type.Urban †</b>	<b>-1.10810</b>	<b>0.56952</b>	<b>-1.946</b>
	Basal.Area	0.04506	0.11676	0.386
<i>A. rubrum</i>	<b>Intercept***</b>	<b>1.5514</b>	<b>0.2962</b>	<b>5.238</b>
	Type.Urban	-23.8583	9179.6579	-0.003
	<b>Basal.Area***</b>	<b>0.7103</b>	<b>0.1421</b>	<b>5.000</b>
<i>A. saccharum</i>	Intercept	-3.744e-02	4.908e-01	-0.076
	Type.Urban	-2.304e+01	1.437e+04	-0.002
	<b>Basal.Area**</b>	<b>2.833e-01</b>	<b>9.864e-02</b>	<b>2.872</b>
<i>P. serotina</i>	<b>Intercept**</b>	<b>-1.5098</b>	<b>0.5277</b>	<b>-2.861</b>
	<b>Type.Urban***</b>	<b>3.1519</b>	<b>0.6473</b>	<b>4.869</b>
	Basal.Area	0.2363	0.1740	1.359
<i>S. albidum</i>	Intercept	-0.03255	0.62431	-0.052
	Type.Urban	-0.03255	0.75654	0.255
	Basal.Area	-2.12568	1.42095	-1.496
<i>Betula sp.</i>	Intercept	0.48061	0.44908	1.070
	<b>Type.Urban***</b>	<b>-4.24071</b>	<b>1.17848</b>	<b>-3.598</b>
	Basal.Area	-0.03464	0.45203	-0.077
<i>F. Americana</i>	<b>Intercept***</b>	<b>-1.0123</b>	<b>0.3921</b>	<b>-2.582</b>
	<b>Type.Urban*</b>	<b>-1.7109</b>	<b>0.7015</b>	<b>-2.439</b>
	<b>Basal.Area †</b>	<b>1.3632</b>	<b>0.7282</b>	<b>1.872</b>

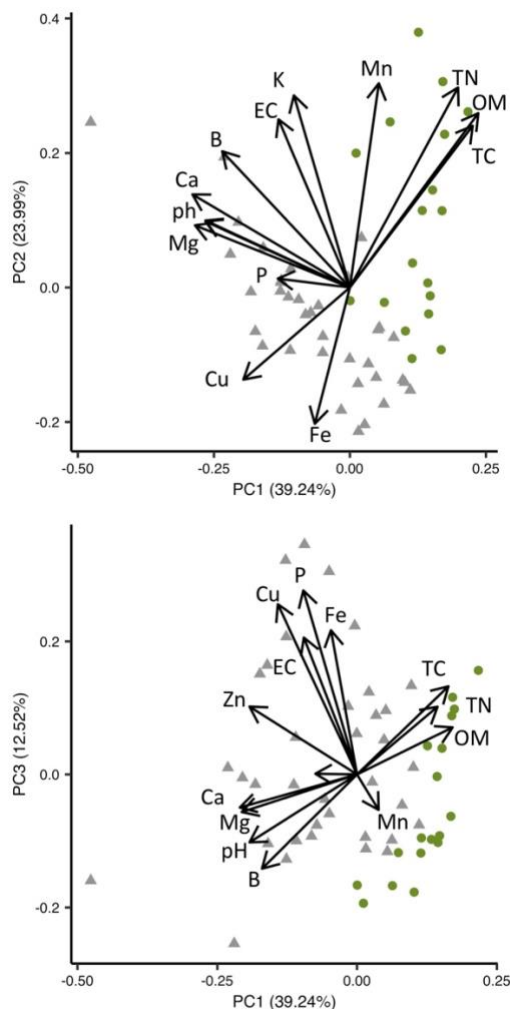


**Figure S1** Canopy density in urban (grey) and rural (green) forests was controlled for during plot selection to minimize differences in natural regeneration associated with light availability.

Canopy density was not significantly different; Mann-Whitney U test (Mann and Whitney 1947).

Boxes indicate the interquartile range (25th and 75th percentile) and the line shows the median.

Error bars show  $\pm 1.5$  times the interquartile range to the 25th and 75th percentiles. Outlier points are beyond 1.5 times the interquartile range.



**Figure S2** Characteristics of soils from urban (grey triangles) and rural (green circles) oak-hickory forests in the NYC metro area. From the principal-component analysis (PCA) we identified strong clustering by site type (urban, rural). The first axis (PC1) explained 39.24% of the total variance in soil data and was strongly correlated with pH, as well as Ca and Mg. Urban soils had significantly higher pH. The second axis (PC2) explained an additional 23.99% of the variance and was most strongly correlated with Mn and Total Nitrogen (TN). Axis 3 (PC3) explained an additional 12.52% of the variance and was most strongly correlated with P, Cu, and Fe.

**Chapter 4: Early-establishment limitation in urban and rural forests: seed predation and herbivory limit tree seedling recruitment in urban forested natural areas.**

## ABSTRACT

1. Urban forested natural areas are important, and common, habitats in cities that support local and regional biodiversity and provide a suite of ecosystem services for residents. Research suggests that early seedling recruitment is limited for tree species in urban forests. As a result, the management of these sites has depended upon direct planting. A question for ecologists and managers alike is what processes in seedling establishment constrain the natural regeneration of native canopy trees.
2. We conducted a seed addition experiment in urban and rural oak-hickory forests located in the New York City metropolitan area. Small mammal exclosures were used to compare the importance of seed predation and seedling herbivory on seedling establishment, seedling survival, and relative establishment limitation for four native (*Quercus rubra*, *Carya tomentosa*, *Acer rubrum*, *Prunus serotina*) and two non-native (*A. platanoides*, *Ailanthus altissima*) tree species.
3. Urban and rural forests are both significantly establishment limited. Seedling establishment and survival is generally lower in urban forests. Only *P. serotina* showed no difference in seedling emergence between urban and rural forest. Seedling survival was more variable and species-specific.
4. Seed predation and herbivory limit both urban and rural forests, but the pressure is greater in urban than rural forests. Seed predation had a greater negative effect on seedling establishment than other site factors, including percent understory vegetation cover.
5. The establishment of oak and hickory species was limited in both urban and rural forests. Independent of forest type, both maple species were the most successful species to recruit seedlings. The transition from oak to maple species has been observed in red oak forests throughout the region.

6. *Synthesis and applications.* Alternatives to direct planting, including natural regeneration and broadcast seeding, represent a more cost-effective and sustainable management approach in urban forested natural areas. Traditional approaches for managing natural regeneration need to be modified in urban forests to account for greater barriers to seedling establishment. Our research shows that small seeded species may be managed through natural regeneration and seed augmentation strategies. Larger-seeded species may require less passive restoration approaches, including direct planting, to assure establishment.

**Keywords** establishment limitation, forest ecology, herbivory, recruitment dynamics, seed predation, seed limitation, urban ecosystems, urban silviculture

## Introduction

As urban ecology has matured, there has been a call for more process-based research (Shochat et al., 2006; McDonnell & Hahs, 2013). Understanding how urban conditions influence ecological function has important implications for application and urban conservation efforts. This will identify ecological mechanisms that limit and support ecosystem function and allow for urban adapted management strategies that promote the long-term sustainability of urban greenspaces and the many ecosystem services they generate.

With respect to urban plant ecology, multiple frameworks have been developed to better understand species abundance and distribution, by placing an emphasis on functional traits and early recruitment processes, from seed production through seedling establishment (e.g. Williams et al., 2009; Kowarik et al., 2017; Gelmi-Candusso & Hämäläinen, 2019; Piana et al., 2019).

Plant recruitment dynamics in urban ecosystems can be influenced by multiple co-occurring and often exacerbated factors common to most cities. Urban-associated habitat fragmentation and land transformation, altered climate and moisture regimes, biotic invasion, pollution (e.g. elevated atmospheric carbon and nitrogen), and human activity, both direct and indirect, are observed to have species-specific effects that may limit or facilitate recruitment success (as reviewed in Piana et al., 2019). A core question to all these studies is whether urban ecosystems are functionally different, and if so, what that means for management and restoration practice.

This study focuses on plant recruitment dynamics in urban forested natural areas. Urban forested natural areas are dominated by naturally regenerating plant populations and, as a result, are more similar to rural forest ecosystems than other components of the urban tree canopy, such as street trees, landscaped parks, and backyards. These greenspaces provide critical ecosystem services for residents (e.g. Hasse et al., 2014) and habitat for local, and even regional, biodiversity (e.g. Ives et al., 2016; Lepzyck et al., 2017). For many cities, urban forested natural areas are also quite common. Natural areas make up approximately 85% of municipal parkland in



the United States (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). As such, these forests provide a disproportionate amount of the ecosystem services generated for the city and, consequently, are of particular interest to environmental managers.

However, there are many ecological challenges to the long-term sustainability of forested natural areas. There is strong evidence that natural regeneration, especially early seedling establishment, is limited in urban forested natural areas. Multiple studies comparing urban and rural forests, as well as urban-rural gradient studies, have identified lower woody plant seedling abundance and native species richness in urban forests (Airolo, 1984; Guntenspergen et al., 1997; Zipperer et al., 2002; Burton et al., 2005; Cadenasso et al., 2007; Pennington et al., 2010; Trammell & Carreiro, 2011; Overdyck & Clarkson, 2012; Wallace et al., 2017). A recent multi-year study of seed rain and natural regeneration in temperate deciduous forests suggest that urban forest sites are more seedling limited than rural equivalents, and that establishment, not seed limitation factors (e.g. seed production, dispersal), strongly limit early recruitment (Chapter 3). Increased establishment limitation in urban forested natural areas may result from multiple factors, both biotic (e.g. invasive plants, pests, herbivores) and abiotic (atmospheric pollution, altered disturbance regimes). While speculated as key drivers in urban forests, less studied are post-dispersal seed predation and early herbivory, ecological processes known to exert significant influence on early recruitment dynamics in rural forest systems (Louda, 1989; Hurtt and Pacala, 1995; Clark et al., 1999; Hulme, 1996; Hulme, 1998; Levine & Murrell, 2003; Clark, Poulsen, & Levey, 2012; Larios et al., 2017).

Early seedling establishment may be significantly limited in urban forested natural areas (Chapter 3), yet there is also evidence that recruitment to advance seedling and sapling stages may not be different in urban and rural sites (Chapter 2). As comprehensive assessments of urban natural areas become more common, we are gaining a more nuanced perspective on the range of

habitat quality and conditions that exist in our cities. Urban forests are not all degraded. In New York City for example, urban forested natural areas are characterized by native species in the canopy and midstory (Pregitzer et al., 2019). We limit ourselves as ecologists and practitioners when using the term “urban” to broadly describe habitats within cities and to inherently mean degraded forest condition. In such sites, are traditional ecological forest management strategies for natural regeneration appropriate? Current urban forest management practice emphasizes resource intensive approaches, often relying on direct planting of large tree stock (DiCicco, 2014; Simmons et al., 2016; Pregitzer et al., 2018).

We ask the following questions: (1) What is the difference in relative establishment limitation between urban and rural forests? (2) What is the contribution of seed predation and seedling herbivory to establishment limitation and how does the magnitude of these site filters differ between urban and rural forest sites? (3) What environmental factors drive seedling establishment in urban forests? Are these the same for all canopy tree species dominants? We addressed these questions through a seed addition experiment that included small mammal exclosures. Seedling establishment and survival was recorded for native and non-native species over a two-year period. We hypothesized that (1) overall establishment limitation would be greater in urban forest sites, (2) that seed predation would increase as a limiting filter in urban forests, and (3) there would be no difference in recruitment limitation for exotic species among forest site types. Identifying the potential to leverage natural regeneration in urban sites may provide a more cost-effective and sustainable management framework for these forests.

## **Methods**

### ***Experimental Design***

The experiment was conducted in the same sites and plots as those identified in Chapter 3 (See Chapter 3 for site description and selection methods). We tested the relative importance of establishment limitation and the impact of seed predation and herbivory on seedling recruitment through a seed addition and small-mammal exclosure experiment. Seed addition experiments provide a means for quantifying recruitment limitation (Nathan & Muller-Landau, 2000; Clark et al., 2007). Our study species included four native tree species that are canopy dominants and subdominants, including *Quercus rubra*, *Carya tomentosa*, *Acer rubrum*, *Prunus serotina*, as well as two common exotic tree species, *Acer platanoides* and *Ailanthus altissima*. These species were selected because they are present in all forest types and represent different dispersal syndromes and seed sizes.

Two seed stations (3.5 x 2.5 m) were installed in each forest plot (n=24) to quantify recruitment limitation and seed predation and seedling herbivory pressure. Each seed station was divided into sixteen 0.28 m radius (0.25 m<sup>2</sup>) seed addition sub-plots, with 0.5 m between each seed addition plot to provide access for data collection. Within each seed station, exclosures were installed on 8 sub-plots. Predation cages were constructed with 12.5 mm hardware cloth, installed a minimum of 5 cm below soil surface, and secured with garden stakes (Fig. 1).

Within each experimental seed addition sub-plot, conspecific seed from one of the six study species were randomly added to a caged or uncaged plot. To mimic natural dispersal conditions, *A. rubrum*, *A. platanoides*, *P. serotina*, and *A. altissima* were placed at the surface of each plot. *Q. rubra* and *C. tomentosa* were depressed 2.5-5.0 cm in the soil, to mimic secondary dispersal patterns. Haas and Hecke (2005) found that buried acorns were more likely to germinate than unburied seeds. By following these methods, this study will determine the establishment limitation of a secondary-dispersed oak or hickory seed. Fifty seeds were added to each of the *Q. rubra* and *C. tomentosa* plots, and 150 seeds were added to all other plots. Seed density was related to ambient seed rain, previously established across all plots in a related study (Chapter 2;

Chapter 3). We recognize methodological critiques of previous seed addition and recruitment limitation studies (Clark et al., 2007), however, the constraints of this study did not allow us to augment seed at multiple densities. Instead, we selected seed addition quantities related to the maximum seed density found in a single seed trap, with seed collected in 2016. Control plots did not receive seed addition and were monitored for natural recruitment for each of the study species.

The experiment was conducted from September 2017 to June 2019. Seed addition occurred in September 2017 for all but *A. rubrum*, which was added in May 2017 to mimic natural dispersal patterns. Germination was monitored every 72 hours from April to mid-June. Germination was monitored in spring 2017 for *A. rubrum* and control plots only, and in 2018 and 2019 for all plots. All emerged seedlings were mapped and tagged to record survival over time. Seedling survival was sampled after one growing season in late-August 2018 and again in June 2019. Debris, primarily leaf litter was removed from cages at a minimum bi-weekly. Each November leaf litter from the surrounding area was placed within each caged plot so that differences in leaf litter depth were minimized.

### ***Environmental and Microsite Characteristics***

Multiple ecological factors were measured that may contribute to differences in seedling recruitment. In each seedling quadrat we recorded cover of vegetation, coarse woody material, fine woody material, leaf litter, bare soil, trash and human debris, rock, and impervious surface (constructed or other). Leaf litter depth was measured in each seedling sub-plot in late July and early August 2018 and all measurements were taken more than one day after a rain event to avoid possible compaction effects. Five estimates of leaf litter depth were recorded for each quadrat by inserting a wooden probe into the leaf litter and marking the top of the litter layer along the

dowel. Litter was then removed until the interface of the litter layer with the humus layer was found. The difference between these two points was measured to the nearest 0.5 cm. We also measured soil compaction using a handheld penetrometer (Soil Pocket Penetrometer BCL-315, Certified MTP, Palm Bay, FL), taking the average of four readings in each quadrat. A spherical densiometer (Forestry Suppliers Concave Spherical Densiometer Model-C, Forestry Suppliers Inc., Jackson, MS) was used to estimate percent canopy cover. At each quadrat we took the average of four readings, one in each cardinal direction, taken at a height of 0.5 m. We also ran a basic soil analysis for each sub-plot. Soil samples were collected in December 2016 at five randomly selected locations within each sub-plot, using a 2.5 cm diameter soil probe and sampling to 10 cm depth. Samples were processed by the Rutgers University Soil Testing Laboratory (<https://njaes.rutgers.edu/soil-testing-lab/>) and analyzed for nutrient availability (P, K, Ca, Mg, Fe, Mn, Zn, Cu, B, S), lead (Pb), and aluminum (Al), cation exchange capacity, soil organic matter, pH, and total Nitrogen. All samples were processed by the Rutgers University Soil Testing Laboratory. We used principal component analysis (PCA) to compare differences between urban and rural sites, as well as among urban plots only (Supplemental S3). We used axes scores for the urban plots only to reduce the number of variables included as covariates in data analysis.

### ***Data Analysis***

We sowed 67200 seeds, 3647 of which successfully germinated (5.4% of all seeds). Of these germinants, 1422 survived for 18 months of the study (2.1% of all seeds). To test the relative importance of seed predation and herbivory for early recruitment limitation in urban and rural forests, we fitted and evaluated generalized linear mixed models (GLMM) to: (1) the proportion of seedlings that emerged as a function of the number of seeds added to a given quadrat; (2) the proportion of seedlings that survived to 18 months as a function of the maximum number of

emerged seedlings in each quadrat; and (3) relative establishment limitation, defined here as the proportion of seedlings that survived to 18 months as a function of the number of seeds added to each quadrat. The latter is the equivalent of relative establishment limitation as described by Clark et al. (2007). To account for natural regeneration, for each model, we subtracted the average density of seedling recruits in control plots from the average density of seedling recruits in experimental plots.

Models were fit for all-species pooled together, as well as for each individual species. Site type (urban or rural) and the exclosure treatment (caged or uncaged) were included as explanatory variables in all models. Species and plot were included as random effects in the all species model. Plot was included as a random effect for all species-specific models. The random effects of each model quantify variation in seed predation and seedling mortality among sites and species. We also ran a separate species-specific model for the urban plots only, to test how seedling establishment is limited by the environmental and microsite site factors. Species-specific models were fit with the proportion of seed germinated as the response variable and exclosure treatments, percent canopy cover, percent vegetation cover, leaf litter depth, and soil PCA axis 1, axis 2, and axis 3 included as covariates. Plot was included as a random effect in these models. All models were all fit with a binomial error distribution and a logit-link, using Laplace approximation (glmmTMB package) for maximum likelihood estimation of the parameters and testing the statistical significance of fixed effects with Wald Z statistics (Brooks et al., 2017). All statistical analyses were performed in R 3.6.0 (R Development Core Team, 2019).

## **Results**

### ***Emerged seedlings***

In the all species model, site type (urban, rural), treatment (caged, uncaged), and their interaction were all significant factors in determining the proportion of seeds that successfully germinated (Fig. 2 & Table S2). The proportion of emerged seedlings was greater in urban compared to rural forests, and the exclosures had a positive effect on the proportion of seed that germinated in both urban and rural forests (urban uncaged=1.6%; urban caged=5.1%; rural uncaged=7.1%; rural caged=10.7%). The significant interaction between site type and treatment indicates that the effect of exclosures on germination success was greater in urban forests, indicating that among all species, seed predation and early herbivory pressure is greater in urban compared to rural forests.

Species-specific responses were similar to the all species model. For all species, except *P. serotina* and *C. tomentosa*, we found significant interactions between site type and treatment. For these species, caging had a stronger positive effect on germination in urban forests, meaning urban seed predation and early herbivory is more limiting in urban forests (Fig. 3 & Table S2). The two maple species, *Acer platanoides* (urban uncaged=3.0%; urban caged=10.0%; rural uncaged=18.1%; rural caged=25.8%) and *A. rubrum* (urban uncaged=2.4%; urban caged=8.5%; rural uncaged=8.5%; rural caged=14.2%), had the highest proportion of seeds that germinated in both urban and rural forests. Seed removal was significantly limiting for *C. tomentosa* in both urban and rural forests. We do not report a significant interaction for *C. tomentosa*, however, this is the result of a Type II error, as no seeds successfully germinated outside of exclosures in urban forests (urban uncaged=0.0%; urban caged=0.1%; rural uncaged=0.1%; rural caged=4.5%). For *P. serotina*, caging was the only factor that significantly determined seed germination. The proportion of *P. serotina* seed that germinated was not significantly different in caged plots in urban (3.6%) and rural forests (2.9%), nor was it different in uncaged urban (1.3%) and rural (1.4%) forests.

### ***Seedling survival***

In the all species model, treatment (cage, no-cage) and the interaction between site type and treatment were significant factors in determining seedling survival (Fig. 2 & Table S3). There was no significant difference in the proportion of seedling survival in caged plots in urban (42.1.2% survival) and rural (47.2%) forests. There was, however, a significant difference in the proportion of seedlings that survived in uncaged plots in rural (29.6%) and urban (20.7%) forests. The significant interaction between site type and treatment supports the conclusion that the effect of exclosures on the proportion of seedlings that survived was greater in urban forests, meaning among all species early herbivory pressure is greater in urban compared to rural forests.

Species-specific models of seedling survival were more variable and were constrained by the total number of seedlings in our experiment. The interaction between site type and treatment was significant for *P. serotina* (urban uncaged=31.6%; urban caged=73.0%; rural uncaged=65.8%; rural caged=74.0%), where the effect of small mammal exclosure on seedling survival was greater for urban forest sites (Fig. 4 & Table S3). For *Q. rubra*, caging had a positive effect on seedling survival and was the only significant factor (urban uncaged=50.0%; urban caged=48.0%; rural uncaged=12.5%; rural caged=28.9%). Seedling survival for *A. rubrum* was greater in rural sites and positively correlated with exclosure (urban uncaged=16.5%; urban caged=31.2%; rural uncaged=35.8%; rural caged=53.9%). Site type and caging did not affect seedling survival for the non-native *A. altissima* and the model for *C. tomentosa* failed to converge due to limited number of individuals, but there was greater seedling survival in caged quadrats.

### ***Establishment limitation***

Establishment limitation, the proportion of seedlings that survived to 18 months as a function of the number of seeds added to each quadrat, was high in both urban and rural forests. In the all



species model, site type, treatment, and their interaction were significant factors in determining establishment limitation (the proportion of seedlings that survived the length of the study, as a function of total seeds added) (Fig. 2 & Table S4). Establishment limitation was greater in urban compared to rural forests and the exclosures decreased establishment limitation in both urban and rural forests (urban uncaged=99.7%; urban caged=98.8%; rural uncaged=97.8%; rural caged=94.5%). The significant interaction between site type and treatment shows that the effect of exclosures on the establishment limitation was greater in urban forests, meaning among all species, seed predation and herbivory pressure were greater in urban compared to rural forests.

Establishment limitation was greater than 90% for all species. Site type, treatment, and their interaction were all significant in species-specific models for *P. serotina* (urban uncaged=99.6%; urban caged=97.4%; rural uncaged=99.1%; rural caged=97.9%), *A. rubrum* (urban uncaged=99.6%; urban caged=97.4%; rural uncaged=97.0%; rural caged=92.3%), and *A. platanoides* (urban uncaged=99.4%; urban caged=95.9%; rural uncaged=94.9%; rural caged=88.7%) (Fig. 5 & Table S4). For both *Q. rubra* (urban uncaged=99.9%; urban caged=99.2%; rural uncaged=99.0%; rural caged=96.9%) and *C. tomentosa* (urban uncaged=100.0%; urban caged=99.4%; rural uncaged=99.8%; rural caged=96.7%), treatment and site type were significant factors. Total establishment limitation exceeded 99% for *A. altissima* in both sites and among treatments (urban uncaged=100.0%; urban caged=99.9%; rural uncaged=99.7%; rural caged=99.5%).

### ***Microsite factors and urban seedling establishment***

Significant differences between urban and rural forests were observed among multiple environmental factors. The PCA analysis of soil data determined distinct clustering between urban and rural plots (Fig. S4). The percent vegetation cover was greater in urban (39.4%)

compared to rural (22.2 %) forests ( $W=25972$ ,  $p<0.001$ ). Leaf litter depth was lower in urban (4.0 cm) than rural (5.4 cm) forests ( $W=57884$ ,  $p<0.001$ ). There was no difference in canopy cover (urban=88%; rural=88%;  $W=37190$ ,  $p=0.386$ ), meaning differences in light availability do not drive our results. When accounting for multiple environmental covariates in the urban-specific GLMM, exclosure treatments were still found to significantly increase seedling emergence for all species, except *C. tomentosa* and *A. altissima*. Vegetation cover, a proxy for competition, was negatively correlated with seedling emergence for *A. rubrum*, *A. platanoides*, *P. serotina*, and *A. altissima*. Soil PCA axis 3, which was most associated with metal contamination, significantly limited the emergence of both *Acer* species.

## Discussion

In our study, early-establishment was a significant ecological barrier for seedling recruitment in both urban and rural forests. Establishment limitation exceeded 90% for all species, even when excluding small mammals. These findings corroborate existing research in rural temperate deciduous forests (e.g. Clark et al., 1998) and broad trends observed across plant communities, where establishment limitation strength is typically greater than seed limitation (Clark et al., 2007). Our findings confirm the hypothesis that early-establishment limitation is greater in urban forests, and identifies seed predation and herbivory as important ecological mechanisms governing urban forest seedling recruitment.

Seed predation is an important driver of seedling establishment that can influence future forest composition and structure (Louda, 1989; Hulme, 1998; Levine & Murrell, 2003; Larios et al., 2017). Although seed predation has been hypothesized as a critical barrier to seedling recruitment in urban forests (Zipperer et al., 2010), our study is the first to confirm that the contribution of seed predation and removal to seedling establishment limitation is greater in urban

forests. Seed predation pressure may increase in urban forests for multiple reasons. First, granivore abundance frequently determines seed predation rates (e.g. Ostfield et al., 1997; Zwolak et al., 2010; Mattos et al., 2013) and there may be a greater abundance of seed predators in cities (Parker & Nilon, 2008). This may be the result of more favorable habitat conditions, the absence of predators (Faeth et al., 2005; Rodewald et al., 2011), and/or subsidized food resources that help sustain larger populations over time (Shochat et al., 2006; Chace & Walsh 2006; Parker & Nilon, 2008; Robb et al., 2008; Galbraith et al., 2015). Urban granivores may also be more aggressive foragers in urban sites, a result of threat of predation (Bowers et al., 1996; Parker & Nilon, 2008; Sarno et al. 2015).

It is also important to note that seed predation pressure may shift over time. It is well established that granivory is influenced by mast years and the identity of masting species (e.g. Schnurr et al., 2002; Lichti et al., 2014). In a comparison of urban and rural forest, seed removal was found to fluctuate in rural forest in response to oak masting. Conversely, there was no difference in urban forest seed removal (Chapter 5). The observed patterns may be year specific and we did not replicate the study over multiple years. Future research should be conducted over multiple years to determine if the temporal pattern of seedling establishment is similarly constant in urban forests.

Seed predation is not the only factor limiting urban seedling germination. Although the strength of seed predation and early herbivory is greater in urban forests, significantly greater seedling emergence was observed in rural caged quadrats compared to urban caged quadrats. This was true at the species-specific level, except for *P. serotina* and *A. altissima*. There are multiple microsite factors that may contribute to these observed differences in recruitment (Piana et al., 2019). For example, despite controlling for soil series type (Charlton and Hollis Series), there were strong differences between urban and rural soil characteristics, including pH, metal concentration, organic matter, and total nitrogen (Fig. S4). Urban soils are quite heterogenous and

variable across small areas (Craul, 1992; Pouyat et al., 2010) and these differences can have strong effects on seedling survival and health (Pregitzer et al., 2016).

Other potential drivers may include, but are not limited to, competition with invasive plants, changes in microsite conditions (e.g. leaf litter depth, woody debris abundance) and changes in microclimate (e.g. moisture and temperature). Although we did not find an influence of leaf litter depth, etc. on seedling germination and survival, we did find that higher vegetation resulted in less seed germination of particular species in the urban sites. This vegetation included more invasive herbaceous and liana species. We also found decreased leaf litter depth in urban quadrats (Fig. S2). Previous urban-rural gradient studies have found leaf-litter depth to be negatively correlated with proximity to urban centers (Kostel-Hughes, Young, & Carreiro, 1998). Decreased leaf litter depth may favor smaller seed species and prevent successful germination of large seed species, such as *Q. rubra* and *C. tomentosa* (Kostel-Hughes, Young, & Wehr, 2005), but that was not clear in our study.

Seedling survival was also limited by early herbivory in both urban and rural forests, and the strength of herbivory was greater in urban forests. However, when comparing caged plots, we did not observe overall differences in seedling survival. This finding suggests that following seedling emergence, site differences in recruitment are driven primarily by early herbivory and not other site factors. This is particularly interesting given the context of our study sites, especially with respect to herbivory pressure from white-tailed deer (*Odocoileus virginianus*). In the past several decades white-tailed deer have become overabundant and are known to significantly reduce seedling recruitment throughout the region (Horsley et al., 2003; Rooney and Waller, 2003; Cote et al., 2004; Aronson & Handel, 2011). In our study, each of the rural forest parks has abundant white-tailed deer populations. However, only one of the urban forest sites has deer regularly present. Therefore, we are observing an increase in herbivory from non-deer herbivores in urban sites that exceeds any pressure of deer in our rural sites. We do not know

what herbivore species were responsible for seedling predation in urban forest sites. To our knowledge there has been no study comparing herbivore identity across edge gradients in urban forests, nor the identity of herbivores between urban and rural forests. There is anecdotal evidence from local forest restoration that the abundance of voles, and their associated seedling herbivory, may be high in urban forested natural areas. Rural forest studies have found herbivore identity to shift in response to distance from forest edge (e.g. Cadenasso & Pickett, 2000). For example, in an oak-dominant forest, meadow voles (*Microtus pennsylvanicus*) were the primary herbivores for tree seedlings near forest edges, while deer, not voles, were the primary herbivores in forest interiors (>30 m from forest edge) (Cadenasso & Pickett 2000). Future research should work to identify herbivores in urban forested natural areas, comparing these populations to rural sites and across different urban conditions.

Although limited to six species, our study does highlight important trends in species-specific responses that may influence future forest composition and therefore management considerations. Specifically, in both urban and rural sites, the two maple species were most successful in germinating and establishing seedlings. The success of maple species in oak dominant forests is a well-documented trend across the range of *Q. rubra* in the eastern United States (Lorimer, 1984; Abrams et al., 1998; McEwan et al., 2011). The non-native *A. platanoides* was the most successful species at establishing in both urban and rural forests. A successful invader in temperate forests, *A. platanoides* displays several competitive advantages including relatively high photosynthetic rates, biochemical defense, and low preference from seed predators and herbivores (e.g. Martin & Marks, 2006; Morrison & Mauck, 2007; Gailbraith-Kent & Handel, 2008; Paquette et al., 2012).

Conversely, the other non-native species, *A. altissima*, did not recruit well. This species is less shade tolerant, which may have driven low germination rates. However, as noted elsewhere, the seeds of *A. altissima* may persist in the seed bank longer than larger seeded tree species and

allow this species to recruit following future disturbances to the canopy (Rebbeck & Jolliff, 2018; Redwood, Matlack & Huebner, 2019). Also, of note is *Prunus serotina*, which did not germinate at high rates. However, once seedlings emerged, they survived at high rates. Among naturally regenerating populations, *P. serotina* was the most common seedling and sapling in our urban forest (Chapter 2; Chapter 3). It appears that while initial establishment barriers may be quite strong for *P. serotina*, it may be able to persist once established, making it an increasingly important species for the future forest.

Our findings have important implications for the management of urban forested natural areas. Direct planting is a common practice in urban forests, but is expensive and resource intensive (DiCicco, 2014; Simmons et al., 2016; Pregitzer et al., 2018). Passive restoration and silvicultural treatments that promote natural regeneration are common in rural systems. An important management question is whether or not such approaches are viable in urban forested natural areas. Our study confirms that there are more intense site filters in urban forests that make the probability of seedling recruitment lower, and as a result, relying on natural regeneration alone may not be a viable management option. Seed addition does increase establishment; however, seed predation and herbivory are strong filters and will limit success. That said, once established, urban seedlings may successfully transition to juvenile and adult stages. A concurrent study of these plots found sapling abundance to be greater in urban forest sites and natural regeneration stocking indices to be the same as rural forests (Chapter 2). As such, modified silvicultural approaches that promote and protect seedling establishment may be successful in establishing robust understory populations of native tree species.

Urban forest research has shown that gaps in the canopy are difficult to restore. Recent research has found that restoration can be successful in these sites (e.g. Johnson & Handel, 2016). However, long-term success is dependent upon intense and continued management, including planting, removal of invasive plants, and chemical treatment (Simmons et al., 2016; Johnson and

Handel, 2019). It is therefore important that we manage intact canopy and develop a robust midstory and understory that is able to capture gaps following disturbance events. With this understanding, despite being different than the current canopy species, *Acer* sp. and *P. serotina*, cherry may be important species that help sustain native tree canopy in our urban forested natural areas. An important decision for forest managers will be whether or not to manage for the current community, oak-hickory, or to consider transitions to other native forest community types. Given the suite of urban conditions and stressors that affect plant recruitment (Piana et al., 2019), the prudent strategy may be to support both current canopy dominants through small seedling transplants and the natural regeneration of species, such as *A. rubrum* and *P. serotina*, that are more resilient to existing conditions.

## Conclusion

Understanding how urban conditions influence ecological processes is important for guiding the management of urban habitats. By identifying how urban ecosystem functions respond, and how they fundamentally may differ from rural equivalents, we can develop targeted management interventions. We show that natural regeneration in urban forested natural areas is not hopeless, and the wealth of traditional ecological forest management knowledge may be relevant. Still, there are distinct differences and exacerbated barriers to native tree recruitment that must be addressed through modified or novel strategies. We argue that such knowledge may benefit ecological management outside of city limits as well. The conditions and stressors of cities are not unique, but in fact common in a time of global change. Experiencing elevated temperatures and often the epicenter of biotic invasions, urban ecosystems may serve as model systems for the future perturbations and changes that threaten rural wildlands. By conducting mechanistic research in cities, and comparing across gradients of human impacts, ecology theory and application will advance.

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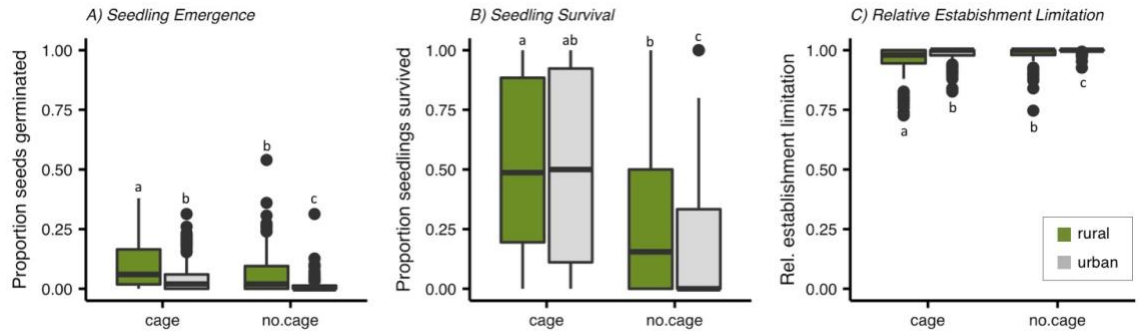
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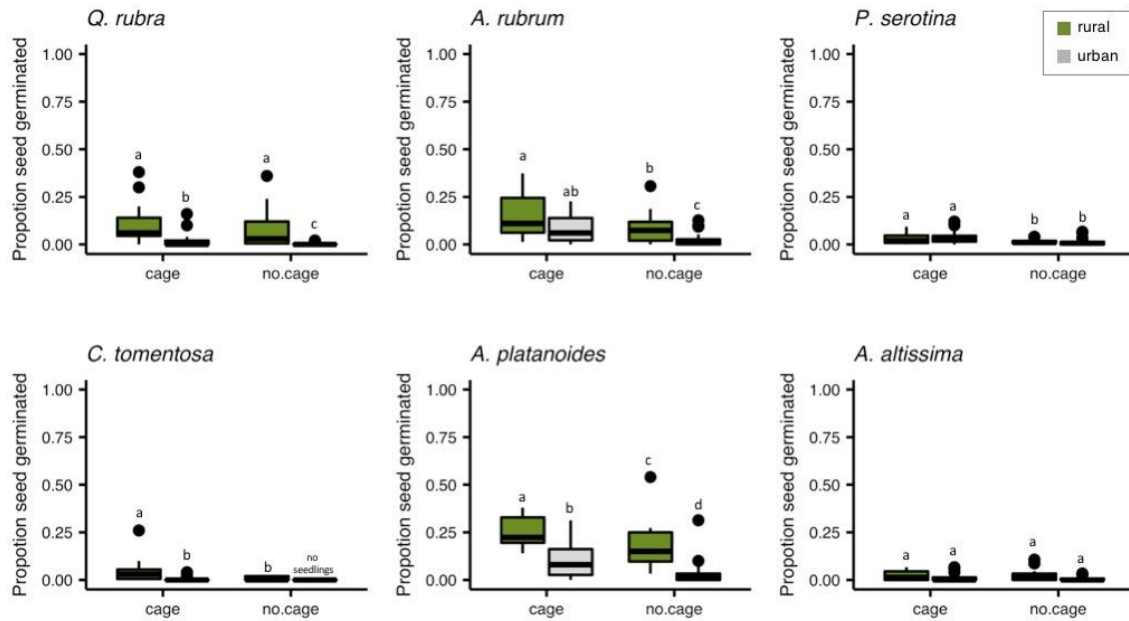
## Figures



**Figure 1** Seed addition experiment with small mammal exclosures at Sterling Forest Park, Tuxedo Park, New York, USA (rural site) (Photo credit M.H. Helmer).



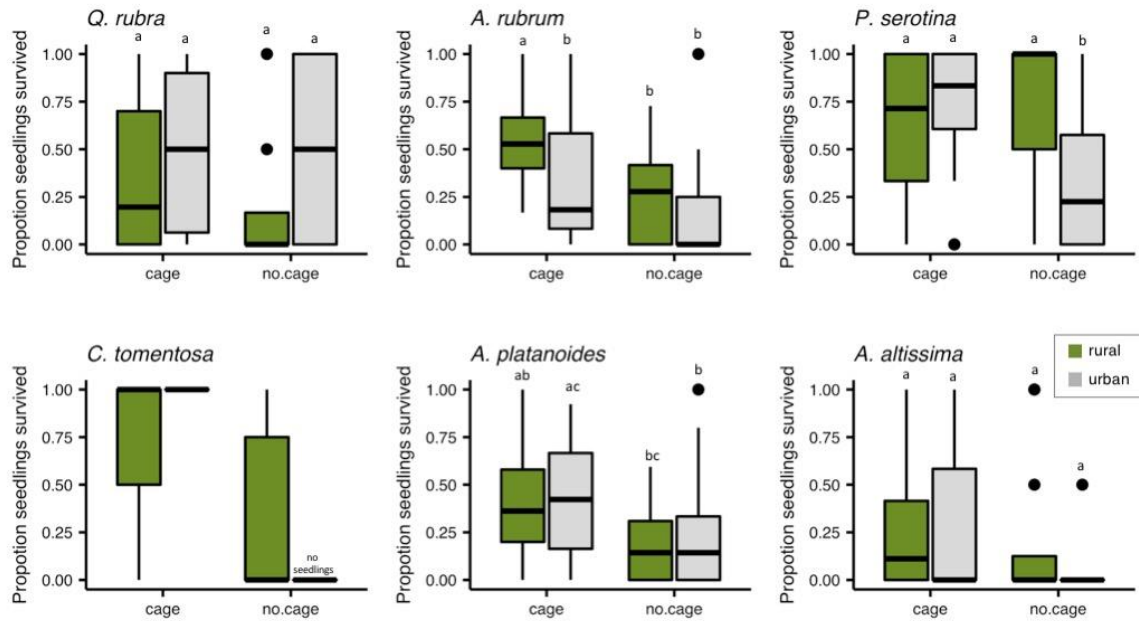
**Figure 2** All species model comparisons for urban (grey) and rural (green) forest for: A) seedling emergence, the proportion of seeds germinated as a function of the number of seeds added to each quadrat; B) seedling survival, the proportion of seedlings survived as a function of the number of seeds germinated; and C) relative establishment limitation, one minus the proportion of seedlings that survived the length of the study as a function of the number of seeds added to each quadrat. Responses that are not significantly different, according to the GLMM, share the same letter ( $P < 0.05$ ) (for full model results see Tables S2-S4). Boxes indicate the interquartile range (25th and 75th percentile) and the line shows the median. Error bars show  $\pm 1.5$  times the interquartile range to the 25th and 75th percentiles. Outlier points are beyond 1.5 times the interquartile range.



**Figure 3** Species-specific seedling emergence in urban (grey) and rural (green) forests. Values are the proportion of seedlings germinated as a function of seeds added to each quadrat.

Responses that are not significantly different, according to the GLMM, share the same letter ( $P < 0.05$ ) (for full model results see Tables S2-S4). Boxes indicate the interquartile range (25th and 75th percentile) and the line shows the median. Error bars show  $\pm 1.5$  times the interquartile range to the 25th and 75th percentiles. Outlier points are beyond 1.5 times the interquartile range.

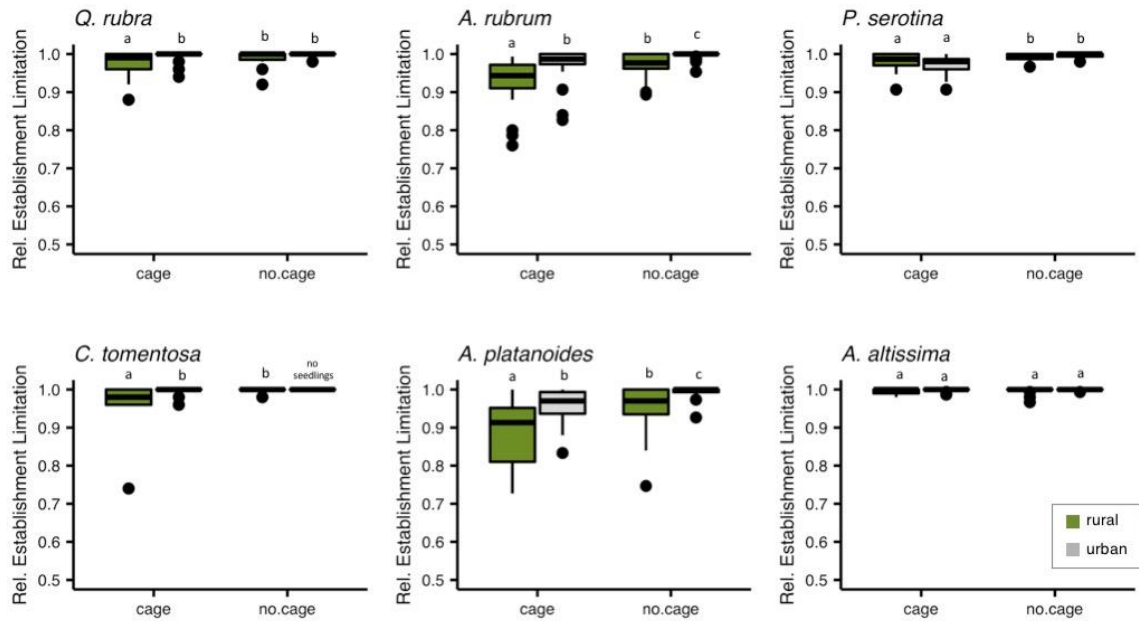




**Figure 4** Species-specific cumulative seedling survival in urban (grey) and rural (green) forests.

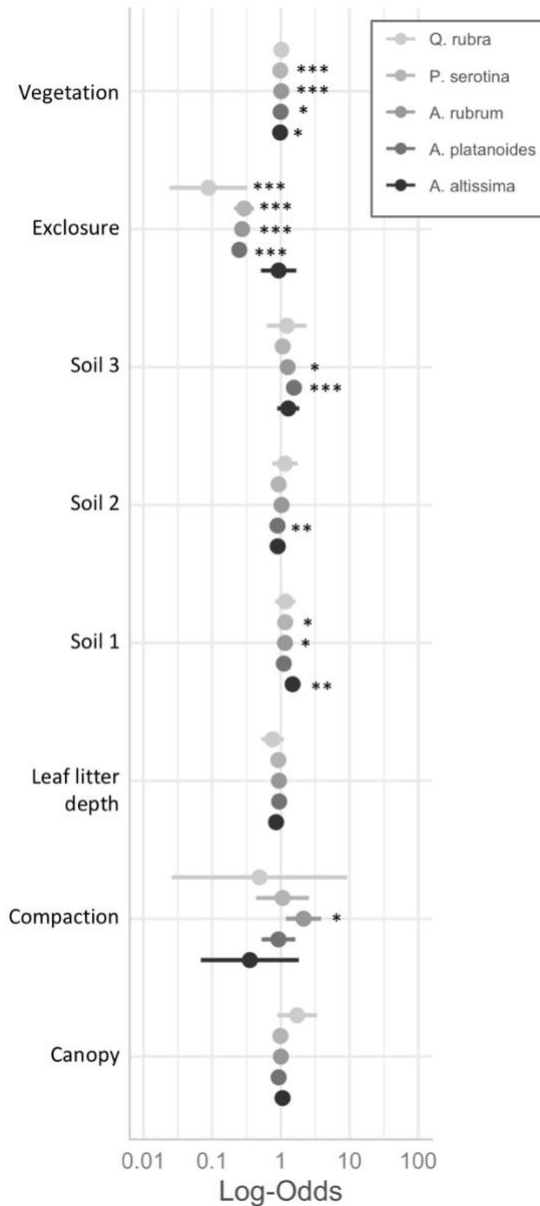
Values are the proportion seedlings survived as a function of total emerged seedlings in each quadrat. Note the model failed to converge for *C. tomentosa* due to limited number of total seedlings. Responses that are not significantly different, according to the GLMM, share the same letter ( $P < 0.05$ ) (for full model results see Tables S2-4). 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.





**Figure 5** Species-specific establishment limitation in urban (grey) and rural (green) forests.

Establishment limitation is one minus the proportion of seedlings that survived as function of seeds added. Values closer to one represent high establishment limitation (low probability of recruitment). Responses that are not significantly different, according to the GLMM, share the same letter (P < 0.05) (for full model results see Tables S2-S4). Boxes indicate the interquartile range (25th and 75th percentile) and the line shows the median. Error bars show  $\pm 1.5$  times the interquartile range to the 25th and 75th percentiles. Outlier points are beyond 1.5 times the interquartile range.



**Figure 6** Microsite and environmental factors that influence seed germination in urban forests.

Covariates included in the model are identified on the y-axis. Soil 1-3 refer to the three most explanatory axes from the PCA analysis for urban sites only. Note, the y-axis reports log-odds, the linear transformation of odds ratios, where 1 unit increase in a predictor results in a coefficient unit increase in the outcome and this holds regardless of the levels of the other predictors. Horizontal lines indicate 95% confidence intervals. Significance from the full models (including all explanatory variables) is indicated as: \* $P < 0.05$ ; \*\* $P < 0.01$ ; \*\*\* $P < 0.001$ .

## **Supplemental Material**

**Table S1:** Study site descriptions.

**Table S2:** GLM(M) results for seed germination models (species-specific, all species).

**Table S3:** GLM(M) results for seedling survival models (species-specific, all species). Bold text identifies significant covariates.

**Table S4:** GLM(M) results for relative establishment limitation models (species-specific, all species).

**Figure S1:** Map of study sites, impervious cover, and human population density.

**Figures S2:** Differences in vegetation cover, canopy density, and leaf litter depth for seed addition quadrats in urban and rural forests.

**Figures S3:** Comparison of urban and rural soil and PCA results.

**Table S1** Study Site Descriptions. Urban conditions were defined by population density (U.S. Census Bureau 2012) and percent impervious cover (USGS 2011). Each of these conditions was assessed at two buffer distances from each study site.

Site	Type	Human Population		% Impervious	
		0.5 km	2.0 km	0.5 km	2.0 km
Van Cortlandt Park	Urban	257.6	77541.7	10.1	27.7
Pelham Bay Park	Urban	246.8	3508.1	7.2	35.6
Inwood Hill Park	Urban	1073.6	121354.2	15.9	33.1
Black Rock Forest	Rural	0.0	486.0	0.8	3.6
Sterling Forest Park	Rural	0.0	167.0	0.1	0.3
Blue Lake Park	Rural	0.0	65.0	0.2	0.4

**Table S2** GLM(M) results for seed germination models (species-specific, all species). Bold text identifies significant covariates. Significance levels are reported as: † P<0.10; \* P<0.05; \*\* P<0.001; \*\*\* P<0.001.

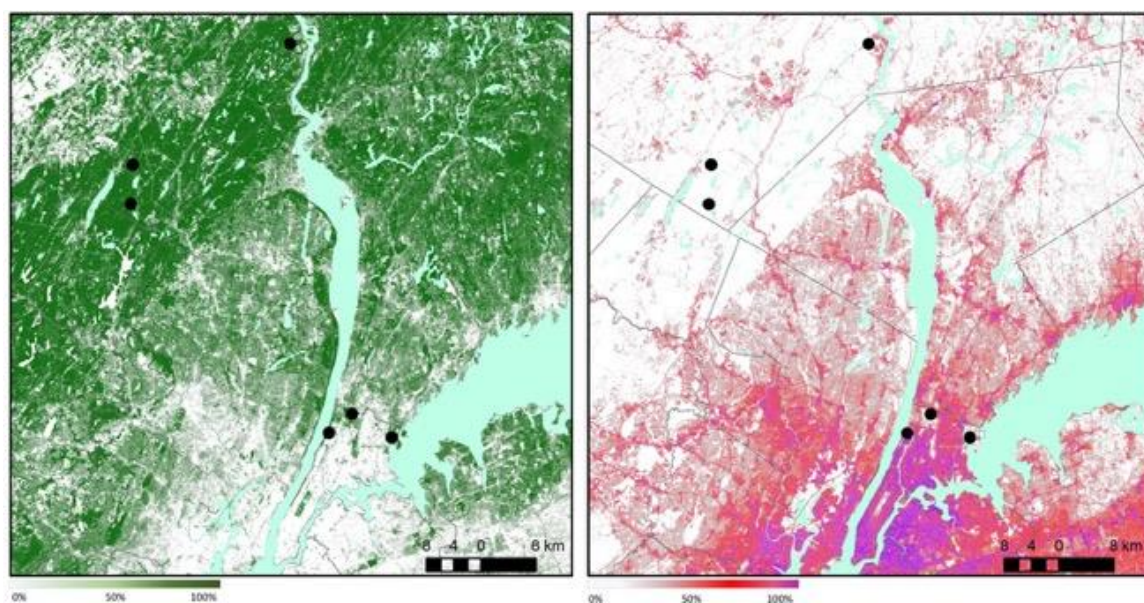
Species	Fixed effect	Estimate	Std. Error	z Value
All Species	<b>Intercept***</b>	<b>-2.64345</b>	<b>0.41337</b>	<b>-6.395</b>
	<b>Type.Urban***</b>	<b>-0.89685</b>	<b>0.19342</b>	<b>-4.637</b>
	<b>Tx.Cage***</b>	<b>-0.48508</b>	<b>0.04675</b>	<b>-10.377</b>
	<b>Type.Urban:Tx.Cage***</b>	<b>-0.76911</b>	<b>0.07984</b>	<b>-9.633</b>
<i>Carya tomentosa</i>	<b>Intercept***</b>	<b>-3.3247</b>	<b>0.3473</b>	<b>-9.572</b>
	<b>Type.Urban***</b>	<b>-2.1719</b>	<b>0.5610</b>	<b>-3.871</b>
	<b>Tx.Cage***</b>	<b>-1.9894</b>	<b>0.4417</b>	<b>-4.504</b>
	Type.Urban:Tx.Cage	-19.0879	12509.1555	-0.002
<i>Quercus rubra</i>	<b>Intercept***</b>	<b>-2.4419</b>	<b>-6.770</b>	<b>-6.770</b>
	<b>Type.Urban***</b>	<b>-2.1435</b>	<b>0.5187</b>	<b>-4.132</b>
	<b>Tx.Cage*</b>	<b>-0.3490</b>	<b>0.1682</b>	<b>-2.075</b>
	<b>Type.Urban:Tx.Cage**</b>	<b>-1.5146</b>	<b>0.5668</b>	<b>-2.672</b>
<i>Prunus serotina</i>	<b>Intercept***</b>	<b>-3.6843</b>	<b>0.2583</b>	<b>-14.266</b>
	Type.Urban	0.1864	0.3237	0.576
	<b>Tx.Cage***</b>	<b>-0.7252</b>	<b>0.2007</b>	<b>-3.613</b>
	Type.Urban:Tx.Cage	-0.3601	0.2542	-1.417
<i>Acer rubrum</i>	<b>Intercept***</b>	<b>-1.95745</b>	<b>0.32462</b>	<b>-6.030</b>
	<b>Type.Urban*</b>	<b>-0.83145</b>	<b>0.41543</b>	<b>-2.001</b>
	<b>Tx.Cage***</b>	<b>-0.60876</b>	<b>0.09039</b>	<b>-6.735</b>
	<b>Type.Urban:Tx.Cage***</b>	<b>-0.75530</b>	<b>0.14432</b>	<b>-5.234</b>
<i>Acer platanoides</i>	<b>Intercept***</b>	<b>-1.0939</b>	<b>0.1827</b>	<b>-5.987</b>
	<b>Type.Urban***</b>	<b>-1.2443</b>	<b>0.2350</b>	<b>-5.295</b>
	<b>Tx.Cage***</b>	<b>-0.4705</b>	<b>0.0677</b>	<b>-6.950</b>
	<b>Type.Urban:Tx.Cage***</b>	<b>-0.8341</b>	<b>0.1221</b>	<b>-6.830</b>
<i>Ailanthus altissima</i>	<b>Intercept***</b>	<b>-4.6038</b>	<b>0.5258</b>	<b>-8.756</b>
	Type.Urban	-0.8863	0.6685	-1.326
	Tx.Cage	0.1369	0.1852	0.739
	<b>Type.Urban:Tx.Cage*</b>	<b>-0.6435</b>	<b>0.3166</b>	<b>-2.033*</b>

**Table S3** GLM(M) results for seedling survival models (species-specific, all species). Bold text identifies significant covariates. Significance levels are reported as: † P<0.10; \* P<0.05; \*\* P<0.001; \*\*\* P<0.001.

Species	Fixed effect	Estimate	Std. Error	z Value
All Species	Intercept	-0.05060	0.42270	-0.120
	Type.Urban	-0.31159	0.26993	-1.154
	<b>Tx.Cage***</b>	<b>-0.72552</b>	<b>0.09603</b>	<b>-7.555</b>
	<b>Type.Urban:Tx.Cage**</b>	<b>-0.52617</b>	<b>0.19336</b>	<b>-2.721</b>
<i>Carya tomentosa</i>	Intercept	NA	NA	NA
	Type.Urban	NA	NA	NA
	Tx.Cage	NA	NA	NA
	Type.Urban:Tx.Cage	NA	NA	NA
<i>Quercus rubra</i>	<b>Intercept*</b>	<b>-0.9687</b>	<b>0.3789</b>	<b>-2.557</b>
	Type.Urban	0.9775	0.6715	1.456
	<b>Tx.Cage†</b>	<b>-0.8041</b>	<b>0.4684</b>	<b>-1.717</b>
	Type.Urban:Tx.Cage	0.6724	1.3446	0.500
<i>Prunus serotina</i>	<b>Intercept***</b>	<b>1.04732</b>	<b>0.25989</b>	<b>4.030</b>
	Type.Urban	-0.05239	0.31412	-0.167
	Tx.Cage	-0.39339	0.42950	-0.916
	<b>Type.Urban:Tx.Cage*</b>	<b>-1.37473</b>	<b>0.54479</b>	<b>-2.523</b>
<i>Acer rubrum</i>	Intercept	0.1379	0.2661	0.518
	<b>Type.Urban**</b>	<b>-1.1045</b>	<b>0.3603</b>	<b>-3.066</b>
	<b>Tx.Cage***</b>	<b>-0.9566</b>	<b>0.1912</b>	<b>-5.003</b>
	Type.Urban:Tx.Cage	0.2602	0.3551	0.733
<i>Acer platanoides</i>	Intercept	-0.31010	0.28371	-1.093
	Type.Urban	0.08988	0.37363	0.241
	<b>Tx.Cage***</b>	<b>-0.63986</b>	<b>0.13314</b>	<b>-4.806</b>
	<b>Type.Urban:Tx.Cage †</b>	<b>-0.54206</b>	<b>0.30933</b>	<b>-1.752</b>
<i>Ailanthus altissima</i>	<b>Intercept †</b>	<b>-2.0994</b>	<b>1.1744</b>	<b>-1.788</b>
	Type.Urban	0.1187	1.5121	0.078
	Tx.Cage	-0.5074	0.5521	-0.919
	Type.Urban:Tx.Cage	-2.2534	1.9704	-1.144

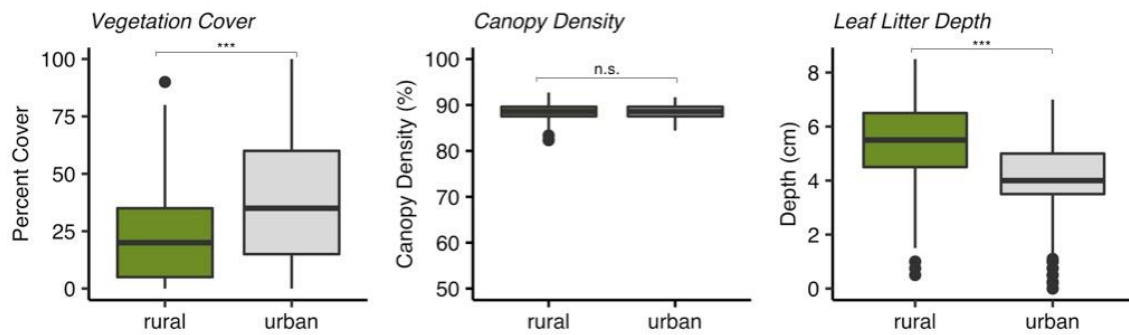
**Table S4** GLM(M) results for relative establishment limitation models (species-specific, all species). Bold text identifies significant covariates. Significance levels are reported as: † P<0.10; \* P<0.05; \*\* P<0.001; \*\*\* P<0.001.

Species	Fixed effect	Estimate	Std. Error	z Value
All Species	<b>Intercept***</b>	<b>-3.53684</b>	<b>0.46205</b>	<b>-7.655</b>
	<b>Type.Urban***</b>	<b>-0.98718</b>	<b>0.24886</b>	<b>3.967</b>
	<b>Tx.Cage***</b>	<b>-0.93531</b>	<b>0.07513</b>	<b>12.449</b>
	<b>Type.Urban:Tx.Cage***</b>	<b>-0.98974</b>	<b>0.15091</b>	<b>6.558</b>
<i>Carya tomentosa</i>	<b>Intercept***</b>	<b>3.717e+00</b>	<b>3.859e-01</b>	<b>9.633</b>
	<b>Type.Urban**</b>	<b>1.821e+00</b>	<b>5.893e-01</b>	<b>3.090</b>
	<b>Tx.Cage***</b>	<b>2.773e+00</b>	<b>7.337e-01</b>	<b>3.779</b>
	Type.Urban:Tx.Cage	1.850e+01	1.378e+04	0.001
<i>Quercus rubra</i>	<b>Intercept***</b>	<b>3.7508</b>	<b>0.3796</b>	<b>9.880</b>
	<b>Type.Urban**</b>	<b>1.4255</b>	<b>0.5343</b>	<b>2.668</b>
	<b>Tx.Cage**</b>	<b>1.1696</b>	<b>0.3880</b>	<b>3.015</b>
	Type.Urban:Tx.Cage	0.6338	0.8580	0.739
<i>Prunus serotina</i>	<b>Intercept***</b>	<b>4.0142</b>	<b>0.2772</b>	<b>14.479</b>
	Type.Urban	-0.1725	0.3474	-0.497
	<b>Tx.Cage***</b>	<b>0.8407</b>	<b>0.2420</b>	<b>3.473</b>
	<b>Type.Urban:Tx.Cage**</b>	<b>1.0806</b>	<b>0.3510</b>	<b>0.3510</b>
<i>Acer rubrum</i>	<b>Intercept***</b>	<b>2.7292</b>	<b>0.3517</b>	<b>7.761</b>
	<b>Type.Urban**</b>	<b>1.4440</b>	<b>0.4652</b>	<b>3.104</b>
	<b>Tx.Cage***</b>	<b>1.0102</b>	<b>0.1357</b>	<b>7.444</b>
	<b>Type.Urban:Tx.Cage**</b>	<b>0.9259</b>	<b>0.2887</b>	<b>3.208</b>
<i>Acer platanoides</i>	<b>Intercept***</b>	<b>2.1518</b>	<b>0.1988</b>	<b>10.823</b>
	<b>Type.Urban***</b>	<b>1.1649</b>	<b>0.2609</b>	<b>4.465</b>
	<b>Tx.Cage***</b>	<b>0.8639</b>	<b>0.1071</b>	<b>8.063</b>
	<b>Type.Urban:Tx.Cage***</b>	<b>1.0308</b>	<b>0.2281</b>	<b>4.520</b>
<i>Ailanthus altissima</i>	<b>Intercept***</b>	<b>6.3937</b>	<b>0.8293</b>	<b>7.710</b>
	Type.Urban	1.2420	0.9520	1.305
	Tx.Cage	0.3715	0.4358	0.853
	Type.Urban:Tx.Cage	1.4235	1.1653	1.222

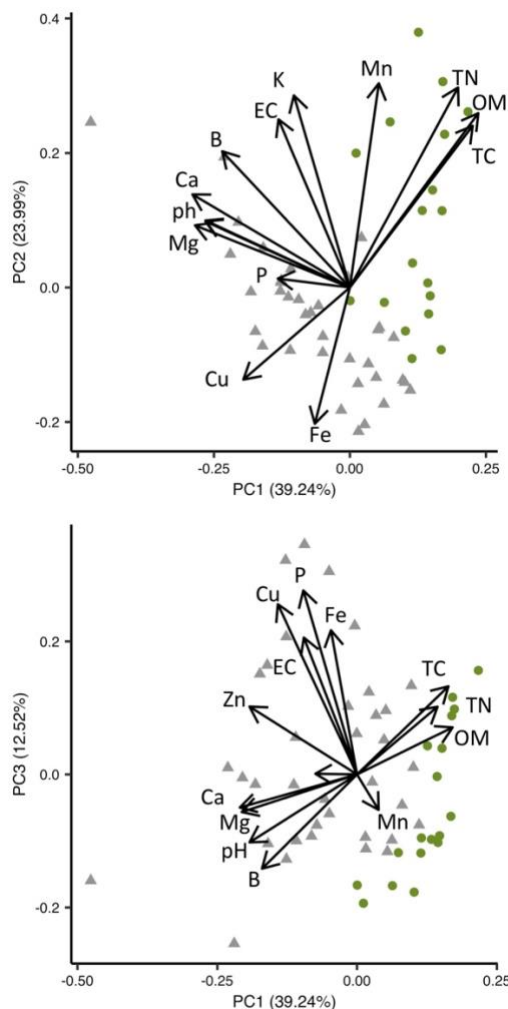


**Figure S1** Urban and rural forest site locations in relation to (left) percent regional forest canopy cover and (right) percent impervious cover (National Land Cover Database 2016; U.S. Census Data 2016).





**Figure S2** Differences in vegetation cover, canopy density, and leaf litter depth for seed addition quadrats in urban (grey) and rural (green) forests. Significance levels are reported as: †  $P < 0.10$ ; \*  $P < 0.05$ ; \*\*  $P < 0.001$ ; \*\*\*  $P < 0.001$ ; Mann-Whitney U test (Mann and Whitney 1947). Boxes indicate the interquartile range (25th and 75th percentile) and the line shows the median. Error bars show  $\pm 1.5$  times the interquartile range to the 25th and 75th percentiles. Outlier points are beyond 1.5 times the interquartile range.



**Figure S3** Characteristics of soils from urban (grey triangles) and rural (green circles) oak-hickory forests in the NYC metro area. From the principal-component analysis (PCA) we identified strong clustering by site type (urban, rural). The first axis (PC1) explained 39.24% of the total variance in soil data and was strongly correlated with pH, as well as Ca and Mg. Urban soils had significantly lower pH. The second axis (PC2) explained an additional 23.99% of the variance and was most strongly correlated with Mn and Total Nitrogen (TN). Axis 3 (PC3) explained an additional 12.52% of the variance and was most strongly correlated with P, Cu, and Fe.

**Chapter 5: Evidence of functional shifts in urban ecology: temporal dynamics of post-dispersal seed removal in urban and rural forests**

## Abstract

Testing and understanding the functional differences between rural and human-dominated habitats is a critical focus for urban ecology theory and the basis for sustainable management in a rapidly urbanizing world. Seed predation may represent a significant, and previously overlooked, barrier for plant recruitment in urban forests. We conducted a three-year cafeteria experiment in the New York City metropolitan area comparing seed removal of woody species in urban and rural oak-hickory forests. Seed removal fluctuated among years in rural forests but was interannually sustained and moderately high in urban sites. Additionally, in both urban and rural forests, native species experienced greater seed removal than non-native species. Our results support the hypothesis that urban forests deviate from temporal patterns of seed predation that are characteristic of forests dominated by masting tree species. These findings represent an urban-driven shift in a basic ecological process with important implications for plant recruitment and therefore future forest composition and structure, function, and associated ecosystem services.

**Keywords:** Forest ecology, granivory, invasion, mast dynamics, non-native plants, seed predation, seed removal, mechanistic urban ecology

## Introduction

Urban ecosystems are affected by many biophysical and social conditions that can alter biodiversity and ecological function (Pickett et al. 2011). Around the world, observational studies for multiple taxa provide evidence of shifting patterns of species abundance, distribution, and community composition between urban and rural sites, and across gradients of urbanization and human impact (e.g. Aronson et al. 2014, Beninde et al. 2015). Determining the ecological mechanisms that drive these community shifts is an important arena of research. There is a

growing call for functionally based urban ecology studies (Shochat et al. 2006, McDonnell and Hahs 2013). Such research and an improved functional understanding of urban ecosystems will inform not only sustainable management within cities, but also regional and global conservation practices confronted with the challenge of an increasingly urbanized and human-impacted world.

Urban forested natural areas are important reservoirs for biodiversity and provide a significant proportion of ecosystem services within many of the world's largest and densest cities (e.g. Lawrence et al. 2013, Pregitzer et al. 2018). These sites are also areas where natural regeneration can occur and are functionally more like their rural counterparts than other components of the urban forest canopy (e.g. street trees, park trees, backyards). However, current management practice in urban forested natural areas is resource intensive and relies on planting (Pregitzer et al. 2018). Given the structural similarity between urban and rural forested natural areas, passive restoration and traditional approaches to ecological forest management that leverage natural regeneration may be a more sustainable alternative. Such management strategies require understanding of the functional responses of these reproduction systems to urban conditions.

Research comparing urban and rural forested natural area composition and structure suggests that plant recruitment dynamics are affected by urban conditions and stressors. When compared to rural forests, researchers report greater non-native seedling species richness and reduced native seedling abundance in urban forests (e.g. Guntenspergen et al. 1997, Zipperer et al. 2002, Cadenasso et al. 2007, Pennington et al. 2010, Trammell and Carreiro 2011). Differences in urban forest composition are well documented, but the ecological mechanisms driving these changes are not. Empirical research has identified different processes that can have a negative impact on native plant recruitment in urban forests. These include herbivory, competition from invasive plants, and the absence of natural disturbance regimes such as fire (O'Brien et al 2012, Labatore et al. 2016, Ettinger et al. 2017). Many of those experiments do not,

however, directly compare urban and rural sites. Functional shifts in urban plant communities are also highlighted by trait analyses and hierarchical trait filter models (e.g. Williams et al. 2009, Aronson et al. 2016). However, these approaches only point towards potential mechanisms and must be paired with process-based experiments to identify specific causes. Recognizing this need, urban plant population frameworks that emphasize plant demography and identify potential barriers in plant life history have been developed to synthesize research and identify knowledge gaps (e.g. Kowarik and von der Lippe 2018, Piana et al. 2019). These works suggest that early-establishment processes, from seed production to germination, are under-studied in cities, but may be affected by urban conditions and influence recruitment dynamics and community assembly.

Seed predation is one such process. In non-urban systems, post-dispersal seed predation is known to significantly alter plant recruitment and community composition (Louda 1989, Hulme 1998, Levine and Murrell 2003, Larios et al. 2017). Some studies suggest that seed predation may better explain plant abundance and distribution than seed dispersal (e.g. Orrock et al. 2006). In temperate deciduous forests of the eastern United States, dominant tree species such as maples and oaks, have been recorded to suffer post-dispersal predation exceeding 80%, and sometimes nearly 100% (Myster and Pickett 1993, Meiners 2005). Given these high rates of seed predation, interannual-variation can be critical to successful plant recruitment. In oak-dominated temperate deciduous forests, interannual variation in seed predation patterns is well-known (e.g. Sork 1983) and such shifts have been correlated with annual fluctuations in local seed production and granivore populations (Ostfeld et al. 1996, Schnurr et al. 2002, Clotfelter et al. 2007).

Elevated seed predation has been hypothesized to limit native plant recruitment in urban forests (Rudnický and McDonnell 1989, Labatore et al. 2016), but there is little empirical research that supports this contention or that directly compares rural and urban sites. Also, those experiments that do compare seed predation have been conducted for a single year, missing

potential temporal dynamics (Bowers et al. 1996, Pufal et al. 2015). Despite this research gap, there is indirect support that seed predation may be influenced by urbanization. Consumer abundance frequently determines seed removal rates (Ostfeld et al. 1997) and seed predator population density may be higher in urban forests (Rudnicki and McDonnell 1989). Global change factors, such as fragmentation, biotic invasion, and nitrogen deposition, may also influence seed predation. Given that many of these factors co-occur in urban systems, they may serve as a first approximation for urban-based dynamics. For example, fragmentation may increase granivory because small mammals tolerate this land change better than their predators (e.g. Adler and Levins 1994). Invasive plants may increase granivory because consumers are subsidized by the invader (Orrock et al. 2015). Additionally, atmospheric nitrogen deposition may increase seed production, altering mast dynamics and seed predation patterns. Given the confluence of these drivers in urban sites, might such effects be exacerbated?

In this experiment, we tested the hypothesis that there are no differences in urban and rural forest seed removal, a potentially important ecological mechanism and driver of observed shifts in urban plant communities. Using a cafeteria study design, replicated over three years, we tested the patterns of seed removal of native and non-native species in urban and rural oak-hickory forests. It is important to note that by definition our study measures seed removal, not seed predation, although, as we note, the majority of observations were predation events. Such methods may sometimes confound secondary dispersal for predation (Van der Wall et al. 2005). To our knowledge, this is the first multi-year study comparing urban and rural seed removal dynamics. The results from this study improve our understanding of the contribution of post-dispersal seed removal and predation to recruitment limitation in urban forests, and advance our knowledge of the influence of urbanization on plant community assembly.

## **Materials and methods**

### ***Study sites***

The experiment was conducted in six oak-hickory forest sites located in the greater New York City metropolitan area (Appendix S1: Fig. S1). Oak-hickory is the most common forest community type in New York City natural areas (Forgione et al. 2016) and is regionally common throughout the northeast corridor, one of the most densely developed regions in the United States. Three urban forest sites were located in forested natural areas in the Bronx (Van Cortlandt Park and Pelham Bay Park) and Manhattan (Inwood Hill Park). Three rural forests sites were located in the New York Highlands region (Sterling Forest State Park, Sterling Forest-Blue Lake Park, and Black Rock Forest). All sites were located more than 15 km apart. Urban and rural sites were defined by the percent population density and the percent of impervious surface in two buffer classes: plot scale (500 m) and site scale (2 km) (Appendix S1: Table S1). Given that site conditions influence seed predation (e.g. Myster and Pickett 1993, Ostfeld et al. 1997, Schnurr et al. 2004), we controlled for forest community, structure, age, slope, and aspect in test location to minimize local impacts on granivore abundance and behavior.

### ***Experimental design and data collection***

We used a cafeteria study design to measure seed removal of seven woody species that are common in the region and were present at each site (Fig. 1). Five native tree species were selected: *Quercus rubra*, *Prunus serotina*, *Acer rubrum*, *Sassafras albidum*, and *Carya tomentosa*. We also included two common non-native tree species: *Acer platanoides* and *Ailanthus altissima*. Collectively, these species were selected to represent a range of seed size and dispersal mode.

Six plots were installed at each forest site. All plots were randomly located, a minimum of 200 m from next nearest plot, and greater than 30 m from forest edge. In each plot, seed trays



were installed in two parallel transects, offset by 2 m and oriented east-west. Seed trays consisted of 10 cm diameter plastic plant saucers, the base of which was perforated to allow for water drainage. Each tray was stabilized with a single landscape staple. Within each plot seed trays were randomly assigned one of the seven tree species and stocked with ten conspecific seeds. Seeds for the experiment were collected locally (within 80 km of all sites) each year and stored at room temperature until the start of the experiment. The samaras of winged seeds (*A. rubrum*, *A. platanoides*, and *A. altissima*) were removed to minimize secondary dispersal from seed trays and the pulp of fleshy seeds removed to mimic conditions found after primary bird dispersal. *Quercus* seeds were marked with a scratch to distinguish our placed seeds from naturally dispersed propagules that may have been introduced to a seed tray. Seed removals were recorded after 21 days. The experiment was conducted three times, in October of 2016, 2017, and 2018. Given that nocturnal foraging activity and behavior may change in response to light regimes and predators (e.g. Brown et al. 1988), we initiated the experiment during the same moon phase each year (phase=first quarter, approximately 50% visible).

### ***Data Analysis***

We used generalized linear models (GLMs) and mixed-effects models (GLMMs) to examine the effect of forest site type on seed removal. Seed removal was calculated as the proportion of seeds removed after 21 days as a function of the total number of seeds placed in each tray (n=10). Seeds removed included all eaten, partially eaten, and seeds missing from the tray. For all species except *C. tomentosa*, the majority of seeds were left partially eaten in the tray and were classified as predated, not removed. To test the hypothesis that seed removal differs between site type (urban vs. rural), we fit a model for all species pooled, where site, year, and their interaction were included as fixed effects, and species and plot were random effects terms. The random effects quantify variation in seed removal among sites and species. General linear models were fit for

each individual species, where site type, year, and their interaction were included as fixed effects. We also compared the relative differences in seed removal among species in urban and rural sites, where species and site were included as fixed effect. We fit all models with a binomial error distribution and logit link, using Laplace approximation for the maximum likelihood estimate of the parameters and testing the significant of fixed effects with Wald Z statistics. Estimated marginal means were used for all post hoc tests. All statistical analyses were conducted using the ‘lme4’ and ‘emmeans’ packages in R 3.6.0 (Bates et al. 2011, R Development Core Team 2019, Lenth and Lenth 2018).

## Results

When pooling all species, the best-fitting model (AIC=3915.5) included year, site type (urban and rural), and their interaction (Fig. 2, Appendix S2: Table S1 and S2). Seed removal was significantly different between urban and rural sites, however the relationship between site types varied over time. The proportion of seed removed in rural sites was significantly different among the three years, with particularly lower observed seed removal in 2017. Conversely, there was no significant difference in annual seed removal in urban sites. Given these different responses, seed removal between urban and rural sites also varied among observation periods. In 2016, seed removal was significantly greater in rural (74.5%) than urban (60.4%) sites. However, in 2017, rural seed removal (20.3%) was significantly lower than urban seed removal (61.0%). In 2018 rural seed removal increased (65.0%) and was similar to seed removal in urban forest sites (67.0%).

Similar temporal patterns were observed in the species-specific models (Fig. 3). The best fitting species-specific models also included site type, year, and their interaction, with the exception of *C. tomentosa*, for which all seeds were removed each year in all sites (Appendix S2:

Table S1 and S2). Seed removal was different in rural sites across years and there were no significant annual differences in urban seed removal (Fig. 3). The only exception to this was *C. tomentosa*, as mentioned previously, and *Q. rubra*, for which seed removal was lower in 2016 than 2018. We also found differences in total seed removal among species in both urban and rural forest sites (Fig. 4: Appendix S2: Table S3). The rank of seed removal was similar between site types and was generally correlated with seed size (larger seeds exhibited greater proportion of seed removed). The exception to this trend were the two non-native species. Specifically, in both urban and rural sites, seed removal for *A. rubrum* was greater than *A. platanoides* and *A. altissima*, both species with larger average seed mass.

## Discussion

This research provides evidence of an urban-driven shift in a plant recruitment process with implications for future urban forest conditions, management, and ecosystem function and services. We observed a potential decoupling of seed predation from annual seed production and a significant shift in urban forest recruitment and community dynamics from contemporaneous rural sites. Our experiment does not support the blanket statement that seed predation and removal is greater in urban forests. Instead, over the three years of our experiment, urban forest sites experienced moderately high and sustained seed predation. This temporal pattern differed from the interannual variability in seed removal rates detected in rural forest sites. Additionally, we found that the removal of *A. rubrum*, the native maple species, was greater than two non-native seed species. These findings correlate with removal preference in non-urban preference studies, and suggest that seed predation preference may act as an additional biotic filter that contributes to the competitive advantage for non-native plants in urban habitats.

### ***Functional shifts in urban seed predation dynamics?***

It is clear that seed predation in urban forests may deviate from temporal patterns of seed removal in rural forests, but the mechanisms driving this change are not. Seed predation patterns in temperate deciduous forests respond to seed production and mast years (e.g. Orrock et al. 1996, Schnurr et al. 2002), as seed predation may significantly decrease one year after low acorn production years and increase following mast years. Similar response patterns between mast years and seed predation were observed in the rural sites of our study. A concurrent seed dispersal study (Chapter 2) and acorn mast inventory conducted at Black Rock Forest (Schuster, W., *Personal Communication*, January 23, 2018) confirm mast years for *Q. rubra* in 2014, 2015, and 2017 in nearby rural forest sites. In 2016, rural forest *Q. rubra* acorn production was low and corresponded with reduced seed predation in 2017. There was, however, no observed decrease in *Q. rubra* acorn production in urban forest sites in 2016.

More research conducted across multiple cities will be required, but our findings potentially signal desynchronized mast dynamics between urban and rural sites. It is important to note that masting may not always be synchronized, even at local spatial scales (Wang et al. 2017), and such differences may not be generalizable. An alternative hypothesis for the observed patterns in seed removal is that there is a fundamental shift in mast dynamics and annual seed production in urban forests. Specifically, lower interannual variation in total seed production could support larger and or more constant granivore populations. Increased temperature and longer growing seasons, atmospheric carbon, and nitrogen deposition increases the growth and productivity of some plant species (e.g. Gregg et al. 2003, O'Brien et al. 2012, Zhao et al. 2016). This may impact mast and community dynamics. Atmospheric nitrogen deposition (Lovett et al. 2000, Gregg et al 2003), has been reported to increase annual oak seed production and alter pre- and post-dispersal seed predation dynamics (Bogdziewicz et al. 2016). Urban oak-hickory forests

may be decoupled from regional mast patterns and experience elevated and less variable seed production for these reasons.

The observed patterns of seed predation may also result from urban-driven differences in seed predator abundance, composition, and behavior, independent of changes in forest mast dynamics. Consumer abundance frequently determines seed removal rates (e.g. Ostfield et al. 1997, Zwolak et al. 2010, Mattos et al. 2013) and studies have observed greater abundance of granivores in urban sites (Parker and Nilon 2008). Greater abundances of granivores may be the result of increased resource availability in cities. It has been suggested that increased resource availability may be an important driver for functional shifts in urban ecosystems (Shochat et al. 2006). For example, in cities, the abundance of human-generated food resources, such as human refuse or bird feeders, may support larger granivore populations, void of bottom-up effects, and shift community compositions (Chace and Walsh 2006, Parker and Nilon 2008, Robb et al. 2008, Galbraith et al. 2015). Community shifts to synurbic small mammal and bird species are also observed in cities. For birds, such changes include an increase in generalists and granivorous species (Chace and Walsh 2006). Other granivores, such as squirrels, have been found to be more vigilant foragers in urban sites (Bowers et al. 1996, Parker and Nilon 2008, Sarno et al. 2015), a finding that may represent the decoupling of predator-prey relationships in cities, with the potential to have broad effects on ecological processes (e.g. Faeth et al. 2005, Rodewald et al. 2011). Additionally, changes in habitat composition and structure, including the presence of invasive plants, may alter foraging behavior by granivores in both space and time (Guiden and Orrock 2017, Bartowitz and Orrock 2016).

Regardless of the mechanism(s), our experiment signals that the interannual variation of seed predation is altered in these urban environments. Urbanization has been hypothesized as a driver of biotic homogenization of ecological communities (McKinney 2006). Might there be a similar functional homogenization that occurs in urban natural areas? Moving forward, research

should be expanded to consider the interaction between multiple community processes related to seed predation, including the relationship between regional and urban-rural mast dynamics, granivore community composition, and interannual shifts in granivore populations. Such research may contribute to understanding functional ecology in urban ecosystems and contribute to our understanding of urban adaptations and their potential microevolutionary consequences (Johnson and Munshi-South 2017).

***Preference for native species and evidence of enemy release?***

Our experiment did not explicitly test seed-predator preference; however, the observed species-specific seed removal rates align with preference studies conducted in temperate deciduous forests. We observed distinct, species-specific patterns of removal. Furthermore, the intensity and temporal patterns of seed removal differed between urban and rural sites, but the relative rank of species-specific removal did not. Patterns of seed removal have been determined to be species-specific (Meiners and Stiles 1997), and preference for large seeded species may be higher (Price 1983, Moles et al. 2003). Within temperate forests, mast dynamics may also influence post-dispersal seed fate (Lichti et al. 2013). Our results confirm these general rules and seed removal did increase with seed size, regardless of site type, except for the two non-native species. In all three years, *A. altissima* and *A. platanoides* had the lowest seed percent removal of any species, including *A. rubrum* seeds which on average weigh less. The greater removal for the smaller native *A. rubrum* over *A. platanoides*, an exotic congener, suggests a preference for native seed by granivores in both urban and rural forests.

Given the reported increased abundance of granivorous and generalist species in urban forests (e.g. Chace and Walsh 2006), we hypothesized that in urban forest sites there would be less discrimination between species and relatively greater observed seed removal for non-native

species. However, when comparing seed removal for each species, the relative rank was similar for urban and rural forests. This, as well as the lower seed predation for non-natives observed in our urban forest, has important implications for urban plant invasion and community dynamics. Both *A. altissima* and *A. platanoides* are prevalent in NYC and other urban forest natural areas (Pregitzer et al. 2018). Lower rates of seed removal may contribute to the competitive advantage of these species and support their continued dominance.

Seed predation can be an important biotic filter governing plant invasion dynamics (e.g. Reader 1993, Nunez et al. 2008, Connolly et al. 2014). Post-dispersal seed consumers have been observed to have differential effects on native and non-native species. Some non-native species may experience targeted granivory and suppression of plant establishment (Allington et al. 2013); others experience lower seed predation rates and escape from specialist and natural enemies (Pearson et al. 2011, Maron et al. 2014, Lucero and Callaway 2018). These divergent responses correspond to two competing hypotheses, “enemy release” (Keane and Crawley 2002) and “biotic resistance” (Elton 1958), which are commonly referenced to explain the success of non-native plant establishment and invasion. Our results support the enemy release hypothesis as a possible driver of non-native woody plant establishment success. There are multiple experiments that depict the competitive advantage of *A. platanoides* over native congeners (e.g. Galbraith-Kent and Handel 2012), including lower observed seed predation rates (Meiners 2005). These factors, which extend from seed to seedling to adult phases in plant life history, may synergize a plant’s competitive advantage and successful invasion (Meiners 2005, Galbraith-Kent and Handel 2012).

### ***Implications for conservation and advancing a mechanistic urban ecology***

Urban forested natural areas provide 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). These urban greenspaces need careful management. The long-term sustainability of ecologically robust urban natural areas depends on the recruitment of native tree species. As urban ecology research advances from descriptive to mechanistic-based studies, we are beginning to identify ecological barriers to recruitment at different life stages. These findings advance urban ecology and provide practitioners with knowledge to manage urban ecosystems sustainably (Piana et al. 2019). For example, cities worldwide have established ambitious urban forest initiatives, such as the MillionTreesNYC Initiative, that cite canopy expansion and planting goals (Nilon et al. 2017). The work of ICLEI, a worldwide consortium for urban environmental improvements, includes urban forest initiatives (ICLEI 2019). However, planting is resource intensive and does not leverage the natural processes of forest dynamics, including natural regeneration, that are commonly associated with rural forest management. For urban forest managers who wish to maintain or increase native species in the canopy, can natural regeneration be relied upon? Or is planting the only option? Our experimental results support the conclusion that effects of seed predation must be considered both when establishing native species and limiting non-native plant invasion. Strategies focused on natural regeneration may be handicapped and require supplemental plantings of targeted species.

In their call for mechanistic urban ecology, Shochat and colleagues (2006) recognized the potential for urban conditions to shift ecological processes through increased resource availability and disrupted trophic interactions. Our findings support this perspective and point towards important functional shifts in urban forest ecosystems. It has been proposed that urban ecosystems might be model systems or harbingers for the fate of global ecosystems (Grimm et al. 2008). Identifying the specific socio-ecological factors that drive the observed changes in seed predation will allow us to determine if non-urban forests may be at risk for similar functional



changes as a result of anthropogenic forces. The contribution of seed predation to overall recruitment limitation in urban and human-impacted plant populations needs continuing attention.

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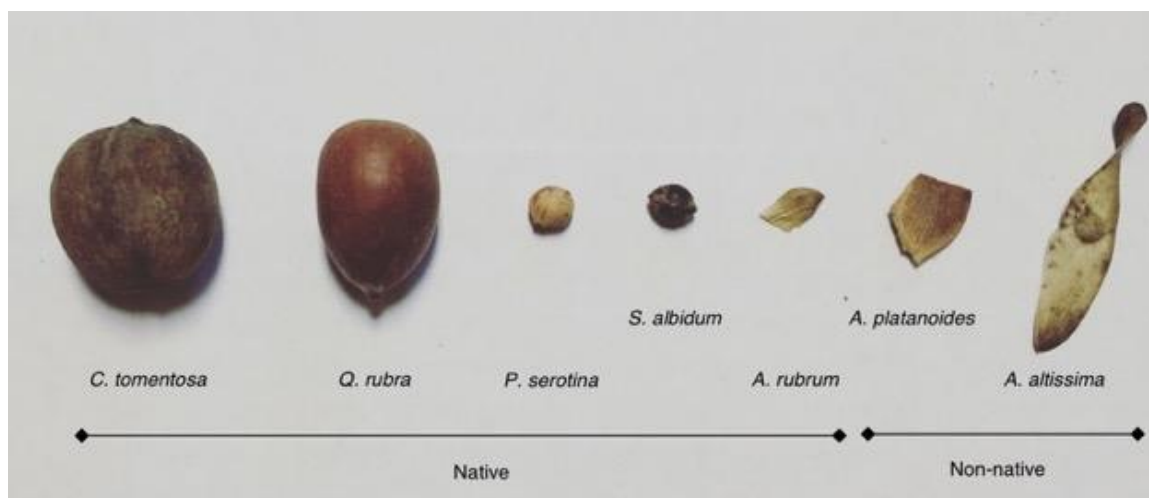
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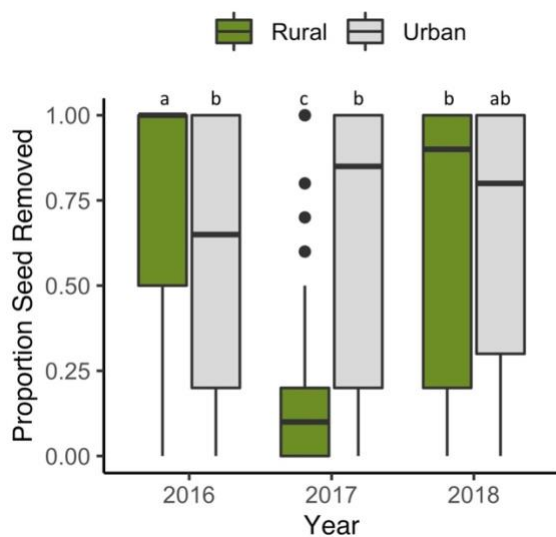
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## Figures



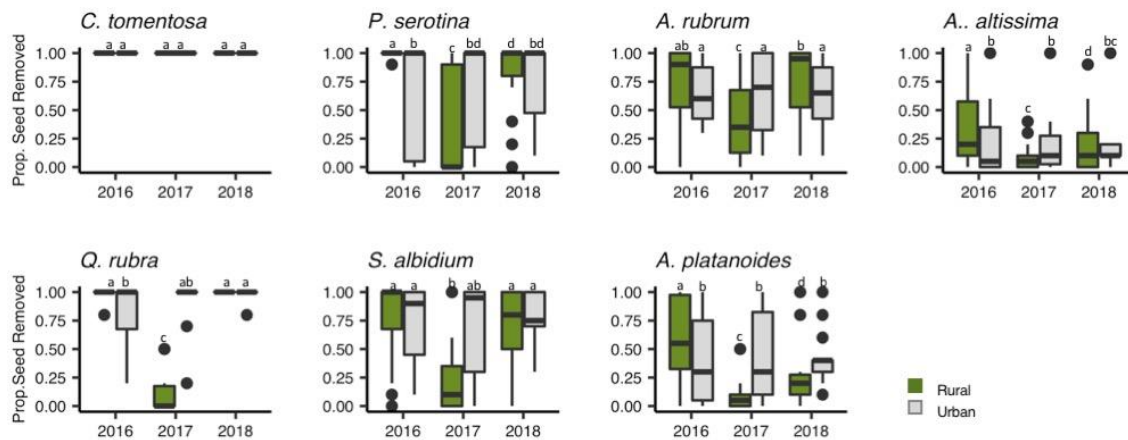
**Figure 1** Seed removal was compared between eight tree species, native and non-native, that are common to urban and rural oak-hickory forests in the northeast U.S. Species were selected to represent a range of seed size and dispersal modes.



**Figure 2** Seed removal, by year, in urban (grey) and rural (green) forest sites (all species pooled).

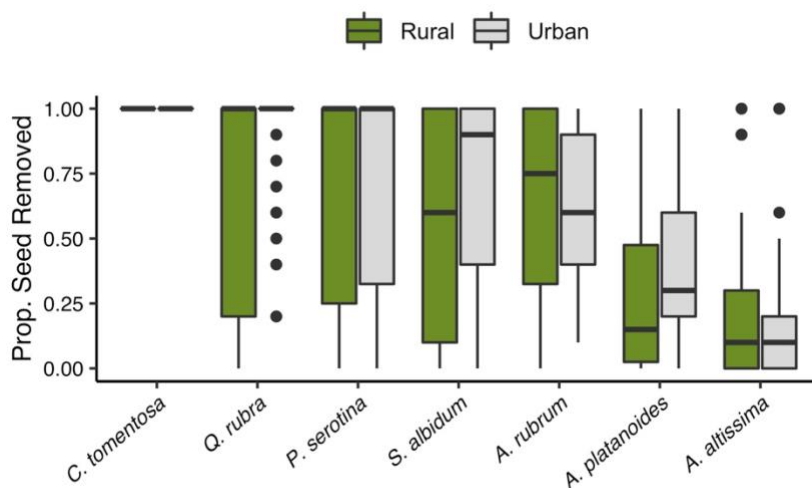
Responses that are not significantly different, according to the GLMM, share the same letter ( $P < 0.05$ ). Boxes indicate the interquartile range (25<sup>th</sup> and 7<sup>th</sup> percentile) and the line shows the median. Error bars show  $\pm 1.5$  times the interquartile range to the 25<sup>th</sup> and 75<sup>th</sup> percentiles. Outlier points are beyond 1.5 times the interquartile range.





**Figure 3** Species-specific seed removal, by year, in urban (grey) and rural (green) forests.

Responses that are not significantly different, according to the GLM, share the same letter ( $P < 0.05$ ). Boxes indicate the interquartile range (25th and 7th percentile) and the line shows the median. Error bars show  $\pm 1.5$  times the interquartile range to the 25th and 75th percentiles. Outlier points are beyond 1.5 times the interquartile range.



**Figure 4** Total species-specific seed removal in urban (grey) and rural (green) forests (all years pooled). Native study species are ordered by average seed mass from left to right. The average seed mass of the two non-native species, *A. altissima* and *A. platanoides* (far right), is greater than the native *A. rubrum*. Boxes indicate the interquartile range (25th and 7th percentile) and the line shows the median. Error bars show  $\pm 1.5$  times the interquartile range to the 25th and 75th percentiles. Outlier points are beyond 1.5 times the interquartile range.

## **Supplemental Material**

**Appendix S1:** Study site description and map.

**Table S1:** Summary of impervious cover and human population density in surrounding areas of study sites.

**Figure S1.** Map of study sites, impervious cover, and human population density.

**Appendix S2:** Model results.

**Table S1:** AIC model selection of explanatory variables for all-species and species-specific seed removal.

**Table S2:** GLMM results for the most parsimonious models for all species and species-specific seed removal.

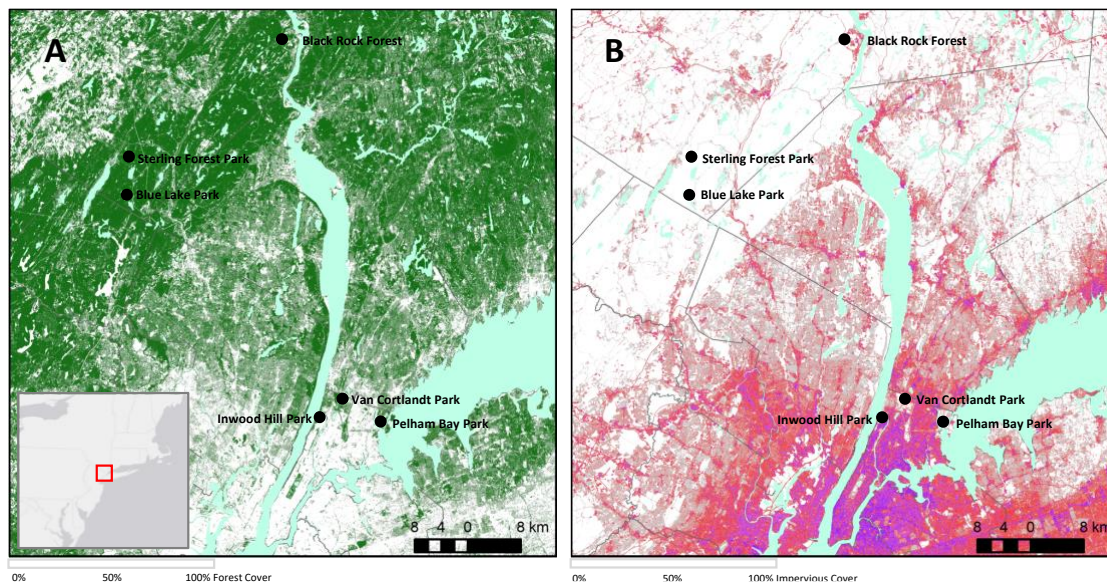
**Table S3:** GLM results for seed removal among species in urban and rural sites (all-years pooled).

## Appendix S1

**Table S1** Study Site Descriptions. Urban conditions were defined by population density (U.S. Census Bureau 2012) and percent impervious cover (USGS 2011). Each of these conditions was assessed at two buffer distances from each study site.

Site	Type	Human Population		% Impervious	
		0.5 km	2.0 km	0.5 km	2.0 km
Van Cortlandt Park	Urban	257.6	77541.7	10.1	27.7
Pelham Bay Park	Urban	246.8	3508.1	7.2	35.6
Inwood Hill Park	Urban	1073.6	121354.2	15.9	33.1
Black Rock Forest	Rural	0.0	486.0	0.8	3.6
Sterling Forest Park	Rural	0.0	167.0	0.1	0.3
Blue Lake Park	Rural	0.0	65.0	0.2	0.4

## Appendix S1



**Figure S1** Study site locations in New York City and New York Highlands region. Urban and rural forest sites were differentiated by (A) percent regional forest canopy cover and (B) percent impervious cover (National Land Cover Database, Homer et al. 2015).

## Appendix S2

**Table S1** AIC model selection of explanatory variables for all-species and species-specific seed removal. We asked how site type, year, and their interaction influenced seed removal. Most parsimonious models are bolded, with those less than two AIC units considered equally parsimonious.  $\Delta_i$  (AIC) =  $AIC_i - \min(AIC)$ ;  $w_i$  (AIC) = the rounded Akaike weights.

Model	Fixed Effect	AIC <sub>i</sub>	$\Delta_i$ (AIC)	$W_i$ (AIC)
<i>All Species</i>	Null (Random Effects Only)	4889.468	974.0	<0.001
	Site Type	4888.135	972.7	<0.001
	Year	4411.739	496.3	<0.001
	Site Type + Year	4410.409	494.9	<0.001
	Site Type * Year	3915.477	0.0	1.000
<i>Ailanthus altissima</i>	Site Type	636.4802	35.5	<0.001
	Year	618.3740	17.3	<0.001
	Site Type + Year	618.0555	17.0	<0.001
	Site Type * Year	601.0256	0.0	1.000
<i>Acer platanoides</i>	Site Type	826.5611	114.1	<0.001
	Year	792.6127	80.1	<0.001
	Site Type + Year	776.6802	64.2	<0.001
	Site Type * Year	712.5041	0.0	1.000
<i>Acer rubrum</i>	Site Type	789.9393	63.1	<0.001
	Year	759.0550	34.2	<0.001
	Site Type + Year	761.0550	32.2	<0.001
	Site Type * Year	726.8113	0.0	1.000
<i>Carya tomentosa</i>	Site Type	4	6.0	0.644
	Year	6	4.0	0.237
	Site Type + Year	8	2.0	0.087
	Site Type * Year	10	0.0	0.032
<i>Prunus serotina</i>	Site Type	1137.8598	131.0	<0.001
	Year	1030.8360	133.0	<0.001
	Site Type + Year	1032.8310	238.0	<0.001
	Site Type * Year	899.8774	0.0	1.000
<i>Quercus rubra</i>	Site Type	815.3453	545.9	<0.001
	Year	593.8610	324.4	<0.001
	Site Type + Year	459.0778	189.6	<0.001
	Site Type * Year	269.4471	0.0	1.000
<i>Sassafras albidum</i>	Site Type	960.0970	120.6	<0.001
	Year	906.3043	66.8	<0.001
	Site Type + Year	878.8151	39.3	<0.001
	Site Type * Year	839.5028	0.0	1.000

## Appendix S2

**Table S2** GLMM results for the most parsimonious models for all species and species-specific seed removal (Fig. 2 and Fig. 3). Significance levels are reported as: †  $P < 0.10$ ; \*  $P < 0.05$ ; \*\*  $P < 0.001$ ; \*\*\*  $P < 0.001$ .

Model	Fixed Effect	Estimate	Std. Error	z value
<i>All Species</i>	Intercept***	2.2922	0.9385	2.442
	Urban***	-1.0001	0.2976	-3.360
	Year2017***	-3.3231	0.1263	-26.321
	Year2018***	-0.7837	0.1120	-6.997
	Urban:Year2017***	3.4003	0.1645	20.667
	Urban:Year2018***	1.0378	0.1543	6.724
<i>Acer platanoides</i>	Intercept*	0.3594	0.1515	2.372
	Urban**	-0.6730	0.2138	-3.148
	Year2017***	-2.8323	0.3168	-8.940
	Year2018***	-1.5490	0.2324	-6.665
	Urban:Year2017***	2.8550	0.3819	7.476
	Urban:Year2018***	1.5032	0.3158	4.760
<i>Acer rubrum</i>	Intercept***	1.0692	0.1709	6.257
	Urban*	-0.5227	0.2305	-2.268
	Year2017***	-1.4979	0.2290	-6.540
	Year2018	0.2160	0.2489	0.868
	Urban:Year2017***	1.5704	0.3175	4.946
	Urban:Year2018	-0.1920	0.3316	-0.579
<i>Quercus rubra</i>	Intercept***	4.4886	0.7111	6.313
	Urban***	-2.7970	0.7402	-3.779
	Year2017***	-6.6859	0.7532	-8.876
	Year2018	15.6297	1056.4949	0.015
	Urban:Year2017***	7.7262	0.8405	9.192
	Urban:Year2018	-12.8328	1056.4952	-0.012
<i>Prunus serotina</i>	Intercept***	5.187	1.003	5.173
	Urban***	-4.444	1.015	-4.377
	Year2017***	-5.931	1.015	-5.841
	Year2018***	-3.617	1.022	-3.540
	Urban:Year2017***	6.035	1.041	5.799
	Urban:Year2018***	4.095	1.050	3.901
<i>Ailanthus altissima</i>	Intercept***	1.0692	0.1709	6.257
	Urban*	-0.5227	0.2305	-2.268
	Year2017***	-1.4979	0.2290	-6.540
	Year2018	0.2160	0.2489	0.868
	Urban:Year2017***	1.5704	0.3175	4.946
	Urban:Year2018	-0.1920	0.3316	-0.579
<i>Sassafras albidum</i>	Intercept***	1.2528	0.1793	6.988
	Urban	-0.3248	0.2439	-1.331
	Year2017***	-2.4115	0.2504	-9.631
	Year2018*	-0.5345	0.2395	-2.232
	Urban:Year2017***	2.1518	0.3389	6.349
	Urban:Year2018*	0.7961	0.3402	2.340
<i>Carya tomentosa</i>	Intercept	2.812e+01	2.447e+05	0
	Urban	-1.585e-07	2.643e+05	0
	Year2017	1.585e-07	1.580e+05	0

	Year2018	2.173e-22	2.596e+05	0
	Urban:Year2017	NA	NA	NA
	Urban:Year2018	1.585e-07	2.852e+05	0



## Appendix S2

**Table S3** GLM results for seed removal among species in urban and rural sites (all-years pooled)

(Fig. 4). Significance levels are reported as: †  $P < 0.10$ ; \*  $P < 0.05$ ; \*\*  $P < 0.001$ ; \*\*\*  $P < 0.001$ .

Model	Fixed Effect	Estimate	Std. Error	z value
<i>All years pooled</i>	Intercept***	-0.84730	0.09391	-9.023
	A. rubrum***	1.42588	0.12986	10.980
	A. altissima**	-0.39478	0.13953	-2.829
	C. tomentosa	17.96568	333.38082	0.054
	P. serotina***	1.76618	0.13380	13.200
	Q. rubra***	1.67702	0.13257	12.650
	S. albidum***	1.10049	0.12785	8.608
	SiteType_Urban***	0.52604	0.12813	4.105
	A.rubrum:Urban**	-0.52604	0.18030	-2.918
	A.altissima:Urban***	-0.75334	0.19811	-3.803
	C.tomentosa:Urban	-0.52604	388.78551	-0.001
	P.serotina:Urban**	-0.51694	0.18607	-2.778
	Q.rubra:Urban***	1.14327	0.22709	5.034
	S.albidum:Urban	0.13964	0.18174	0.768