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A long-term evaluation of applied nucleation as a strategy to facilitate forest restoration

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Abstract. Applied nucleation is a restoration technique that seeks to facilitate woody-plant establishment by attracting birds or other animals that may introduce seeds of dispersal-limited species. In 1991, an experimental test of applied nucleation was initiated in an abandoned landfill in New Jersey, USA. Trees and shrubs were planted into 16 10 × 10 m plots, covering <3% of the 6-ha site. In 2010–2011, we sampled the plant community to test the impact of the treatments on forest cover and plant biodiversity. Site-wide forest cover increased substantially in the 19 years since planting from none to 59%. The original planted plots had significantly higher stem density, particularly of bird-dispersed species, than unplanted areas. Species composition outside the planted plots was dominated by the wind-dispersed *Fraxinus americana* and several small-seeded bird-dispersed species, but there were few species indicative of later successional stages. The expected model of successional development via the nucleation model that rates of colonization would be highest near plantings and that forest cover would spread outward from established clusters was not supported after this time span. Given the site's isolation from potential sources of woody propagules, the experimental treatments may not have been enough to overcome many species' dispersal limitation. Regardless of the mechanism, however, the treatments transformed the once essentially treeless site into a densely wooded habitat, and did so at a rate faster than other descriptions of reforestation following disturbances or land-use changes in the region. Despite the relatively low species richness of the community, this experiment demonstrated that reforestation of even severely degraded habitat can be achieved with minimal management after site preparation and cluster plantings.

Key words: *bird dispersal; cluster planting; dispersion; landfill; New Jersey Meadowlands; propagule limitation; reforestation; restoration; seed sources*

Introduction

Links between restoration science and succession theory must be forged to improve restoration and reclamation practices (e.g., Bradshaw 1997, Dobson et al. 1997, Pickett et al. 2001, Young et al. 2005, Walker et al. 2007). A variety of restoration techniques are specifically designed to either mimic natural successional processes or influence potential pathways. Strategies such as the addition of topsoil, seeding, or transplantation are designed to overcome edaphic, dispersal, or other limitations to recruitment and survival (e.g., Bradshaw 1987, Wong 2003, Lamb et al. 2005, Bonilla-Moheno and Holl 2010, Fields-Johnson et al. 2012). The assumption underlying many of these methods is that natural ecological processes, including succession, will predominate after the period of active management has ended (Holl 2002, Onaindia et al. 2013). A further assumption is that these natural processes will maintain or even advance the desired goals of the restoration activities.

Applied nucleation is a restoration strategy that explicitly relies on successional processes to aid in forest recovery (Rey Benayas et al. 2008, Corbin and Holl 2012). Trees or other types of vegetation are planted in clusters or habitat islands, which then serve as focal areas for propagule establishment (McDonnell and Stiles 1983). Over time, new recruits establish and the nuclei expand to facilitate site-wide forest recovery (Corbin and Holl 2012). The planted nuclei not only are expected to increase rates of tree establishment and reforestation, but are also expected to influence

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woody-plant community composition by attracting birds or other animals that may introduce seeds of species that otherwise might be strongly limited by seed dispersal (e.g., Robinson and Handel 2000, Rey Benayas et al. 2008, Cole et al. 2010, Corbin and Holl 2012, de la Peña-Domene et al. 2014). This method is thought to mimic the natural nucleation processes of woody establishment in non-forested lands, when initial pioneers establish in nuclei around which other species establish (Yarranton and Morrison 1974, McDonnell and Stiles 1983, Archer et al. 1988, Del Moral and Bliss 1993).

In 1991, Robinson and Handel (2000) established an experimental test of reforestation via applied nucleation on a 6-ha closed landfill in New Jersey, USA. Nine species were planted in 16 plots distributed throughout the site (21 trees per plot) with minimal post-planting management. During the first 4 years of sampling after planting, plots where trees and shrubs were planted had three- to four-times denser stem recruitment than unplanted control plots, primarily due to differences in bird-dispersed seedlings. Recruitment of bird-dispersed species outside the plots was concentrated in or around the planted plots, but recruitment of wind-dispersed species was more evenly spread. By the end of the fourth growing season after planting, 26 woody species had new individuals introduced into the community, 20 of them from sources outside the experimental plantings.

The findings of Robinson and Handel (2000) are consistent with reports from later, similar experiments in tropical forest (Zahawi and Augspurger 2006, Holl et al. 2013, Zahawi et al. 2013, Piiroinen et al. 2015) and in Mediterranean woodland (Rey Benayas et al. 2008). Planted nuclei are typically visited by birds more frequently, and seed inputs and seedling survival are higher, compared to unplanted areas (Zahawi and Augspurger 2006, Rey Benayas et al. 2008, Cole et al. 2010, Holl et al. 2011, 2013, Zahawi et al. 2013, Piiroinen et al. 2015). The experiments are also consistent with observations in tropical forests that "remnant trees" left standing in otherwise-deforested habitat act as focal points for bird and bat visitation (Fischer et al. 2010) and subsequent tree regeneration (Schlawin and Zahawi 2008, Sandor and Chazdon 2014). These results indicate that applied nucleation shows promise as a strategy to restore forest cover and to facilitate the establishment of a diverse canopy (Corbin and Holl 2012).

Still unanswered is how longer term succession and reforestation will proceed. Specifically, will clusters continue to facilitate the colonization of bird-dispersed species that are often slow to colonize isolated sites? Also, how will forest recovery proceed outside the initial plantings, spreading outward from the foci as predicted by the nucleation model of succession, or will colonization be independent of the location of the initial plantings? Answering these questions to understand restoration trajectories requires longer term monitoring of experimental tests.

Here we provide a long-term evaluation of the experiment established by Robinson and Handel (2000) by reporting conditions 19 years after trees and shrubs were planted in an applied nucleation design. This represents the longest term examination of reforestation via applied nucleation of which we are aware. We tested two specific hypotheses related to the nucleation model of succession: (1) Bird-dispersed woody species' recruits will concentrate in and near planted nuclei to a greater extent than wind-dispersed species' recruits, and (2) tree establishment will concentrate in and near planted clusters and spread outward over time. More generally, we also assessed whether the site preparation and tree and shrub planting treatments were sufficient to facilitate site-wide recovery of woody-plant community composition. Indications that reforestation could take place with minimal post-planting management would be encouraging for the broader issue of reforestation following severe habitat degradation.

Methods

Site conditions and preparation

The experimental site was a 6-ha rectangular area atop a shallow closed landfill in the New Jersey Meadowlands (40°45′06″ N, 74°07′24″ W) that had been operated by the Town of Kearney, New Jersey, until the early 1960s. Upon cessation of daily operations, the landfill was treated with a thin layer of excavated subsoil and construction debris (D. Smith, *personal communication*) and left untended. By the early 1990s, the surface consisted of rubble and exposed trash, with a sparse cover of weedy, mostly herbaceous, vegetation (Fig. 1a; Robinson and Handel 2000).

The surrounding landscape, from before the initial planting to the present, is an urban matrix of freeways and industrial sites, interspersed by estuarine marshland dominated by common reed (*Phragmites australis*) (Sullivan 1998). Robinson and Handel (2000) reported a sparse, species-poor mixture of trees and shrubs within 50 m of the site and a large ($n > 1000$) population of quaking aspen (*Populus tremuloides*) at another abandoned landfill ~0.5 km to the west. There was very little other upland woody vegetation within 5 km of the site at the time of planting. The creation of an upland woodland that could serve as habitat for migrating and resident birds in an area where such habitat is otherwise scarce was an explicit landscape-scale goal of the project (Robinson and Handel 2000).

To enhance soil resources to support woody-plant growth, inorganic sandy loam soil was imported from a nearby construction project and composted leaf mulch was obtained from a municipal yard-waste collection program. These two layers, 60-cm inorganic soil topped

FIG. 1. Photographs of the experimental site at the New Jersey Meadowlands, USA: (top) in 1990, prior to experimental treatments, with the skyline of Newark, New Jersey, visible in the background; and (bottom) in 2010, 19 years after experimental treatments were initiated.

by a 30-cm organic layer, were spread over a 150 × 400 m area using earthmoving equipment. To reduce erosion and weed establishment, the freshly covered site was then sown with a commercial annual grass mixture, predominantly Japanese millet (*Echinochloa frumentacea*).

Experimental layout and plantings

After site preparation, 16 clusters of trees and shrubs were planted in fall 1991. Each cluster, consisting of 21 woody plants selected from 6 species, was planted into a 10 × 10 m plot. There were four different experimental treatments, assigned in a 2 × 2 factorial design: plant size (large vs. small) was crossed with inclusion of N-fixing species (with N-fixers vs. without N-fixers; Table 1). These treatments were designed to test the influence of woody-stem height on disperser attraction and the benefits of N-fixers for soil development (Robinson and Handel 2000). The 16 planted plots (n = 4 for each treatment), along with eight unplanted "control" plots were located within the 6-ha site in a random array, and stratified to prevent neighboring plots having the same treatment. The total planted area was <3% of area of the site. Spacing was somewhat irregular in order to avoid spots with insufficient substrate or impeded drainage. The edge-to-edge distance to the next nearest plot ranged from 32.8 m to 83.7 m (mean ± SD = 48.3 m ± 12.4 m).

The species composition of the plantings was chosen to produce abundant fruit soon after transplanting, and to ensure that fruit production by individual species within each plot would collectively attract foraging birds throughout the year (Robinson and Handel 2000). The trees and larger shrubs were obtained from commercial nurseries, while some of the smaller plants (*Rhus copallina*, *Rubus* spp., and *Sambucus canadensis*) were excavated from successional sites in the region. Experimental trees and shrubs were sorted by size and species composition to match the four treatments. Plant sizes were adjusted so that that the average heights of trees and shrubs in the Large treatments would be approximately twice the average heights in the Small treatments.

Wire fencing (1 m tall) was installed around all 16 planted plots and 4 of the 8 control plots to reduce browsing damage from rabbits (*Sylvilagus floridanus*). The unfenced controls served as controls for potential frugivore perching on fence posts. All plots were watered during dry periods for the first two growing seasons.

Some plant and insect pests were unintentionally introduced via site preparation and transplanting. For example,

TABLE 1. Species composition of the trees planted into plots at the experimental site at the New Jersey Meadowlands, USA, in 1991.

Species	Common name	Treatment
Acer rubrum	Red maple	Without N-fixers
Cornus amomum	Grey dogwood	Without N-fixers
Morella (=Myrica) pensylvanica	Bayberry	With N-fixers
Prunus serotina	Black cherry	Both
Rhus copallina	Winged sumac	Both
Robinia pseudoacacia	Black locust	With N-fixers
Rubus allegheniensis	Common blackberry	Both
Rubus occidentalis	Black raspberry	Both
Sambucus canadensis	Elderberry	Both
Viburnum dentatum	Arrowwood	Both

Note: For treatment, "both" indicates with and without N-fixers.

the weedy tree-of-heaven (*Ailanthus altissima*) was apparently imported with the leaf mulch. In summer 1992, ~2000 stems of this species were removed to avoid confusing recruitment arising as an artifact of the site preparation. This removal was mostly successful, although a small number were recorded during later sampling. Insect pests, notably the locust borer (*Megacyllene robiniae*) and the eastern tent caterpillar (*Malocosma americanum*), were likely imported with nursery material and were found on several experimental plants. These pests were controlled by hand-picking, though their activities were found to reduce the growth and reproduction of several trees and did cause some mortality. All but 18 of the 336 trees and shrubs survived through the first growing season (fall 1992); the actinorrhizal shrub bayberry (*Morella* (=*Myrica*) *pensylvanica*) was the species most prone to mortality. Plants that died during the early period of the experiment were replaced in spring 1992. See Robinson and Handel (2000) for additional details including site preparation, species composition of plantings, and initial responses.

Site preparations were intended to provide homogeneous growth conditions throughout the site. However, an approximately 25 × 25 m area in the northwest corner of the site became dominated by a dense stand of *Phragmites* with little woody vegetation (Appendix S2: Fig. S1). Impeded drainage there was the likely cause (G. Robinson, *personal observation*). One planted plot was located within this area, and while its trees survived the first sampling period through 1994, they did not persist until subsequent resampling (see *Results*).

2010–2011 sampling

In summer 2010 we located 22 of the original 24 plots. Only two of the four unfenced control plots were found, so this treatment was excluded from these analyses. We recorded the identity and diameter at breast height (dbh; at 1.4 m height) of all woody stems in each plot. We were not able to distinguish stems that were planted in 1991 from those that recruited from other sources. Recruitment outside the planted plots was surveyed using 42 2 m wide belt transects between adjacent plots. Transect locations were chosen so as to stratify sampling evenly throughout the experimental site. The length of each transect varied, mirroring the distance between plots. We resampled a small number of plots ($n = 5$) and transects ($n = 11$) in summer 2011 to correct for errors made in plot mapping in 2010. Data sampled in the 2 years were pooled and analyzed as a single data set.

In addition to sampling woody stems in the plots and transects, we recorded the identity of each plant species found across the experimental site including herbaceous species and woody stems shorter than 1.4 m height, to provide an updated record of plant community composition.

Four soil cores (10 cm depth) were collected in each of 11 of the original plots, including planted plots and controls. Cores were first used to measure depth of the O horizon, as a test for a residual organic layer remaining from the 1991 experimental substrate application. Cores were then pooled per plot, dried (103°C for 48 h) and analyzed at the Cornell Nutrient Analysis Laboratory (Ithaca, New York, NY, USA) for the percentage of carbon and nitrogen using a ThermoQuest CHN Analyzer (CE Elantech, Milan, Italy), and for the percentage of organic matter via loss on ignition.

Analysis of aerial photography

We estimated vegetation coverage at three time points (2004, 2007, and 2010) using aerial photographs collected by the New Jersey Geographic Network and obtained from Google Earth (40.751821° latitude, −74.123290° longitude; Appendix S2: Fig. S21). Images represented summer months when vegetation was visible, and featured resolution sharp enough to discern individual trees. Each image was overlain with a 630-cell grid (kmz format), corresponding to ~10 m × 10 m per cell. Because visual interpretation of vegetation cover can be subjective, percent woody cover in each cell and in each image was estimated independently by four different researchers. The mean of the four estimates in each cell was used for subsequent analysis.

The location of planted and unplanted control plots were identified within the grid on each Google Earth image using field-generated GPS locations. In order to estimate the percent cover of vegetation within and surrounding each plot in each image, we calculated the mean percent cover of the nine cells arranged around each plot center in a 3-cell × 3-cell grid.

Data analysis

We tested for differences in woody-plant density, mean woody basal area, and species number in planted vs. control plots using Kruskal–Wallis tests. Separate analyses were conducted for all species, bird-dispersed species, and wind-dispersed species. Differences among planting treatments were analyzed using a factorial ANOVA in which plant size and presence of N-fixers were main effects.

To examine how woody-plant density varied with distance from each type of plot, we first summed the number of stems within 5-m increments of each transect, and then calculated the distance to the closest planted and unplanted plot. (The closest plot was not necessarily one of the transects' endpoints.) Because the resulting data set had a high number of observations in which no stems were found within a 5-m increment, it violated the assumptions of regression even using alternative distributions such as Poisson

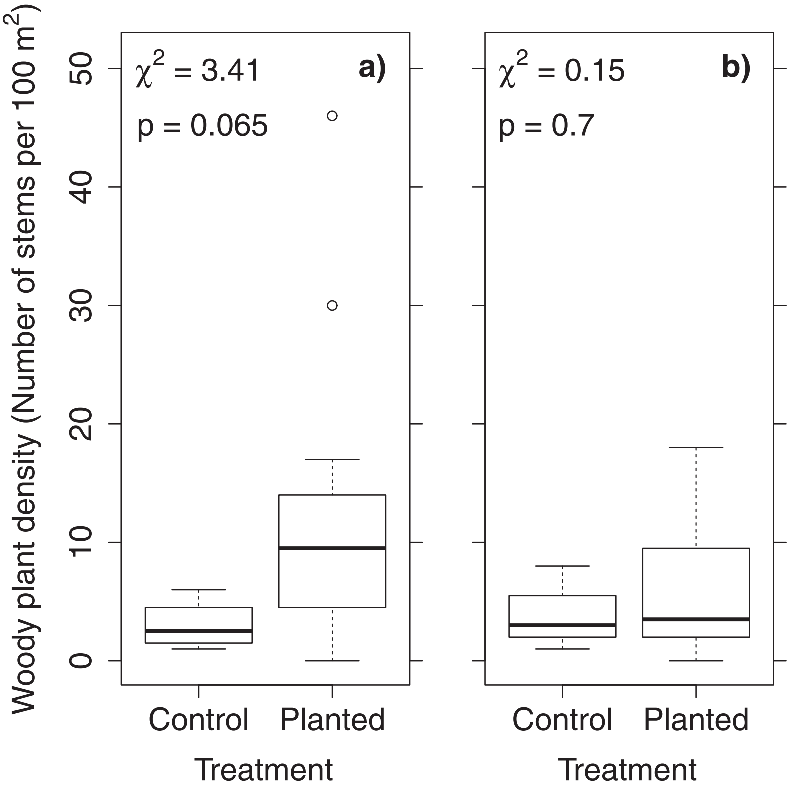

FIG. 2. Woody-plant density in unplanted control vs. planted plots of (a) bird-dispersed and (b) wind-dispersed species. The χ^2 and P values from Kruskal–Wallis tests are shown. See *Methods* for details. The box in each box-and-whiskers plot represents the 25th and 75th percentiles, while the line in the middle of the box is the median (50th percentile). The top and bottom whiskers extend to the most extreme data points that are no more than 1.5 times the interquartile range from the box. Open circles are outliers beyond the whiskers.

or quasi-Poisson. Instead, we calculated the mean number of stems in all transect increments that fell within 5-m "bins" from each type of plot (e.g., 0–5 m, 5–10 m, et cetera). We then conducted a weighted regression in which distance (from planted or unplanted plots) was the independent variable and mean stem density per bin, weighted by the number of values for each bin, was the dependent variable. Mean stem density was square root-transformed. Each analysis was performed separately for all woody plants, bird-dispersed species only, and wind-dispersed species only.

In order to analyze whether woody plants closer to planted or control plots were larger than those further away, we calculated mean woody basal area per individual within each 5-m increment. Unlike the analysis of stem density, increments along a transect with no stems were excluded from the analysis. We conducted regression analysis on the relationship between distance from each type of plot and log-transformed mean basal area per individual in each increment.

We tested for differences in percent woody-plant cover between planting treatments ("planted" or "control") in the sequence of three aerial photographs using repeated measures ANOVA ("aov" function in R). Once percent woody cover was arcsin-transformed in order to meet assumptions of ANOVA, we tested for the main effects of Treatment, Year, and the Treatment × Year interaction using appropriate within-plot and between-plot error terms.

All analyses were conducted using R, version 3.02 (R Development Core Team 2013).

RESULTS

Plant survey and soil characteristics

Sixteen species in plots and 21 species in transects were recorded in 2010–2011. There were 25 woody species and 18 herbaceous species recorded across the entire site. Only four of the species, *Cornus amomum*, *Prunus serotina*, *Rhus copallinum*, and *Robinia pseudoacacia*, were planted in 1991. Two-thirds (16) of the woody species and nearly half (8) of the herbaceous species were observed in the 1991–1995 sampling (Appendix S1: Table S11). Nine of the woody species and eight of the herbaceous species were of nonnative origin. The tallest trees observed (*Populus tremuloides*) were >20 m. Average tree height throughout the forested canopy was ~10 m, and only rarely was the canopy <4 m (Fig. 1b).

Soil horizons in the 44 cores were all well mixed, without a distinct O horizon. The top 10 cm of soil had mean percent carbon, nitrogen, and organic matter content of 6.3%, 0.4%, and 9.3%, respectively. The mean C:N ratio in soil samples was 14.5.

Woody-plant composition in planted and fenced control plots

Planted plots were dominated by bird-dispersed species (68% of the recorded stems), and 58% of these stems were a single genus, the bird-dispersed *Morus* spp. The next most abundant species were the wind-dispersed *Fraxinus americana* (14%) and *R. pseudoacacia* (12%). The long-term influence of the experimental clusters was an indirect one, as only 21 (8%) of the 278 woody plants, from four different species, were of species included in the 1991 planting mixture.

Stem density was more than twice as high in planted plots compared to fenced control plots (χ^2 = 3.61, P = 0.057), due largely to the nearly four-fold difference in the number of bird-dispersed stems in planted plots vs. controls (χ^2 = 3.41, P = 0.065; Fig. 2a). There was no difference in the density of wind-dispersed woody plants between the planted and fenced control plots (χ^2 = 0.15, P = 0.7; Fig. 2b). Variability in stem density among planted plots was high, ranging from 0 trees in a poorly-draining area in the northeast of the site, dominated by Phragmites (See Methods; Appendix S2: Fig. S21), to three plots with >30 stems per 100 m (Fig. 2). Total basal area per plot was marginally higher in planted plots (χ^2 = 3.22, P = 0.073), though there was no difference in mean basal area per individual between planted and control plots (χ^2 = 2.01, P = 0.15; Fig. 3). As was the case for stem density, there was high variability in basal area per plot, especially among planted plots. There were roughly equal numbers of species in planted and fenced control plots (3.3 [SD = 1.4] vs. 2.8 [SD = 1.0] species per 100 m2; χ^2 = 1.07, P = 0.3). The difference was even smaller when species planted in 1991 were excluded from the analysis (2.8 species [SD = 1.3] vs. control 2.5 [SD = 0.6] species per 100 m2).

There were no differences in the number of stems, basal area, or number of species among the four planting treatments (all P > 0.7). There was also no interaction between planting size and the presence of N-fixers (P = 0.4). A separate analysis, considering only bird-dispersed species, similarly yielded no significant difference among the planting treatments (all P > 0.4) (Appendix S3: Fig. S1).

Woody-plant composition outside fenced plots

Wind-dispersed species were a majority (58%) of the stems outside the fenced (planted and control) plots, and 43% of the recorded stems were a single species, the wind-dispersed *F. americana*; another 25%

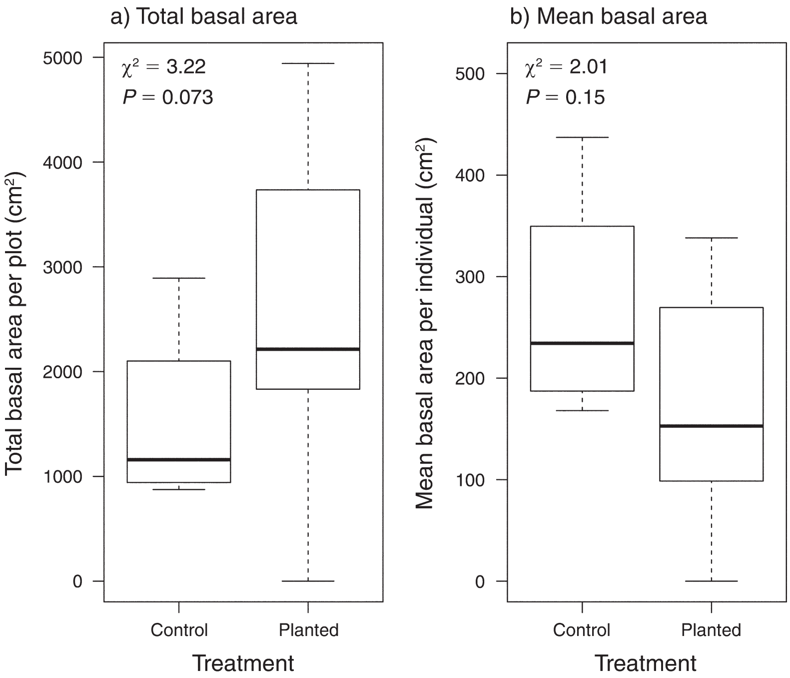

FIG. 3. (a) Total basal area per plot and (b) mean basal area per individual in unplanted control and planted plots. The χ^2 and P values from Kruskal–Wallis tests are shown. See *Methods* for details. Boxplot details are as in Fig. 2.

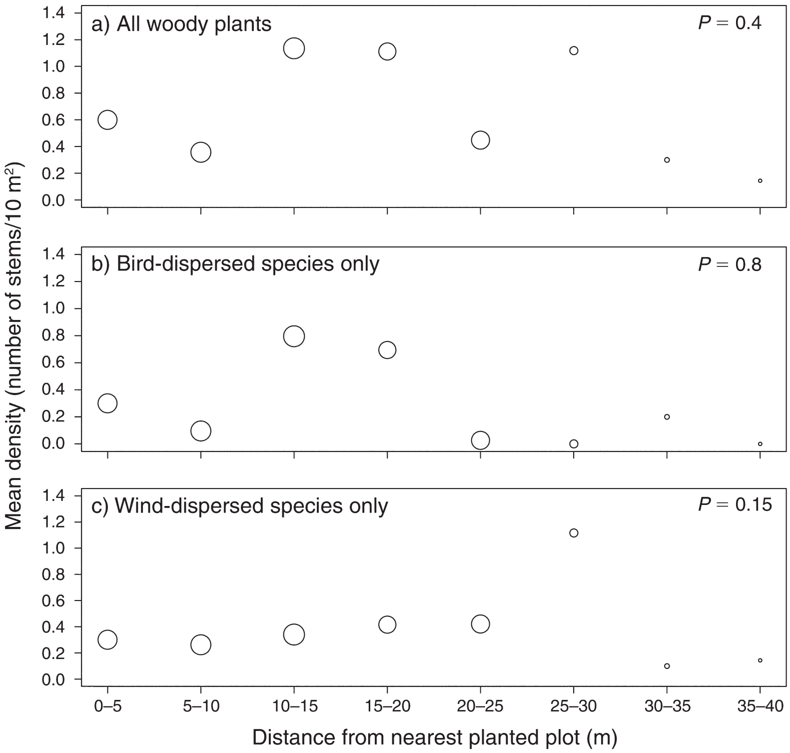

FIG. 4. Mean number of (a) all woody species, (b) bird-dispersed species, and (c) wind-dispersed species per 10 m^2 as a function of distance from planted plots. Each circle is the mean of all transect samples that fell within 5 m "bins." The size of the circle is scaled according to the number of observations, in order to visualize the effect of the weighted regression. *P* values are from regressions of distance from the nearest planted plot vs. mean stem density per 5-m transect increment, weighted by the number of values for each bin. See *Methods* for details.

were one of three species of bird-dispersed shrubs (*Rhus copallinum*, *R. glabra*, and *R. typhina*).

The density and basal area of woody plants that colonized the site outside of planted plots were not correlated with their proximity to planted plots. Weighted regression analysis found no significant relationship between mean density and distance from the nearest planted plot (all $P > 0.1$; Fig. 4), nor did individuals located closer to planted plots have a larger basal area (all $P > 0.4$; Fig. 5).

Progression of woody cover

Our analysis of aerial photographs showed that percent woody cover on the entire site increased significantly between 2004 and 2010 (RM ANOVA, Year $F_{2,34} = 36.9$, $P = 0.0001$), from 24% (SD = 26) in 2004 to 56% (SD = 37) in 2007, and to 59% (SD = 38) in 2010. We did not find, however, that percent woody cover was higher in planted plots than in unplanted plots (RM ANOVA Planting Treatment, $F_{1,17} = 0.5$, $P = 0.5$), or an interaction between planting treatment and the year of the aerial photograph (RM ANOVA, Treatment × Year, $F_{2,34} = 0.1$, $P = 0.9$).

DISCUSSION

After 19 years of vegetation development, we did not find evidence for either of the two hypothesized patterns of recruitment predicted by the nucleation model of succession, namely that the recruitment of bird-dispersed woody species would concentrate in and near planted nuclei, and that planted nuclei would expand over time as new establishment concentrated near their edges. Woody-stem density was the same at close and far distances from planted plots, and we did not find larger stems in areas close vs. far from planted plots as we would expect if the earliest colonists were on the edges of clusters. Furthermore, the progression of forest cover over time, as estimated from aerial photographs, was similar in planted and unplanted controls.

Regardless of the mechanism, however, the experimental treatments of soil and organic matter addition followed by tree and shrub planting transformed the once essentially treeless site into a densely wooded habitat. The community included a substantial proportion of bird-dispersed species, but was dominated by wind-dispersed and small-seeded, bird-dispersed species. Still, even relatively simple woodlands such as this

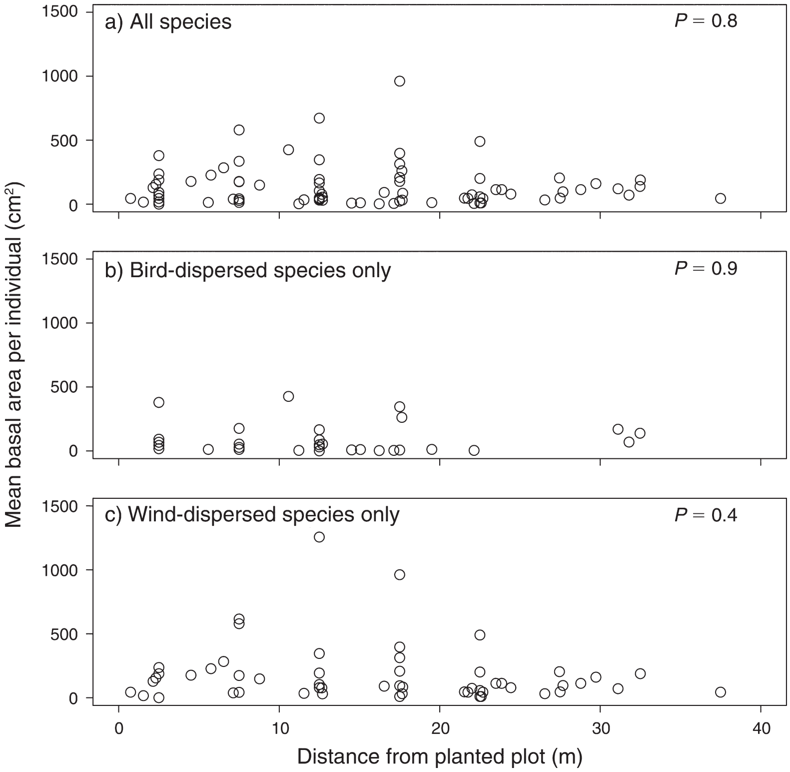

FIG. 5. Mean basal area of (a) all species, (b) bird-dispersed species, and (c) wind-dispersed species within 5-m increments of sampled transects as a function of the distance from planted and control plots. *P* values are from regressions of the distance from the nearest planted plot vs. log-transformed mean basal area per individual in each 5-m increment.

are likely to offer greater value in terms of biodiversity and ecosystem services than the barren landscape that existed before treatments were initiated in 1991 (Yurlina 1998, Robinson and Handel 2000, Costanza et al. 2006).

Effect of treatments on rate of colonization and species composition

Woodland development occurred despite the poor soil conditions on the old landfill. Our importation of deeper, improved substrates in 1991 likely mitigated the severe limitation to tree establishment that is often observed in unimproved landfills or surface mines (e.g., Bradshaw 1997, Prach et al. 2001, Prach and Hobbs 2008). By contrast, planted trees and shrubs survived and new woody recruits appeared in the first years after the experimental treatments (Robinson and Handel 2000). There was also no evidence of the installed layers of inorganic and organic layers when soils were resampled in 2012, and organic matter content was comparable to native forests in the region (e.g., Finzi et al. 1998, Aitkenhead and McDowell 2000).

The rate of forest establishment, from 0% prior to 1991 to 59% in 2010, was relatively fast compared to other descriptions of reforestation following disturbances or land-use changes in temperate North America (e.g., Hanks 1971, Inouye et al. 1987, Pickett et al. 2001, Meiners et al. 2002, Cook et al. 2005). For example, Hanks (1971), in a survey of 22 old-field sites in New Jersey's inner coastal plain, found that trees were typically absent in the first 10–15 years following agricultural abandonment, and that tree cover averaged only 14% in sites that were 25–40 years old. Incoming tree propagules in our study encountered a nearly open competitive landscape (with the exception of the seeded annual grass cover) created by the soil installation in 1991. As a result, forest cover likely increased more rapidly than if perennial pasture grasses and other herbaceous species had been able to establish "priority" (sensu Belyea and Lancaster 1999).

The established community was a simple one, with a species composition that did not differ substantially from what would be expected in other recently disturbed early-successional forests in the region (Sneddon et al. 2008). Though the site included a substantial (>40%) proportion of bird-dispersed species such as *Morus* spp. and *Rhus* spp., many others typical of later successional stages including *Amelanchier* spp., *Cornus* spp., *Prunus* spp., and

Quercus spp. were rare or absent. We note that many aggressive bird-dispersed invasive shrub species of this region such as *Berberis thunbergii*, *Lonicera* spp., and *Rhamnus cathartica* were also not recorded at our site. Urban woodland restorations often require continual management against invasive species. This very slow accretion of invasive species we observed is encouraging, but it may not persist over future decades in the midst of this highly invaded landscape.

Without an unplanted site to serve as a control for the influence of clusters, we cannot definitively demonstrate that the plantings influenced species composition across the whole experimental site. Studies on other sites, however, can be useful comparisons. Gallagher et al. (2011), surveyed urban brownfields ~7 km from our site that had been abandoned 30 years prior with no plantings. The dominant trees were all wind dispersed: *Betula populifolia* (35% cover), *Populus deltoides* (16% cover), and *P. tremuloides* (14% cover). Shrubs were primarily *Rhus* spp., as they were at our site. A second study, undertaken ~50 km from ours, can serve as a reference for another kind of treatment, namely widespread planting. The Edgeboro (New Jersey, USA) landfill was abandoned in the 1960s until 1976, when the 800-m^2 site was treated with 60 cm of mineral and topsoil, and then planted with 190 shrubs and trees. Robinson et al. (1992) reported that 14 years later, 18 of the 19 planted species survived, and that an additional 18 species of trees, shrubs, and vines colonized from outside the site. Besides many of the wind-dispersed species we observed at our site, Robinson et al. (1992) also reported stems of the bird-dispersed American crabapple (*Pyrus coronaria*), blackjack oak (*Quercus marilandica*), and black cherry (*Prunus serotina*), which we did not observe.

Whether clustering the trees vs. a denser, plantation-style design (e.g., Robinson et al. 1992) would be more effective is unknown. We note that the clustered design requires fewer trees and, therefore, may be less expensive than plantation designs (Corbin and Holl 2012, Holl and Zahawi 2014). Comparing clustered and plantation planting designs is an explicit component of the experimental designs of other studies (e.g., Zahawi et al. 2013), and should be helpful for understanding the tradeoffs between the methods.

Applied nucleation as a reforestation strategy

Other studies, including ones in tropical rainforest (Zahawi and Augspurger 2006, Holl et al. 2011, Zahawi et al. 2013, Piiroinen et al. 2015) and Mediterranean oak woodland (Rey Benayas et al. 2008) have reported experimental tests of the applied nucleation method through 2–13 years after planting. Those studies have found that clusters facilitate woody establishment, but like ours, have not demonstrated that they can consistently facilitate the establishment of desired later successional, animal-dispersed species. For example, Zahawi et al. (2013) found that, 4 years after planting, establishment of animal-dispersed seedlings was twice as high in planted plots vs. unplanted controls, but that the newly established species were predominantly early-successional and other smaller seeded species. They also found that the rate of seedling establishment outside the area of the initial planting area was slow (likely a function of the short duration of the study), but also that clusters were spreading. Rey Benayas et al. (2008) documented that planting clusters of *Quercus ilex* ssp. *rotundifolia* in abandoned cropland increased soil organic matter and inorganic N content, but the plantings have expanded very little in ~20 years since establishment (Rey Benayas et al. 2015). Further monitoring of these sites would reveal longer term successional dynamics.

While our long-term study did not support the nucleation model of succession, our plantings may have, nonetheless, attracted dispersers to accelerate and otherwise influence site-wide tree establishment. Robinson and Handel (2000) hypothesized that a clustered planting design could result in a random pattern of tree recruitment when a site possesses abundant dispersal agents that frequently move between clusters. Localized trees in degraded landscapes, either introduced or remnants of once extensive woodlands, can be foci of species introductions over long periods (Schlawin and Zahawi 2008, Sandor and Chazdon 2014). Importantly, recruitment within plots did not vary with height of the original trees, which suggests that planting smaller stems, which are often less expensive, can still be effective.

Almost all of the newly established woody plants were from sources outside the site, showing the influence of the broader landscape on successional processes at the site. However, the site is situated in a highly urbanized, heterogeneous and species-poor landscape (see Plate 1 in Robinson and Handel 2000). Applied nucleation may be particularly sensitive to a site's landscape context: it is a tool intended to enhance dispersal of species dispersed by birds, bats, and other mammals, but it may not do so if source populations of these species are too distant (Corbin and Holl 2012). Distance to seed sources is a well-known influence on the pace and direction of succession (Fastie 1995, Turner et al. 1998, Luck and Daily 2003, Cook et al. 2005) and restoration (Holl 2007, Brudvig 2011), as only the best-dispersing plants are able to be part of the pool of potential recruits to an isolated site.

Implications for management

These data, 19 years after the initiation of experimental treatments, demonstrate the efficacy of improving forested habitat quality on severely degraded urban sites to advance forest biodiversity and structure and their many ecological services. Though not all regional species, particularly ones with larger seeds, have appeared over these 19 years, and individuals are more concentrated within the planted clusters than in the rest of the site, substantial recovery has indeed occurred. The site resembles other successional forests in the region, yet the woodland has developed at a faster rate than would be expected if no planting treatments had been undertaken. The ability of a woodland to develop on the modified substrate is encouraging evidence that restoration is possible even in stringent edaphic conditions, once simple amendments are applied.

Though the mechanism for recovery is not entirely clear, it is notable that the rapid colonization took place, even though <3% of the site was planted with trees, at a fraction of the cost than site-wide planting treatments that are sometimes undertaken (Lamb et al. 2005). Furthermore, these nearly two decades since initiation did not include any landscape management activities (i.e., watering, fertilization, staking, pruning, or removal of invasive species stems) that are administrative and financial burdens for many public authorities that control our urban habitats (Handel et al. 2013).

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DATA AVAILABILITY

Data associated with this paper have been deposited in Dryad: http://dx.doi.org/10.5061/dryad.m4m9v.