Factors driving natural regeneration beneath a planted urban forest

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ABSTRACT

Cities around the world are investing in urban forest plantings as a form of green infrastructure. The aim is that these plantations will develop into naturally-regenerating native forest stands. However, woody plant recruitment is often cited as the most limiting factor to creating self-sustaining urban forests. As such, there is interest in site treatments that promote recruitment of native woody species and simultaneously suppress woody non-native recruitment. We tested how three, common site treatments—compost, nurse shrubs, and tree species composition (six-species vs. two-species)—affected woody plant recruitment in 54 experimental plots beneath a large-scale tree planting within a high-traffic urban park. We identified naturally regenerating seedling and sapling species and measured their abundance six-years after the site was planted. This enabled us to examine initial recruitment dynamics (i.e. seedlings) and gain a better understanding of seedling success as they transition to the midstory (i.e. saplings). Seedling and sapling recruitment (native and total) was greater in areas with higher canopy cover. The combination of the nurse shrub treatment with compost and species composition (six-species) treatments increased seedling recruitment by 47% and 156%, respectively; however, the nurse shrub treatment by itself decreased seedling recruitment by 5% and native seedling recruitment by 35%. The compost treatment alone had no effect on the total number of recruits but resulted in 76% more non-native seedlings. The sizes of these treatment effects were strongly dependent on whether the forest plantings were in open areas, versus areas with existing tree canopy, the latter condition facilitating recruitment. Our findings therefore suggest that combinations of site treatments, paired with broad canopy tree species, may be most effective for promoting regeneration of native species resulting in more self-sustaining urban forests.

1. Introduction

Urbanization of forests and open areas is rapidly increasing around the world (Nowak et al., 2002). As cities grow denser and expand their footprint, urban trees and forests will become an increasingly important way to enhance quality of life through their provision of ecological, economic, health, social, and aesthetic services (Pataki et al., 2011). In recognition of the value of these services, many cities are investing in afforestation efforts and restoring degraded forests, with the goal of generating self-sustaining native forests (Sullivan et al., 2009; McPhearson et al., 2010; Clarkson et al., 2012; PlaNYC Reforestation Overview, 2015). Although cities are dedicating substantial resources to these projects, there is limited information on restoring, creating, and managing new urban forests so that they develop toward sustainable entities.

Large-scale tree plantings have been successful in establishing native forests in degraded tropical lands (Parrotta, 1992 Guariguata et al., 1995; Parrotta et al., 1997; Brockerhoff et al., 2008), but urban systems present a unique set of circumstances. These include frequent human-caused disturbances (Rebele, 1994; Grimm et al., 2000), modified soils (Craul, 1985; Pavao-Zuckerman, 2008), high edge-to-interior ratios, and invasion from introduced plant species (Alson and Richardson, 2006; Cadotte et al., 2017) all of which have the potential to negatively impact restoration goals (Cadenasso and Pickett, 2001). Few studies to date have examined forest development in urban areas post-planting and of those that do, most cite lack of native woody plant recruitment as one of the biggest hurdles to achieving a sustainable restoration (McClanhan and Wolfe, 1992; Robinson and Handel, 2000; Oldfield et al., 2013; Labatore et al., 2017).

Woody plant recruitment is an important component of forest development (Greene et al., 1999; Aide et al., 2000). By examining species composition of woody plants regenerating in the understory of new tree

plantings, it is possible to infer the future species composition and the capacity of the plantings to self-perpetuate (Franklin and DeBell, 1988). However, in urban settings planted species often do not recruit, or recruit sparsely and instead local seed sources from nearby ex-situ trees fill in gaps (Robinson and Handel, 2000). This has implications for reforestation projects with the goal of steering species composition towards a "native-dominated" forest (PlaNYC Reforestation Overview, 2015; Morgenroth et al., 2016) because local seed sources are often from non-native, invasive species and not the desired planted species. These projects favor the regeneration of native or planted tree species over non-native invasive ones because invasive trees have been found to negatively impact biodiversity (Van Wilgen and Richardson, 2014), forest structure (Asner et al., 2008), and ecosystem services (Richardson et al., 2014).

Some of the factors found to limit recruitment of planted tree species in urban settings include competition at the ground level in the form of weeds or other ground cover (Rawlinson et al., 2004; Ruiz and Aide, 2006) and above-ground competition in the form of canopy cover and shade (Nakamura et al., 2005; Michalak, 2011). Degraded soils can be a barrier to regeneration in urban settings as soil nutrients, beneficial microbes such as mycorrhizae, and moisture may be limiting (White and McDonnell, 1988; Rebele, 1994; Pavao-Zuckerman, 2008; Oldfield et al., 2015; Pregitzer et al., 2016). In addition, soil compaction may limit root respiration (Craul, 1985). To ameliorate these inhospitable urban conditions land managers will often install costly and time-consuming site treatments prior to planting to create a more favorable environment for the desired planted species (Castro et al., 2002; Saebo and Ferrini, 2006; Oldfield et al., 2014; Dominguez et al., 2015). Compost amendments are one such site treatment with the potential to improve site conditions by increasing the soil's water holding capacity, nutrient availability, and microbial biomass (Cogger, 2005; Davidson et al., 2006; Oldfield et al., 2014). Nurse shrubs are another site treatment expected to improve microclimatic conditions in harsh environments by decreasing soil temperatures, increasing soil moisture, providing organic matter in the form of leaf litter, and in some cases increasing soil nitrogen through fixation (Shumway, 2000; Gomez-Aparicio et al., 2004; Castro et al., 2002). Finally, diversity or species composition of planted trees is another site treatment with the potential to enhance tree growth, alter understory light conditions, and in the case of nitrogen-fixing species, increase available nitrogen (Guariguata et al., 1995; Piotto, 2008).

Understanding the competitive and environmental barriers to woody plant recruitment, and the potential for site treatments to reduce these barriers for target natives, is vital to the successful implementation and maintenance of afforestation and reforestation sites. However, much of the existing research on site treatments and their impact on woody plant recruitment is from high-stress Mediterranean or tropical climates rather than urban areas (Guariguata et al., 1995; Gomez-Aparicio et al., 2004; Piotto, 2008; Castro et al., 2002; Dominguez et al., 2015), has conflicting results (Nakamura et al., 2005; Michalak, 2011), and/or only examined short-term dynamics (< 5 y) and hence may not capture factors that can take several years to have an effect, such as soil conditions (Rawlinson et al., 2004; Ruiz and Aide, 2006). Furthermore, urban forest site treatments are intended to improve environmental conditions such as soil temperature, moisture, and available light for woody plant recruits, but commonly these conditions are not measured, making it difficult to tease out how site treatments translate to outcomes (Oldfield et al., 2013).

To examine how site treatments impact environmental conditions and natural regeneration we explored woody plant recruitment of both planted and non-planted tree species beneath a large, experimental, urban afforestation site in New York City, USA. Specifically, we examined the abundance and composition of natural regeneration in relation to site treatments and conditions known to affect recruitment (Kostel-Hughes and Young, 1998; Prach et al., 2001; Rawlinson et al., 2004; Nakamura et al., 2005; Ruiz and Aide, 2006; Michalak, 2011).

We assessed several site treatments including compost (amended with compost or not amended), planted nurse shrubs (presence or absence), and planted tree species composition (six-species or two-species) (Oldfield et al., 2015). Our study evaluated woody plant recruitment six years after the initial planting of 3–5 year-old woody saplings. By this point in the experiment, planted trees were approximately 10 years old and five of the six planted tree species were producing seeds (Oldfield et al., unpublished dataset). We assessed recruited seedlings and saplings of both the planted species, as well as non-planted species, to gain insights from a 'snap-shot' set of observations into the temporal dynamics as woody recruits shift from the seedling to sapling size classes.

Using these site treatments, coupled with measurements of environmental conditions, we asked the following questions:

i To what extent is natural regeneration occurring within establishing afforestation areas?
ii Do site treatments increase woody plant recruitment and direct species composition towards a native-dominated system, and if so, is this the result of improved environmental conditions?

2. Methods

2.1. Site description and experimental design

We conducted this study within long-term research plots established in partnership with AECOM, Inc., the Yale School of Forestry and Environmental Studies, and the New York City Department of Parks and Recreation (NYCDPR) at Kissena Corridor Park, a recently reforested 40-ha urban park in Queens, NY (40°44′N, 73° 49′W) (Felson et al., 2013a,b). The US Natural Resource Conservation Service (NRCS) classified the soils as the Laguardia-Ebbets complex, which are characterized as well-drained coarse sandy loam with 10% human-transported material (NRCS, 2016); a complete soil analysis of the site can be found in Oldfield et al. (2014). Average temperatures in July and January are 24.9 °C and 0.2 °C, respectively; mean annual rainfall is 109.12 cm (NOAA, 2016).

The experimental plots at Kissena Corridor Park are dubbed the New York City Afforestation Project (NY-CAP) and are part of the MillionTreesNYC initiative. Launched in 2007 by New York City, the MillionTreesNYC Initiative allocated $400 million to NYCDPR over 10 years to plant 1,000,000 trees in parklands, natural areas, and in street tree pits (PlaNYC Reforestation Overview, 2015). As part of this initiative, in the fall of 2010, 54 experimental plots were installed within Kissena Corridor Park's interior (Fig. 1). Experimental plots are divided between the east (n = 26) and west (n = 28) sides of the park. While pre-planting tree cover at Kissena Corridor Park was generally sparse, stands of *Robinia pseudoacacia* (black locust), *Rhus typhina* (staghorn sumac), *Prunus serotina* (black cherry) and a few large individuals of *Acer saccharinum* (silver maple) were present on the east side of the park prior to NY-CAP installation (Fig. 1). The presence of adjacent forest stands coupled with less human traffic distinguished the east side from the more heavily-used and less-forested west side. To account for these differences between the two areas of the park, we grouped plots on the east and on west sides separately and will hereafter refer to them as "forested" and "open" blocks respectively. Prior to planting and plot installation, Kissena Corridor Park was densely overgrown with non-native invasive herbaceous species, such as *Artemisia vulgaris* (common mugwort) as well as native old-field species like *Solidago canadensis* (Canada goldenrod) (Oldfield et al., 2014).

The NY-CAP experimental plots test how three site treatments—compost (amended with compost or not amended), co-planting with nurse shrubs (presence or absence), and species composition (six-species or two-species)—affect afforestation efforts (Felson et al., 2013b; Oldfield et al., 2014; Oldfield et al., 2015). Replication is uneven and is outlined in Appendix A Table A1.

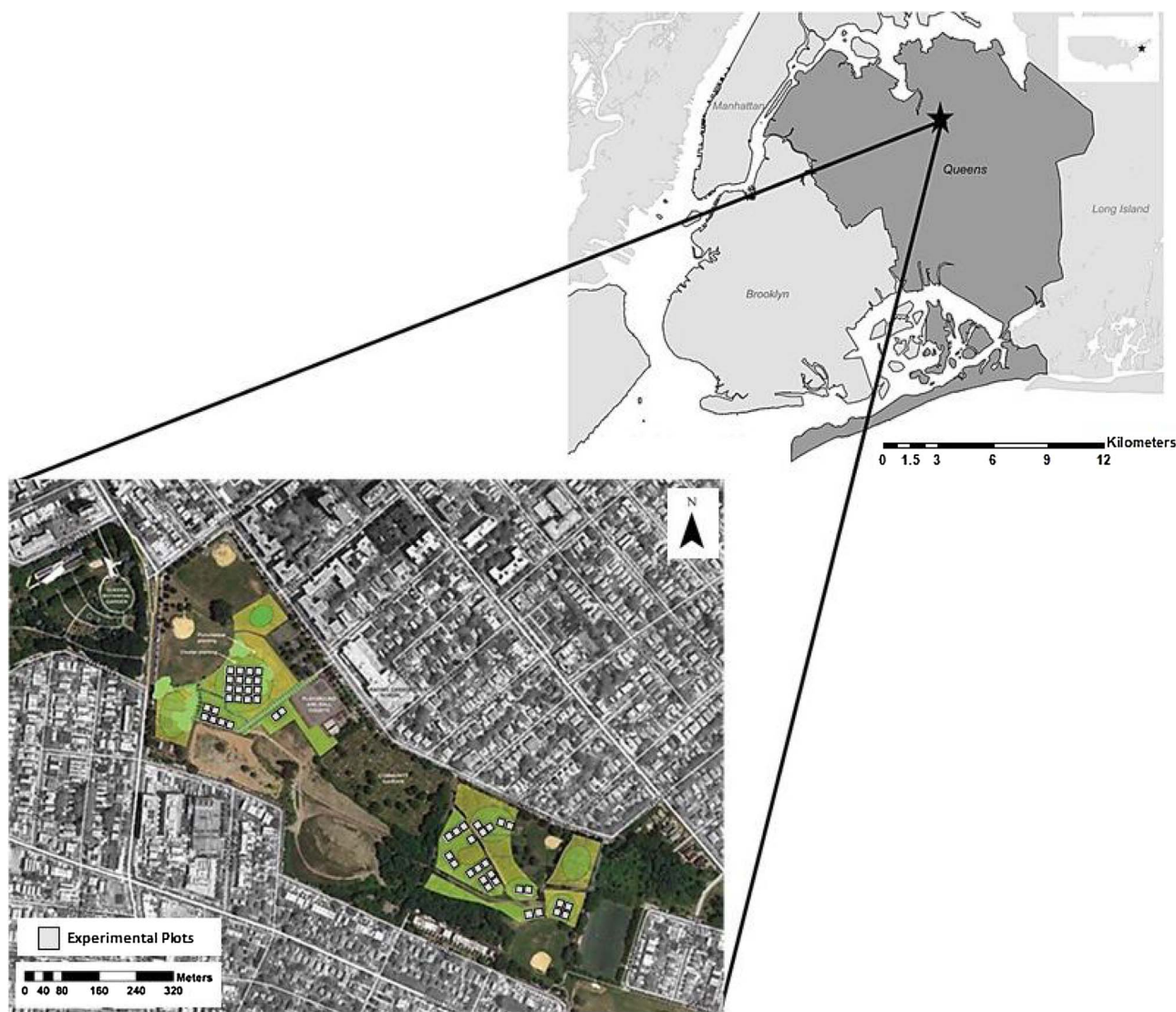In 2010, each 15 × 15 m plot was planted with 56 trees 2.1-m apart

Fig. 1. Aerial view of Kissena Corridor Park with experimental plots in Queens, New York, U.S.A.

from each other (Fig. 2). As NY-CAP is located in a heavily used public park, trees were planted in an offset grid (quincunx pattern) to both blend into the park landscape and to facilitate research (Fig. 2a and b; Felson et al., 2013a). Trees were planted by landscape contractors according to specifications outlined by the NYCDPR through a contractual agreement. Two-species plots were planted with 28 *Tilia americana* (American basswood) and 28 *Quercus rubra* (northern red oak) (Fig. 2a). Six-species plots were planted with eight individuals of *T. americana* and *Q. rubra*, and ten individuals each of *Celtis occidentalis* (hackberry), *Prunus serotina*, *Quercus alba* (white oak), and either *Carya glara* (pignut hickory) on the open west side or *Cayra laciniosa* (shell-bark hickory) on the forested east side (Fig. 2b). The use of two different, but similar, hickory species was owing to limited nursery availability. Plots with the shrub treatment were planted with a mix of native shrubs including *Sambucus canadensis* (elderberry), *Hamamelis virginiana* (American witch hazel), *Lindera benzoin* (spicebush), *Cornus racemosa* (gray dogwood), and *Viburnum dentatum* (arrowwood viburnum) between planted trees (41 shrubs per plot) as well as native herbaceous species including *Apocynum cannabinum* (dogbane), *Asclepias syriaca* (common milkweed), and *Panicum virgatum* (switchgrass). Both shrubs and herbaceous materials were installed at the same time as the tree planting. The compost treatment plots were amended with compost at a rate of 2.5 m^3 per 100 m^2. Compost was incorporated into

the soil with a rototiller to 15 cm depth over the full 15 × 15 m plot. The commercial compost consisted of a blend of nutrient-rich biosolids and clean, ground wood chips. Felson et al. (2013b) provides an overview of the project design and set-up and Oldfield et al. (2014) provides details about trees species selection, site preparation, installation, and compost analysis.

2.2. Measurement of natural regeneration within the plantings

We sampled naturally regenerating seedlings and saplings across all 54 NY-CAP plots in June 2016. Natural regeneration in our plots ranged from recently germinated seedlings to established trees (diameter at breast height (1.37 m) was > 10 cm). We distinguished between "seedlings" and "saplings" based on height: seedlings included any woody plant recruit ≤1.3 m in height and saplings included any recruit > 1.3 m in height. Height is commonly used to distinguish between seedlings and saplings (Chen et al., 1992; Montgomery and Chazdon, 2001; Hall et al., 2003).

We sampled all woody sapling recruits in a center 10 × 10 m plot nested inside the original 15 × 15 m plot, which allowed for a 2.5 m buffer from the plot edge (Fig. 2). We used detailed plot planting maps to distinguish between planted trees and shrubs and woody recruits. For each sapling, we recorded species and diameter at breast height.

Fig. 2. Plot layout of the planted trees, shrubs, and herbaceous material in (a) two-species plots and (b) six-species plots. Natural regeneration measurements were taken within a 10×10 m plot indicated by the dashed lines.

Woody seedling recruitment within the plots was sampled within a 52-m^2 belt transect that ran diagonally from one plot corner to the opposite plot corner (two, 2-m wide transects per plot, which together formed a "cross" across the square 10×10 m area). Within each belt transect we identified individual seedlings to species. Seedling counts within these transects were scaled up to the plot level to make plot-by-plot comparisons.

2.3. Quadrat level sampling

To capture understory cover, we nested two 1-m^2 quadrats within each belt transect 2 m into the 10×10 m plot from a corner tree. Within each quadrat we estimated the percent cover for herbaceous plants, woody seedlings, leaf litter, woody debris, rocks, dumping (human garbage, construction debris, or other anthropogenic materials), and bare ground out of 100% of the quadrat. Within these same quadrats we measured a suite of environmental conditions that are known to affect seedling establishment and growth. We measured volumetric water content as a metric for soil moisture using a time-domain reflectometer (TDR) probe (HS2 HydroSense Soil Moisture Probe, Campbell Scientific, Logan, UT, USA) at 12 cm depth, soil temperature at 5 cm depth (HI 145 T-Shaped Soil Thermometer, Hanna Instruments, Inc., Woonsocket, RI, USA), and photosynthetically active radiation (PAR) as percent diffuse light (LI-191R Line Sensor, LiCor, Inc., Lincoln, NE, USA). We measured PAR at two heights within the quadrat: one at the ground, below the herbaceous/seedling layer, to determine the amount of light reaching the soil surface (hereafter referred to as ground-level PAR) and one above the herbaceous layer at 1 m height to determine the amount of light penetrating the canopy formed by the planted trees and naturally regenerating saplings (hereafter referred to as sub-canopy PAR). We sampled PAR measurements on overcast days between 1000 and 1400 h and calibrated readings with reference measurements in an open field with no canopy cover every 5 plots or as light conditions changed to calculate the percentage of diffuse light. We averaged quadrat measurements for percent cover, soil temperature, soil moisture, sub-canopy PAR, and ground-level PAR to calculate a final value for each plot.

2.4. Statistical analysis

We used a series of generalized linear models (GLMs) and generalized linear mixed models (GLMMs) to assess how site treatments (compost amendments, nurse shrubs, and planted tree composition) affected woody plant recruitment and species composition. We also related site treatments to environmental conditions, and then these conditions to the recruitment observations, to test whether changes in abundance and composition could be explained by improved environmental conditions as a result of the site treatments.

We expected seedlings and sapling recruits to respond differently to site treatments as a result of increased competitive pressure on saplings compared to seedlings (Good and Good, 1972), so we used them as separate response variables in our analysis. To account for the unbalanced replication in our experiment, we used GLMMs with compost, shrub, and tree composition treatments, and their interactions, as fixed effects on the number of seedlings or saplings per hectare (Oldfield et al., 2015). Plots nested within forested/open blocks were included as a random effect to account for the possibility that plots nearer to each other and within a forested/open block may be more similar to one another. Because we were interested in testing how treatments impacted seedling and sapling performance where recruitment was occurring, we excluded plots with no recruitment from our analyses and used GLMMs with a Poisson error distribution and log-link function ($n = 10$ plots for seedlings and $n = 5$ plots for saplings omitted). This method better represents how treatments impacted the magnitude of seedling and sapling recruitment and is more conservative than running analyses on our full dataset. However, when we ran the analysis with the full dataset (using a zero-inflated Poisson regression) we found that both analyses resulted in comparable treatment coefficients (see Table 2 and Appendix A Table A2 for a comparison).

To determine how site treatments steered species composition towards a native or non-native species palette, we used GLMs with a binomial error distribution with treatments and their interactions as fixed effects on the native to non-native ratio. We calculated native to non-native ratio using the number of native and non-native seedlings or saplings per hectare.

To test how site treatments impacted environmental conditions we used GLMs with site treatments (compost, shrubs, and tree composition) and their interactions as fixed effects in four different models for sub-canopy PAR, ground-level PAR, soil temperature, and soil moisture. All response variables were square-root transformed to meet the assumptions of normality.

To assess how these environmental conditions affected seedling

recruitment we used GLMMs with sub-canopy PAR and soil moisture as fixed effects on the number of seedlings per hectare. Ground-level PAR and soil temperature were excluded from this analysis to avoid issues with multicollinearity. We standardized environmental variables, given that the variables were measured with different unit scales (e.g.%PAR vs.% moisture), so that we could compare their relative effects via their model beta coefficients. We nested plot within forested/open block as our random effect variables.

To determine the relationship between environmental variables and the ratio of native to non-native recruits we used GLMs with a binomial error distribution. We set the number of native seedlings or the number of non-native seedlings per hectare as the response variable and standardized sub-canopy PAR and soil moisture as fixed effects. All GLMMs and GLMs had vif values < 0.4, indicating that collinearity was sufficiently low among predictor variables. We used R software (R Core Team, 2013) to complete all statistical analyses, and used the "glmer" function for GLMMs (Bates et al., 2015).

3. Results

3.1. Presence of natural regeneration beneath experimental tree plantings

Natural regeneration ranged from the complete absence of seedling and sapling recruitment ($n = 3$ plots) to plots with over 3,000 saplings ha^{-1} ($n = 2$ plots) and over 60,000 seedlings ha^{-1} ($n = 3$ plots). While these 3 plots with > 60,000 *Prunus serotina* seedlings have an ecological explanation (e.g., presence of nearby, large fruiting parent *P. serotina* plants), including them in our analyses violated the assumptions of our statistical tests. Therefore we dropped these plots from our analyses (including reporting of mean and error values) but this did not affect the model results (for a comparison see treatment coefficients in Appendix A Table A3 and Table 2). Overall, 95% of plots had some form of woody plant regeneration (seedlings mean ± SE = 28,99 ± 379 ha^{-1}, saplings = 1192 ± 139 ha^{-1}). Location within the park (either forested or open block) was a strong determinant of number of woody seedlings and saplings: 68% of all woody plant recruits were found in plots within the forested block (forested mean all recruits ± SE = 5247 ± 570 ha^{-1}, open = 2463 ± 506 ha^{-1}).

We found 18 species of tree seedlings and saplings regenerating (Table 1). Five of the six species that were part of the original tree planting were also present as natural regeneration; the only species not present was *Q. alba* (Table 1). Annual measurements of planted trees confirmed that within most plots, planted trees were setting fruit as early as 2012 (Oldfield et al., unpublished data). Non-planted species such as the non-natives *Morus alba* (white mulberry) and *Ailanthus altissima* (tree-of-heaven), and the natives *Robinia pseudoacacia* and *Rhus typhina*, had the highest abundances and were more evenly distributed across the plots (Table 1).

3.2. Impact of site treatments and environmental conditions on seedlings and sapling abundance and composition

Plots with nurse shrubs had 5% fewer seedlings and 8% fewer saplings than plots that did not receive the shrub treatment, but shrub effects were strongly dependent on compost treatments and species composition (GLMM, $p \leq 0.05$, Table 2, Fig. 3). When plots with shrubs were coupled with compost amendments there were 47% more seedlings (GLMM, $p \leq 0.05$, Table 2, mean with shrubs + compost = 3401 ± 879 ha^{-1}, mean shrubs + no compost = 2321 ± 537 ha^{-1}) and 41% fewer saplings than in shrub plots without compost amendments (GLMM, $p \leq 0.05$, Table 2, mean with shrubs + compost = 942 ± 211 ha^{-1}, mean with shrubs + no compost = 1329 ± 304 ha^{-1}). When plots with shrubs were coupled with the six-species treatment there were 156% more seedlings (GLMM, $p \leq 0.05$, Table 2, mean with shrubs + six-species = 4354 ± 873 ha^{-1}, mean with shrubs + two-species = 1696 ± 350 ha^{-1}) and 15% more saplings

compared with two-species plots (GLMM, $p \leq 0.05$, Table 2, mean with shrubs + six-species = 1242 ± 272, mean with shrubs + two-species = 1071 ± 275 ha^{-1}).

Compost, shrub, tree composition treatments and their interactions did steer species composition in seedlings, but their impact was less evident in saplings (Table 2). Only the compost, species composition, and compost + shrub treatment significantly decreased the ratio of native to non-native saplings recruiting (GLM, $p \leq 0.05$, Table 2). Of the three treatments, compost had the most consistent, negative effect on native recruitment in both seedlings and saplings. Specifically, native seedling recruitment was 24% lower (GLM, $p \leq 0.05$, Table 2, Fig. 4, 1330 ± 411 ha^{-1} vs. 1755 ± 436 ha^{-1}) and native sapling recruitment was 54% lower in compost plots than in no compost plots (GLM, $p \leq 0.05$, Table 2, Fig. 4, 329 ± 97 ha^{-1} vs. 719 ± 178 ha^{-1}).

Site treatments did not significantly affect the environmental variables except for the negative influence of the compost + shrub treatment on ground-level PAR. Plots with compost amendments and shrubs had significantly lower ground-level light (GLM, $p \leq 0.05$, mean ground-story PAR no compost + no shrubs = 17.8% ± 4.6, mean ground-level PAR compost + shrubs = 10.3% ± 3.2).

Independent of treatment, variation in environmental conditions among plots impacted the number and composition of woody plant recruits. Seedling recruitment decreased as sub-canopy PAR increased but increased with soil moisture (GLMM, $p \leq 0.05$, Table 3, Fig. 5). Recruitment responses to sub-canopy PAR potentially reflected competition from herbaceous groundcover, which increased with sub-canopy PAR (LM, $p \leq 0.05$, $r^2 = 0.13$). The ratio of native to non-native species decreased as both sub-canopy PAR and soil moisture increased (GLM, $p \leq 0.05$, Table 3).

4. Discussion

Land managers are investing in the creation and restoration of urban forests and woodlands. For these efforts to be sustainable with minimal human intervention, natural regeneration, especially from the planted material, is essential (Greene et al., 1999; Aide et al., 2000). We found that natural regeneration was present within our afforestation site and that the magnitude and composition of regeneration was impacted by site treatments and their interactions. Interestingly, this study did not detect a relationship between most site treatments and the environmental variables measured. However, when examined alone, increased light in the sub-canopy decreased total recruitment and increased non-native recruitment. Thus, to maximize the benefits of both environmental conditions and site treatments, we recommend that future projects include fast growing species that will achieve early canopy closure in addition to a nurse shrub treatment coupled with either compost amendments or a species-rich plant palette. However, it is important to note that use of compost may also result in a trade-off with increased recruitment from non-planted, non-native, woody species. Thus, projects aimed at achieving a native dominated stand will likely need ongoing management in the form of thinning to control invasive species and promote the establishment of desired species.

While non-native, non-planted species dominated natural regeneration at Kissena Corridor Park, our study did find native recruitment (87,371 non-native vs. 78,496 native seedlings + saplings ha^{-1}). Additionally, records of planted *T. americana, C. occidentalis, Q. rubra, and P. serotina* individuals fruiting as early as 2012 and *Q. alba* individuals in 2014 suggest that planted trees could have contributed to the native recruitment found in this study (Oldfield et al., Oldfield et al., unpublished dataset). Consistent with the literature, the non-planted species that had the highest abundances and widest distributions—*Morus alba, Ailanthus altissima,* and *Robinia pseudoacacia*—were those that disperse via wind or birds (McClanhan and Wolfe, 1992; Robinson et al., 1992; Robinson and Handel, 1993; Clark et al., 1998). Bird dispersal in urban areas has been closely linked with the availability of bird perches (McClanhan and Wolfe, 1992; Robinson and

Table 1
Origin, dispersal mechanisms, relative abundance (% of total recruitment), and distribution (% of plots) of the 18 tree species recruiting in plots at Kissena Corridor Park, New York City, New York, USA in order of decreasing abundance. Origin is either native to NY state (N) or introduced (I). Dispersal is categorized as bird (B), mammal-dispersed (M), gravity (G), wind (W) or vegetative (V). Asterisks denote species that were part of the original plant installation. (USDA NRCS, 2016).

	Common Name	Origin	Seed Dispersal Mechanism	Relative Abundance	Relative Distribution
Morus alba	White Mulberry	I	B, M	Seedlings: 15.46% Saplings: 42.31%	94.44%
*Prunus serotina**	Black cherry	N	B, G, M	Seedlings: 49.63% Saplings: 2.01%	27.78%
Robinia pseudoacacia	Black locust	N	G, B, V	Seedlings: 3.53% Saplings: 26.25%	38.89%
Ailanthus altissima	Tree of Heaven	I	W, V	Seedlings: 13.58% Saplings: 12.04%	53.70%
Rhus typhina	Staghorn Sumac	N	B, V	Seedlings: 12.78% Saplings: 11.20%	24.07%
Acer saccharum	Silver Maple	N	W	Seedlings: 0.91% Saplings: 2.84%	20.37%
*Quercus rubra**	Red Oak	N	G,M	Seedlings: 2.86% Saplings: 0	11.11%
Tilia americana *	American Basswood	N	W	Seedlings: 0.09% Saplings: 0%	1.85%
Ulmus americana	American Elm	N	W	Seedlings: 0.08% Saplings: 0.17%	3.70%
Ulmus pumila	Siberian Elm	I	W	Seedlings: 0% Saplings: 0.50%	5.56%
Populous deltoides	Eastern Cottonwood	N	W	Seedlings: 0.08% Saplings: 1.17%	12.96%
*Celtis occidentalis**	Hackberry	N	B	Seedlings: 0.11% Saplings: 0.17%	3.70%
Cayra spp. *	Hickory	N	G, M	Seedlings: 0.34% Saplings: 0%	3.70%
Cercis canadensis	Eastern Redbud	N	B, M	Seedlings: 0.07% Saplings: 0%	1.85%
Malus spp.	Apple Tree	I	M	Seedlings: 0% Saplings: 0.17%	1.85%
Acer negundo	Boxelder	N	W	Seedlings: 0.26% Saplings: 0.50%	5.56%
Acer campestre	Field Maple	I	W	Seedlings: 0.08% Saplings: 0%	5.56%

Table 2
Results from generalized linear models and generalized linear mixed models exploring the effects of pre-planting plot treatments and their interactions on recruitment in an urban afforestation project in New York City, New York, USA 6 years after tree planting. Plot treatments include co-planting with shrubs (shrub), soil compost amendments (compost), or planted tree composition (two-species or six-species plantings). Species recruiting into plots were native and introduced in origin (see Table 1 for more details). Model coefficients and standard errors significant at $p < 0.05$ are bolded. See Methods for model construction.

Treatment	Seedling Abundance ha^{-1} Coefficient ± std. error	Sapling Abundance ha^{-1} Coefficient ± std. error	Native:Non-native Seedling Ratio Coefficient ± std. error	Native:Non-native Sapling Ratio Coefficient ± std. error
Intercept	7.76 ± 0.32	6.72 ± 0.52	0.68 ± 0.02	0.13 ± 0.02
Shrub	**−0.67 ± 0.01**	**−0.04 ± 0.01**	**−1.47 ± 0.03**	−0.01 ± 0.03
Compost	−0.43 ± 0.42	−0.69 ± 0.38	**−1.27 ± 0.03**	**−0.13 ± 0.05**
Composition	0.03 ± 0.47	0.28 ± 0.38	**−0.22 ± 0.03**	**−0.22 ± 0.03**
Compost*Shrub	**0.62 ± 0.02**	**0.40 ± 0.03**	**1.06 ± 0.04**	**−0.73 ± 0.06**
Shrub*Composition	**0.63 ± 0.02**	**−0.19 ± 0.02**	**2.26 ± 0.04**	0.01 ± 0.04
Compost*Composition	0.46 ± 0.62	0.57 ± 0.54	**0.69 ± 0.04**	**−0.16 ± 0.06**
Compost*Shrub*Composition	0.01 ± 0.03	**−0.28 ± 0.04**	**−1.95 ± 0.05**	0.01 ± 0.08

Handel, 1993). Hence, by planting trees in a sparsely forested urban park, the NY-CAP has likely provided two seed sources: those directly from the planted trees (at an age when fruits/seeds produced are viable) and those sourced indirectly through bird dispersal by providing bird habitat in the form of the planted trees. Therefore, it is likely that native reforestation efforts in cities will have to accept that by establishing native trees, they will also recruit non-native plants that threaten the longevity and replacement of the native plantings.

Our study finds that compost, shrub, and species composition treatments can increase woody plant recruitment in urban sites; however, the direction of their impact varies with treatment interactions. When examined alone, shrub treatments had the unexpected effect of

decreasing the number of woody plant recruits (Table 2). However, when coupled with compost, shrubs increased woody seedling recruitment and decreased sapling recruitment. The combination of improved soil conditions from compost and shade/shelter provided by nurse shrubs may initially facilitate seedling recruitment (Gomez-Aparicio et al., 2005). However, as seedlings grow into saplings this facilitative interaction may shift to a competitive one as saplings compete with planted shrubs for limited water, nutrients, and light (Callaway et al., 1996). In our study, the combination of compost amendments and nurse shrubs resulted in significantly less ground-level light suggesting that planted shrubs may grow more densely in composted plots creating a favorable habitat for seedlings but competing with them as they grow
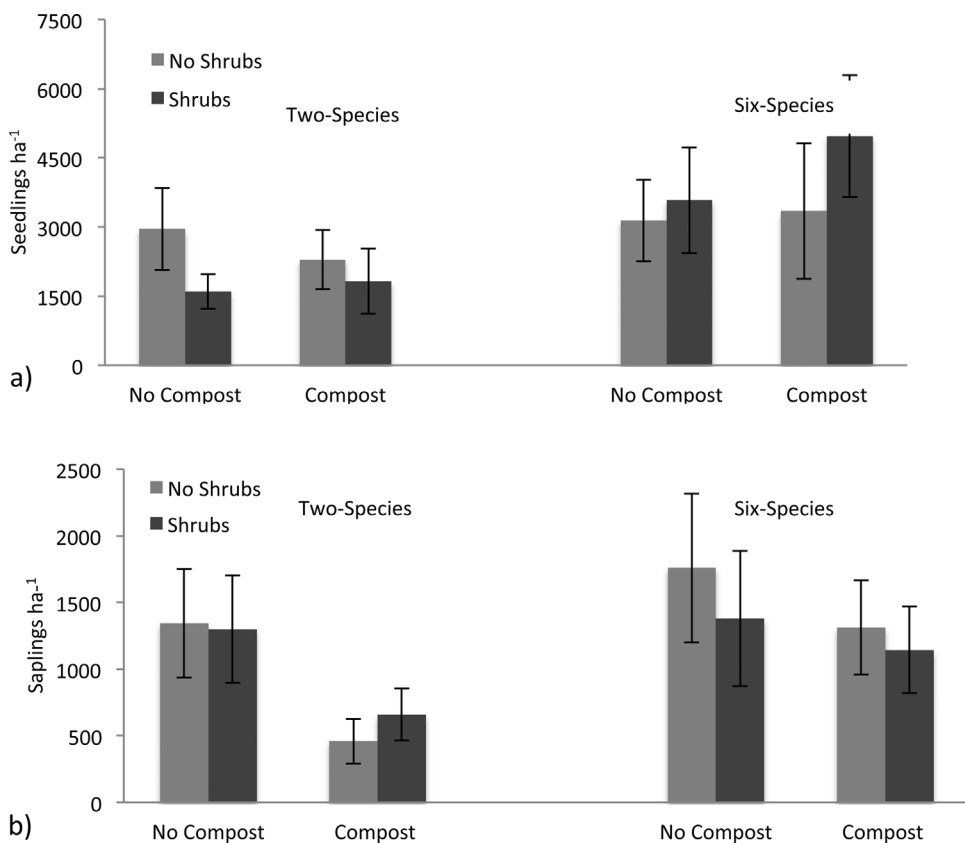
Fig. 3. Mean number of (a) seedlings ha^{-1} and (b) saplings ha^{-1}. There was a significant interaction effect of shrub presence with tree composition (six-species), and also with compost, on seedling and sapling abundance. Error bars represent ± standard error. See Table 2 for treatment coefficients.
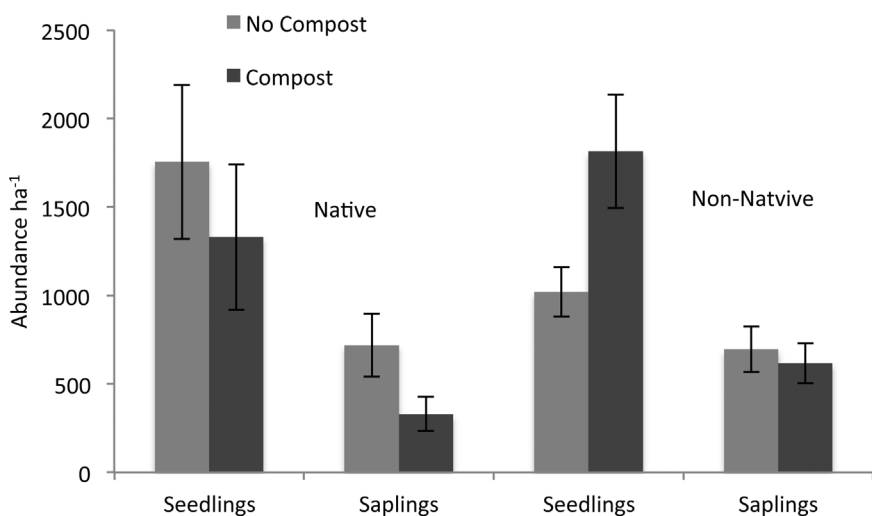

Fig. 4. Mean number of native and non-native seedlings and saplings in compost treatments. The positive effect that compost has on non-native seedling regeneration is clearly apparent with significantly greater non-native seedling recruitment in composted plots compared with plots that were not composted, however this effect drops off in saplings. Compost appears to suppress native regeneration in both seedlings and saplings. Error bars represent ± SE. The replicates are compost, $n = 26$, no compost, $n = 28$. See Table 2 for treatment coefficients.

Table 3
Results from generalized linear models and generalized linear mixed models exploring the effects of environmental conditions on recruitment in an urban afforestation project in New York City, New York, USA. Variables have been standardized so that coefficient size indicates relative impact on seedling recruitment. Model coefficients and standard errors significant at $p < 0.05$ are bolded. See Methods for model construction.

Environmental Condition	Seedling Abundance ha^{-1} Coefficient ± std. error	Native:Non-native Seedling Ratio Coefficient ± std. error
Intercept	6.12 ± 0.98	−0.05 ± 0.01
Sub-canopy PAR	**−1.02 ± 0.44**	**−0.22 ± 0.01**
Soil Moisture	**0.71 ± 0.38**	**−0.61 ± 0.01**

into the sapling stage.

The effect of the shrub treatment on recruitment shifted from negative to positive for both seedlings and saplings when combined with the species composition treatment. This shift may be the result of

greater bird activity in plots with shrubs and six-species. Shrubs provide favorable cover and forage (fruits) for birds (Annand and Thompson, 1997; Soderstrom et al., 2001; Crooks et al., 2002) and six-species plots, in contrast to our two-species plots, included fruiting tree species such
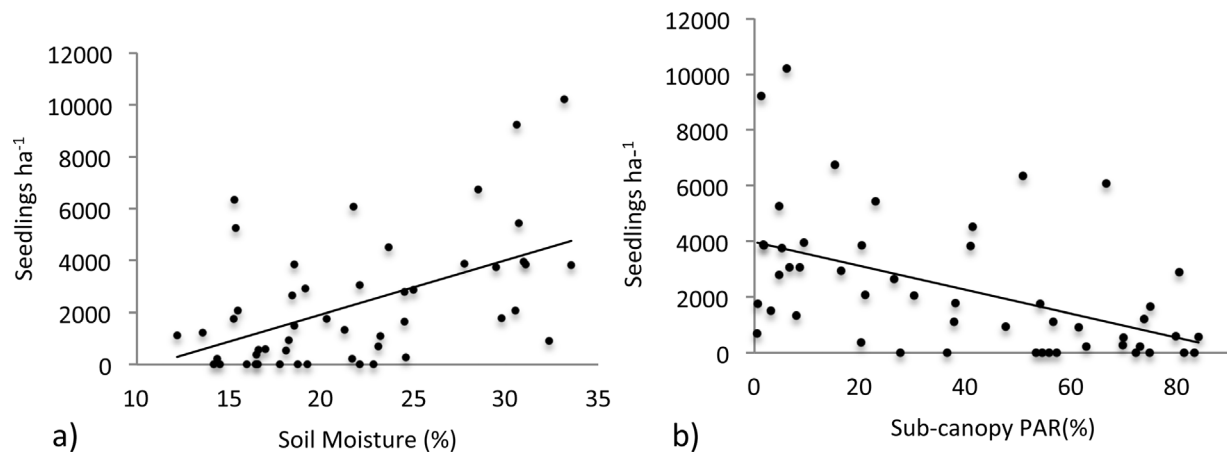
Fig. 5. Fitted regression line with the number of seedlings ha^{-1} in relation to (a) soil moisture (%) and (b) sub-canopy PAR (%). Seedling abundance increased with soil moisture but decreased with increasing sub-canopy PAR. See Table 3 for coefficients.

as *P. serotina* and *C. occidentalis* that are a known food source for birds (Hartung and Brawn, 2005; Deckers et al., 2005; Deckers et al., 2008). By providing both preferred habitat and food source, the shrub + tree composition combined treatments may attract avian dispersers thereby increasing the potential for woody plant recruitment.

While compost alone did not significantly increase woody plant recruitment in our study, it did steer species composition towards a non-native dominated system (Fig. 4). This trade-off between natives and non-natives may be the result of fast-growing non-native invasive species that are able to grow more rapidly and take advantage of enhanced soil conditions (Sakai et al., 2001; Van Kleunen et al., 2000). Similar studies have also found that native species are more competitive than non-natives when in moisture- and nutrient-limiting environments; whereas non-native invasives have higher growth rates and fecundity in nutrient-rich environments (Daehler, 2003; Lake and Leishman, 2003). The use of compost amendments in restoration projects then appears to come with costs as well as benefits. For example, compost amendments at our site increased the growth of planted trees (Oldfield et al., 2014), but ultimately may not establish trajectories that result in a "native-dominated" forest in the long-term if it also promotes—as we find here—recruitment of non-natives over natives.

We did not find a relationship between most environmental variables and site treatments (with the exception of shrub + compost treatment on ground-story PAR). However, we did find that environmental variables impacted both the abundance and species composition of woody plant recruitment. Distinct from high statured and mature rural forests, where larger canopy gaps (measured in our study as higher sub-canopy PAR values) result in greater regeneration (Clinton and Boring, 1994; Gray and Spies, 1996), our study found that larger canopy gaps within tree plantings resulted in dense herbaceous growth and reduced woody plant recruitment (Table 3, Fig. 5), likely because of competition between the herbaceous ground cover and the woody seedlings (Setterfield, 2002). The proportion of non-native to native woody recruits was also greater in open canopy settings (Table 3), suggesting that a dense tall canopy cover coupled with an open understory presents the most ideal environment for native woody plant regeneration, at least at our urban site.

Findings from our study highlight the value of longer-term (> 5 y) studies into the dynamics of urban reforestation projects. Most research on natural regeneration is conducted in the first five years after site establishment (Robinson and Handel, 2000; Rawlinson et al., 2004; Sullivan et al., 2009), or not until more than 25 years later (Robinson et al., 1992; Robinson and Handel, 1993; Hodge and Harmer, 1996; Bornkamm, 2007). However, 5–10 years post planting is a particularly opportune time to identify and distinguish what is able to recruit

(seedlings) and how competition affects what is able to establish (saplings) with a goal of understanding patterns of succession towards canopy closure as well as the potential role that management can play in influencing the eventual outcomes. In our study, the shrub + compost treatment facilitated seedling recruitment but impeded sapling establishment demonstrating the importance in understanding not only the ability of woody species to recruit, but also to compete and establish. Similarly, site treatments had a greater impact on seedling species composition than on sapling composition. This suggests that site treatments may enhance native seedling recruitment but that competitive interactions in the sapling stage overpower treatment effects. Thus ongoing management (i.e. removal of non-native invasive species) will be needed to ensure that native seedlings are able to outcompete non-natives as they grow into saplings. Furthermore, many planted native species can take up to 8–10 years to reach reproductive age. The presence of *Q. rubra* and *Carya* spp. seedlings in our study illuminate the need to conduct research in the longer term to capture data on the regeneration of these later successional species (USDA NRCS, 2016). Future research on recruitment will likely need to consider multiple variables to facilitate monitoring that informs management, such as when seedlings transition to saplings and what age different planted species will begin to fruit.

Urban forests are becoming an increasingly important part of the cityscape given their potential to provide ecological, economic, health, social, and aesthetic services (Dwyer et al., 2000; Carreiro et al., 2007). As land managers continue to plant trees to restore and grow urban forests, understanding the impact that site treatments and environmental conditions have on woody plant recruitment will be essential to effective implementation of restoration projects and efficient management. At six years post-planting, our study demonstrates that natural regeneration of planted and non-planted native tree species can be substantial but is strongly dependent on site treatments and conditions. These site treatments can enhance – or inhibit – recruitment depending on treatment interactions and may result in trade-offs with greater regeneration from non-native species. Further, site conditions, such as forest cover, can promote high recruitment rates. Even with regeneration, the prominence of invasive species at our site suggests that urban sites will need some level of human intervention to be sustainable in the long term. Our results therefore highlight the need to consider ongoing management, interactions among site treatments, and environmental conditions – and how both the seedling and sapling layers respond – when restoration goals focus on establishing and maintaining native-dominated urban forests.

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Acknowledgements

Appendix A

Table A1
Number of plots with each site treatment combination in the New York City Afforestation Project. Site treatments include compost (compost or no compost), co-planting with nurse shrubs (shrubs or no shrubs), and species composition (six-species or two-species).

Number of Plots	Compost	No Compost	Shrubs	No Shrubs	Six-Species	Two-species
9		X		X		X
5	X			X		X
9		X	X			X
5	X		X			X
5		X		X	X	
8	X			X	X	
5		X	X		X	
8	X		X		X	

Table A2
Coefficients for the effect of site treatments on the number of seedlings per ha and number of saplings per ha using zero-inflated Poisson regression. Statistically significant terms $p < 0.05$ are shown in bold text.

Treatment	Coefficient $\pm$ std. error Seedling Abundance ha^{-1}	Coefficient $\pm$ std. error Sapling Abundance ha^{-1}
Intercept	7.99 $\pm$ 0.01	7.20 $\pm$ 0.01
Shrub	**−0.61 $\pm$ 0.01**	**−0.03 $\pm$ 0.01**
Compost	**−0.25 $\pm$ 0.01**	**−1.07 $\pm$ 0.02**
Composition	**0.06 $\pm$ 0.01**	0.27 $\pm$ 0.14
Compost: Shrub	**0.39 $\pm$ 0.02**	**0.39 $\pm$ 0.03**
Shrub: Composition	**0.74 $\pm$ 0.02**	**−0.21 $\pm$ 0.02**
Compost: Composition	**0.32 $\pm$ 0.02**	**0.78 $\pm$ 0.03**
Compost: Shrub: Composition	**−0.26 $\pm$ 0.03**	**−0.28 $\pm$ 0.04**

Table A3
Coefficients for the effect of site treatments on the number of seedlings per ha using GLMMs on plots including the 3 plots with > 60,000 seedlings ha^{-1}. Statistically significant terms $p < 0.05$ are shown in bold text.

Treatment	Seedling Abundance ha^{-1} Coefficient $\pm$ std. error
Intercept	8.10 $\pm$ 0.46
Shrub	**−0.57 $\pm$ 0.01**
Compost	−0.71 $\pm$ 0.01
Composition	0.12 $\pm$ 0.55
Compost: Shrub	**0.53 $\pm$ 0.02**
Shrub: Composition	**0.22 $\pm$ 0.01**
Compost: Composition	0.30 $\pm$ 0.76
Compost: Shrub: Composition	**0.53 $\pm$ 0.02**

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