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RESEARCH ARTICLE

Testing the effect of restoration-focused silviculture on oak regeneration and groundlayer plant communities in urban–exurban oak woodlands

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Throughout their global range, oak-dominated ecosystems have undergone state changes in stand structure and composition. Land managers face an especially acute challenge in restoring oak ecosystems and promoting oak regeneration in urban–exurban areas, where high-intensity silvicultural treatments are often not feasible. To investigate low-intensity management alternatives which could be widely applied in urban–exurban forests, a large-scale adaptive management experiment was implemented in Lake County, IL, in 2012. Five canopy manipulation treatments of varying intensity, timing, and spatial aggregation were replicated across three study areas and oak seedlings were under-planted into treatment units following management. Responses of understory light environment, shrub and groundlayer plant communities, and survival and growth of underplanted oak seedlings were evaluated. Understory light availability, canopy openness, total groundlayer plant cover, and groundlayer species diversity all differed among treatments. However, although understory light availability was significantly increased by canopy manipulation, groundlayer communities and oak seedling survival and growth did not differ among treatments. High overall seedling survival rates suggest current conditions are amenable to oak regeneration, but long-term monitoring will be needed to assess the potential for seedlings to transition to the sapling and canopy layers. Early results demonstrate that canopy-focused silvicultural treatments can affect the understory light environment and, to some degree, groundlayer plant communities. However, underplanting of oak seedlings paired with subcanopy thinning may be sufficient to restore an oak seedling layer, and (when necessary or preferred) canopy manipulation could potentially be deferred until later in the restoration timeline to promote oak recruitment.

Key words: adaptive management, oak ecosystem, regeneration, silvicultural restoration, urban silviculture

Implications for Practice

- In urban–exurban forests and natural areas, low-intensity canopy removals can promote survival and early establishment of planted oaks and increased cover and diversity of groundlayer plants.
- High-intensity canopy manipulation may not be immediately necessary to promote the early establishment of oak seedlings where underplanting is an option.
- More intensive canopy-focused treatments may be prioritized for later in the restoration timeline to promote recruitment of oak advance regeneration at a point where groundlayer competition may have less impact on canopy accession.

Introduction

Over the past ~300 years, oak ecosystems in eastern North America have undergone dramatic alteration, transitioning from open-canopied woodlands dominated by shade-intolerant, xeric-adapted oak species (*Quercus* spp.) to dense-canopied forests with increased dominance of mesophytic species, such as sugar and red maple (*Acer saccharum* and *A. rubrum*) (Abrams 1992; Lorimer 2003). Such shifts constitute a state change in the broader ecosystem, and have been characterized as "mesophication" (Nowacki & Abrams 2008). This pattern has been associated with a range of anthropogenic factors including altered disturbance regimes (especially fire suppression) and resulting shifts in canopy density, suburban and exurban development, browsing and acorn consumption by mammal populations, and the spread of invasive plant and pest species

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Author contributions: DM, RF conceived and designed the overall research program; DM coordinated the management treatments; RF, DM coordinated the monitoring program; JP conducted field data collection and data analysis; JP led manuscript writing; RF, DM edited the final manuscript.

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(Lorimer 1993; Nowacki & Abrams 2008; Arthur et al. 2012). Altered oak ecosystems have been the focus of substantial restoration efforts, largely focused on prescribed fire and management of invasive shrublayer (Dey & Kabrick 2015; Miller et al. 2016). However, the state shift in the system is rarely reversed by the low-intensity, subcanopy-focused restoration approaches employed by managers, due to the significant inertia represented by the high-density canopy and subcanopy of mesic tree species and also the impacts of invasive species and invasional meltdowns (Simberloff & Von Holle 1999) and altered nutrient regimes (Dey & Kabrick 2015).

Although the state change represented by mesophication affects many components of oak ecosystems (including groundlayer diversity, wildlife habitat, and human use), the effects of these shifts have had especially negative consequences for oak regeneration (Larsen & Johnson 1998; Dey & Kabrick 2015). Declines in oak regeneration will have cascading consequences for the future of these ecosystems and the foundational oak species which drive structure and function in the system (Dey 2014). Even in many presently oak-dominated ecosystems, oak seedlings occur at relatively low densities and oak saplings and understory trees are exceedingly rare (Abrams 1992; Carter et al. 2015; Dey & Kabrick 2015). Oak regeneration failures have been attributed to poor initial establishment and slow juvenile growth (Lorimer 1993; Brose & Rebbeck 2016) as well as a lack of seedling and sapling recruitment into the canopy in dense forest stands (Povak et al. 2008). This oak regeneration "bottleneck" has raised concerns about the future sustainability of oak ecosystems throughout North America and addressing this issue will require adaptive management strategies informed by oak silvics in the context of the novel climate, disturbance, and socio-ecological context of modern ecosystems (Iverson et al. 2008; Dey et al. 2010; Knoot et al. 2010).

Altered light regimes associated with mesophication may be a dominant limiting factor driving oak regeneration failures, with negative consequences for other aspects of the ecosystem such as groundlayer plant diversity (Abella et al. 2001; Lorimer 2003). Under dense, mesophytic canopies light availability is generally <20% of full sun (and often <5%), well below optimal growing conditions for most oak species or groundlayer plants associated with open-canopied oak forests and woodlands (Hodges & Gardiner 1993; Ashton & Berlyn 1994; Gottschalk 1994). Without adequate light, seedlings may increase allocation of carbon to aboveground biomass (especially leaf area), which can impede the development of roots and overall vigor of the plant (Gottschalk 1985; Kolb & Steiner 1990). Low light levels also affect the competitive balance between oaks and shade-tolerant species (Kaelke et al. 2001; Brose & Rebbeck 2016), but other environmental factors certainly contribute to these relationships, including temperature and humidity, nutrient and water availability, and microbial communities (Brudvig & Asbjornsen 2009b; Dey & Kabrick 2015). In addition, factors not usually directly related to overstory density (such as browse, herbivory, and disease) can also strongly limit oak regeneration, but the effect of these factors may also be exacerbated by low light availability and intense direct competition (Marquis et al. 1976; Lorimer et al. 1994; Miller et al. 2016). In mesic and dry mesic forests, mortality at the seedling stage may contribute to the bottleneck many oak ecosystems experience with seedling recruitment to the sapling and canopy stages (Dey 2014).

Silvicultural restoration may have some potential to prevent or reverse the transition of oak ecosystems to high-density, maple-dominated forests, especially through a combination of canopy manipulation and repeated fires (or application of fire-surrogate treatments; Albrecht & McCarthy 2006; Brudvig & Asbjornsen 2008; Dey & Kabrick 2015). Land managers and researchers are attempting many different strategies to restore oak ecosystem structure and function and promote oak regeneration (Dey & Kabrick 2015). Most recommended silvicultural practices for oak ecosystems rely heavily on high-intensity treatments and even-aged silvicultural systems (Loftis & McGee 1992; Lorimer et al. 1994; Dey et al. 2008). However, many oak ecosystems now exist within human-dominated landscapes in urban–exurban areas, and even aged regeneration treatments such as clear-cutting or traditional shelterwood may not be suitable in these socio-ecological systems (Konijnendijk et al. 2006; Knoot et al. 2010). A priority of restoration-focused silviculture should be to develop lower intensity management strategies for oak ecosystems that can be applied in urban–exurban forests. Most restoration activities in urban and natural areas forests are limited to treatments such as invasive species removal, sub-canopy thinning, and (in some areas) cool-season surface fires (Hutchinson et al. 2005). These low-intensity interventions can encourage some oak regeneration, but may not remove shade-tolerant species that now often dominate the midstory or canopy in many formerly oak-dominated ecosystems (Kaelke et al. 2001; Dey & Kabrick 2015). Somewhat more intensive treatments such as targeted canopy thinning and gap creation could benefit oak ecosystems by reducing competition experienced by shade-intolerant species from midstory- and canopy-level shade-tolerant trees, as well as increasing environmental heterogeneity and creating beneficial microclimates suitable for oak regeneration and diverse herbaceous communities in the understory (Latif & Blackburn 2010). In restoration-focused management in natural areas and urban sites managers often have the potential to implement extensive planting projects, which could be a valuable method for supplementing natural regeneration of oaks (Paquette et al. 2006; Dey et al. 2012).

The research presented here places silvicultural restoration of oak ecosystems into the context of urban–exurban land management and the constraints placed on management options by an urban socio-ecological landscape setting. The overall goal of this project was to assess the potential for restoration-focused canopy manipulations to affect ecosystem state as evidenced by environmental factors, groundlayer plant communities, and underplanted oak seedling survival and growth. To address this goal we tested three specific hypotheses: (1) Canopy openness and understory light availability would be greater in canopy-focused silvicultural restoration treatments relative to areas receiving subcanopy-only treatment and would increase with intensity of canopy removal; (2) Survival and growth of underplanted oak seedlings would be greater in canopy-focused restoration treatments relative to subcanopy-only treatments and would increase with intensity of canopy removal; (3) Groundlayer communities would differ between canopy-focused restoration treatments and subcanopy-only treatments. This work provides a basis for assessing the utility of restoration-focused silviculture in urban–exurban forest ecosystems and the potential for silvicultural methods adapted to such systems to alter the trajectories of oak ecosystems that have undergone mesophication.

Methods

Study Area and Sampling Methods

This study was conducted in the Southern Des Plaines River Adaptive Management Project (SDPR), which is a long-term adaptive management experiment focused on restoration of oak ecosystem structure and function. The project is directed and maintained by the Lake County (IL) Forest Preserve District (LCFPD) and focuses on testing novel multi-cohort forest management strategies as restoration actions, including a focus on phased, partial canopy removal. A primary goal of the project has been to test low-intensity, canopy-focused silvicultural treatment options that could be applied in natural areas and forests across human-dominated landscapes. The SDPR was initiated in 2011 and is arrayed within areas of remnant dry-mesic oak forest (Fahey & Casali 2017) across three suburban natural areas (Ryerson Conservation Area, MacArthur Woods, and Elm Road Woods) in Riverwoods and Mettawa, Illinois, U.S., along the east flank of the Des Plaines River in the northern part of the Chicago metropolitan region. These sites have a ~20-year history of low-intensity prescribed fire (3–7-year return interval), white-tailed deer (*Odocoileus virginianus*) population management, and mechanical and chemical invasive plant species control (management history details in Data S1). During the period of the study presented here (2011–2017) prescribed burning activities were halted in the study sites to allow for assessment of treatment effects on seedling survival and to promote early establishment of oak seedlings. Modern dry-mesic forests in the areas are characterized by a dense oak-maple-dominated canopy, but were historically more open canopied (Fahey et al. 2014). As in other oak forests in the Chicago region (Carter et al. 2015), oak seedling density is relatively low in the modern forests of the SDPR sites (<200 stems/ha) and oak saplings are exceedingly rare (<10 stems/ha; Fahey et al. 2014). Historically, white oak (*Quercus alba*) dominated woodland and forest ecosystems, and red oak (*Quercus rubra*) and mesophytic species were more common in fire-protected sites (Fahey et al. 2012; Fahey et al. 2014). The climate of the area is continental, with average temperatures from −6 to 23°C, experiencing humid summers and punctuated drought, with mean annual precipitation of ~937 mm.

Treatment Implementation

At each of the three study sites dry-mesic forest management units were delineated in 2011 and divided into 2–10 ha treatment units to which the five SDPR canopy treatments were randomly assigned. Canopy thinning strategies applied in the project vary in intensity, timing, and spatial pattern of removal, but all units received sub-canopy thinning (80% removal of stems <20 cm diameter at breast height; DBH) and invasive shrub removal treatments prior to canopy manipulation in winter 2011 and 2012. The five canopy thinning treatments included: subcanopy removal only (0% canopy basal area removed), light thinning (10% canopy basal area removed), group shelterwood (aggregated removal of 17.5% of canopy basal area), moderate thinning (20% canopy basal area removed), and woodland structure (40% canopy basal area removed; Fig. 1). Initial treatments were implemented in December 2011/January 2012 at MacArthur Woods (but only in 10 of 15 total treatment units to avoid site damage associated with wet, snow-free ground conditions), and in December 2012–Februrary 2013 in the remaining 5 MacArthur units and all units at Elm Woods (10) and Ryerson Conservation Area (15). Prior to treatment implementation three randomly located 0.1 ha circular monitoring plots (17.8 m radius) were established within each treatment unit in a randomized block design, totaling 120 plots (Fig. 1).

After treatment implementation (spring 2012 and 2013) white oak (*Quercus alba*) seedlings were planted in each plot at the plot center and at 5, 10, and 15 m from plot center in each cardinal direction (13 total per plot; Fig. 1). Seedlings were grown from acorns collected in Lake County Forest Preserves, propagated in a nursery, and out-planted at 2 years of age as bare-root seedlings; planting design was developed based on seedling availability at the time of study implementation. Initial heights and diameter at base of the planted seedlings were recorded as baseline data. Seedling locations were marked with pin-flags, but seedlings were not individually tagged due to inconsistent numbering of seedlings by location within plots in initial data collection.

Data Collection

Canopy Structure and Light Availability. Photosynthetically active radiation (PAR) in the understory was measured using a ceptometer (AccuPAR PAR/LAI, LP-80, Decagon Devices) at 1 m aboveground at the seedling planting locations (center of each plot and 5, 10, and 15 m in each cardinal direction, totaling 13 locations per plot). At each location 10 readings were collected 10 seconds apart and averaged. Data were collected once per plot from July to August of 2016 and May to August of 2017, between the hours of 8 am and 5 pm. Above-canopy PAR was estimated at 10-minute intervals using Photon Flux Sensors (PAR Photon Flux Sensor, Decagon Devices) attached to a data logger (EM-50, Decagon Devices) situated in an open field adjacent to the study area at each site. Fraction of above canopy PAR transmitted to the understory (fPAR) was calculated at the plot level by dividing understory PAR measurements by "above canopy" readings taken at the same time as the understory PAR measurements (based on timestamps).

Hemispherical canopy photographs were collected to characterize canopy structure (canopy openness, leaf area index - "LAI") and model annual understory light conditions (estimated

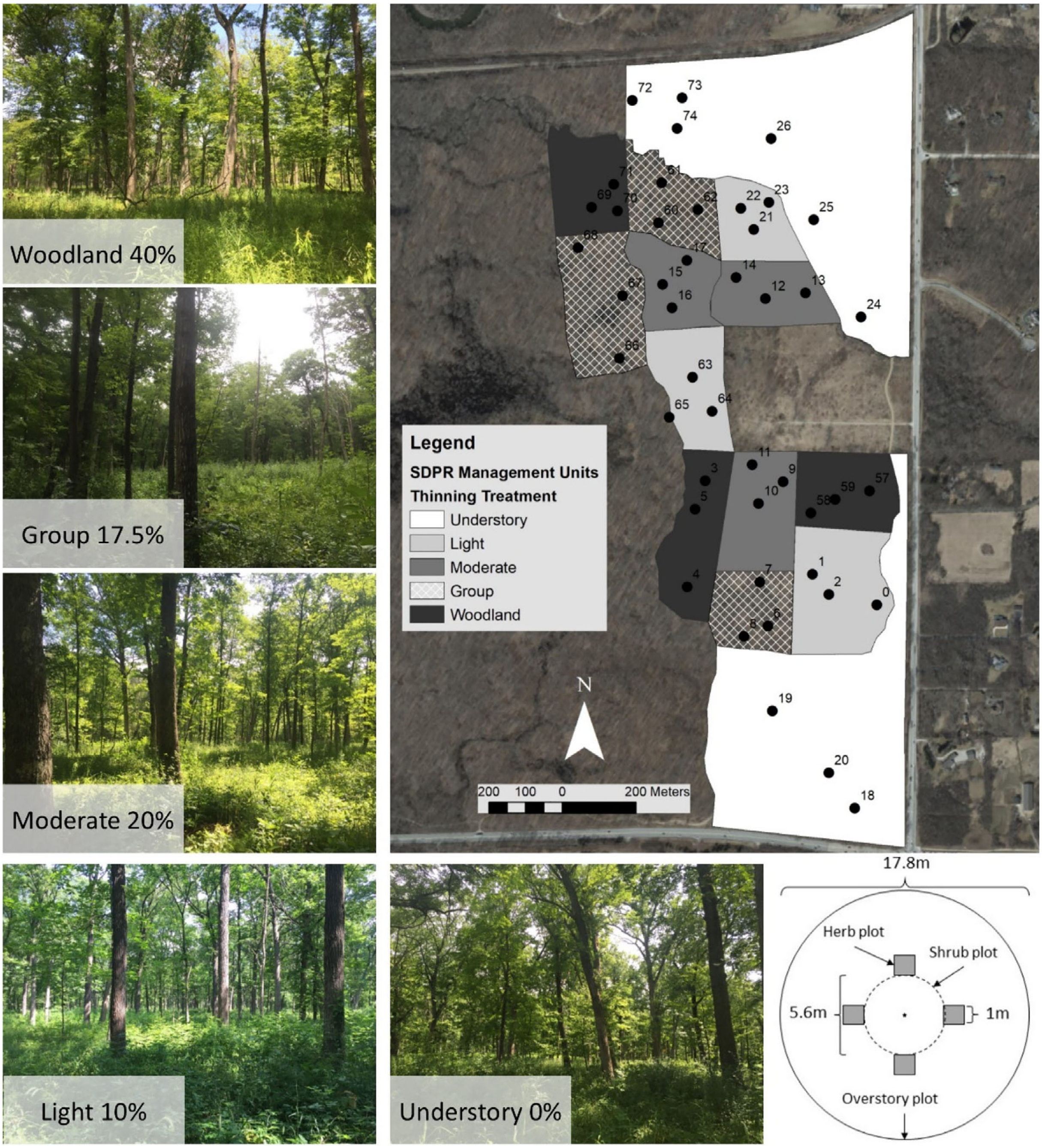

Figure 1. Treatment layout and representative treatment conditions at one of the three SDPR study sites, MacArthur Woods in Mettawa, IL, USA. In the map each polygon represents a treatment unit and each shading level corresponds to a treatment. Points within treatment units represent study plots located within treatment units in a stratified randomized design. In the bottom right corner of the map is a diagram displaying the layout of the sampling plots.

percent of total above-canopy radiation transmitted; referred to hereafter as Gap Light Index or "GLI"; Canham 1988). Photographs were collected at 1 m aboveground in five locations (center of the plot and 5 m in each cardinal direction) in each plot using a Nikon Coolpix digital camera and hemispherical lens. Photos were collected once per plot in July–August 2016 and June–September 2017 on fully overcast days. Images were analyzed using Gap Light Analyzer (GLA) software (GLA, Cary Institute of Ecosystem Studies) and output was averaged at the plot level.

Planted Seedling Survival and Growth

Planted oak seedling status (alive or dead), height (stretched length of the stem, recorded for the longest stem when multistemmed), and diameter at the base of the plant were collected for all seedlings across all three sites, 5 years post-planting in 2016 and 2017. Average height, basal diameter, and basal area were calculated at the plot level for each of the 120 plots and compared to pre-treatment plot averages. Plot-level averages were used because seedlings were not individually tagged, thus individual post-treatment measurements could not be directly matched to pre-treatment seedling measurements.

Ground- and Shrub-Layer Plant Communities

Data on vegetation were collected both prior to treatment in 2011 and 5 years post-treatment in 2016 (30 plots at MacArthur) and 2017 (15 plots at MacArthur and all Elm and Ryerson plots). For canopy trees (>10 cm diameter at breast height—DBH) species, DBH, basal area, location, and crown class were recorded for all stems on the full 17.8 m radius plot. Shrub/sapling layer stem density (woody plants >1 m in height and <10 cm in DBH) was assessed within a 5.64 m radius (0.001 ha) subplot at the center of each plot, tallied by species and size class (<1 cm DBH, 1–5 cm DBH, 5–10 cm DBH). Data on percent cover of groundlayer plants (herbaceous and woody plants <1 m in height) by species were obtained in 4–1 × 1 m quadrats located 5 m from plot center in each cardinal direction in each plot. Stem density was also recorded for woody vegetation <1 m in height and all stems of naturally regenerated oak seedlings were measured (basal diameter, height, height increment for most recent year of growth).

Statistical Analysis

Variation among treatments in light conditions (Transmitted PAR, GLI, canopy openness, LAI) seedling characteristics (survival, height growth, diameter growth, basal area growth), and vegetation conditions (canopy basal area and stem density, sapling/shrub density, seedling density, groundlayer cover, species richness, Shannon's and Simpson's diversity indices) were analyzed using linear mixed effect models with site and treatment included as random effects. When main effects of treatment were significant, post hoc pairwise comparisons were made with Tukey HSD adjustment for multiple comparisons. Where data were non-normal a log transformation was performed to meet parametric and residual assumptions of linear models, where normality was not achieved through transformation the Kruskal–Wallis test was performed in lieu of parametric analysis of variance. Natural regeneration response was assessed based on change in relative stem density of oak species in the tree seedling pool between pre- and post-treatment monitoring.

Multiple regression in a model-selection framework was used to evaluate factors that most effectively explained seedling survival and growth. Sets of mixed-effects linear models that included all possible variations of predictor variables were developed. Several predictors (e.g. canopy openness and LAI) were highly correlated (Data S1; Fig. S1) and thus only models that did not include combinations of strongly correlated ($r > 0.5$) predictors were included in the final model evaluation set. All candidate models included the interaction of treatment unit and site as a random effect. Linear effects models were analyzed using the *lme4* package in R. Model fit was analyzed using Akaike's information criterion (AIC) and AIC weights. All models were ranked by AIC and the models considered to be highly supported by the data were those with ΔAIC <2 in relation to the most highly ranked model. Though model selection was conducted using comparisons of AIC scores, the goodness of fit of highly ranked models was assessed as well. To assess the suitability of these models, R^2 values and coefficients were calculated using the *piecewiseSEM* package in R.

In order to illustrate gradients in groundlayer community composition, Non-metric multidimensional scaling (NMS) ordination was performed on plot-by-species matrices in PC-ORD v. 5.21 (McCune & Mefford 2006) using the "slow and thorough" autopilot setting, which uses 250 runs of real data and 250 Monte Carlo randomizations to assess the robustness of the solution. Prior to running the ordination, species appearing in less than 5% of plots were removed: Elm ($n = 2$), McArthur ($n = 2$), Ryerson ($n = 5$). Ordination was performed for all three sites combined and separately for each individual site. Resource and vegetation characteristics were overlain as bi-plots on the ordination solution and strength of the association with ordination axes was assessed based on Pearson's correlation coefficient (McCune & Grace 2002). Multi-response permutation procedure (MRPP) was used to test for significant differences in species composition among the five treatments. MRPP was conducted with PC-ORD using Sorensen's distance measure (McCune & Grace 2002) on the "All site" data blocked by site, and on individual sites blocked by treatment.

Results

Stand Conditions

Treatments differed in post-treatment canopy basal area ($F_{4,112} = 3.79, p = 0.006$; Table 1) and largely followed intensity of thinning treatments; as understory removal ($p = 0.003$), light thinning ($p = 0.008$), and moderate thinning ($p = 0.04$) treatments differed from the woodland treatment. Proportion change in basal area from pre- to post-treatment also differed among treatments ($F_{4,113} = 3.67$, $p = 0.007$; Table 1), but following adjustment for multiple comparisons only differed significantly between understory removal and the four overstory removal treatments. Mean GLI differed among treatments ($F_{4,110} = 8.35$, $p < 0.01$; Table 2), with significant individual comparisons for both understory removal and woodland treatments relative to all other treatments. Fraction of transmitted PAR reaching the understory (fPAR) also differed among the five treatments ($F_{4,110} = 9.04$, $p < 0.01$; Table 2) and generally increased with intensity of thinning treatments. Canopy openness and leaf area index did not differ significantly among treatments ($F_{4,110} = 1.59$, $p = 0.18$ and $F_{4,110} = 1.51$, $p = 0.21$, respectively; Table 2).

Table 1. Pre- and post-treatment stand conditions and change from pre- to post-treatment condition for each treatment across all three study areas. Results of ANOVA test comparing post-treatment conditions across treatments are indicated and superscript letters indicate significant differences among treatment means based on the Tukey pairwise comparison test.

	Canopy Basal Area (m^2 ha^{-1})		*Shrublayer Density (stems/ha)*		*Groundlayer Cover (%)*	
Treatment	*Pre-treatment*	*Post-treatment, % change*	*Pre-treatment*	*Post-treatment, % change*	*Pre-treatment*	*Post-treatment, % change*
Understory	28.3 ± 1.3	28.0 ± 1.3^a, 0.2	603.8 ± 201.4	702.9 ± 225.4, 16.4	43.4 ± 6.6	81.4 ± 5.4, 87.6
Light	30.5 ± 1.4	26.2 ± 1.3^{ab}, −14.0	986.1 ± 540	592.9 ± 132.2, −39.9	57.0 ± 6.3	96.6 ± 3.6, 69.6
Group	28.4 ± 1.2	23.7 ± 1.5^{ab}, −14.7	480 ± 56.7	995.6 ± 235.4, 107.4	60 ± 6.1	86 ± 4.3, 68.6
Moderate	30.6 ± 1.3	25.1 ± 1.3^{ab}, −17.1	1750.5 ± 993.5	880 ± 197.9, −49.7	58.8 ± 5.6	94.2 ± 3.8, 60.2
Woodland	28.4 ± 1.8	22.4 ± 1.8^b, −21.0	2,582.9 ± 1943.7	748 ± 168.8, −71.0	45 ± 4.5	96.2 ± 6.1, 113.7
ANOVA results		$F_{4,110} = 3.79$ $p < 0.01$		$F_{4,110} = 0.59$ $p = 0.67$		$F_{4,110} = 2.77$ $p = 0.03$

Planted Seedling Survival and Growth

After 5 years, overall seedling survival was not significantly different among the five treatments or the three sites ($F_{4,109} = 0.456$, $p = 0.768$; Table 3). There was also no clear trend in the survival of seedlings based on the intensity of thinning (Table 3). Mean growth in seedling height ranged from 19.9 cm in the understory removal treatment to 29.2 cm in the group shelterwood treatment (Table 3), but did not differ significantly among the treatments ($F_{4,107} = 1.263$, $p = 0.300$). There was also no significant difference in seedling diameter growth ($F_{4,107} = 0.802$, $p = 0.531$), basal area growth ($F_{4,106} = 0.967$, $p = 0.437$), or leaf count ($F_{4,107} = 1.77$, $p = 0.14$) among the treatments (Table 3).

Highly supported multiple regression models for seedling survival, height growth, and diameter growth all included combinations of the same four predictors: GLI, canopy basal area, change in basal area, and percent cover of groundlayer (Data S1; Table S2). For seedling survival, four highly supported models (<2 ΔAIC) accounted for >99% of the weight in the model set and the null model had very little support (ΔAIC = 109.10, $w < 0.001$). A model including GLI and percent groundlayer cover as predictors had the highest weighting ($w = 0.37$) and had high predictive power ($R^2 = 0.55$). In this model, survival increased with greater GLI and lower percent groundlayer cover. For height growth, three highly supported models (<2 ΔAIC) accounted for >88% of the weight in the total model set and the null model had very little relative support (ΔAIC = 96.52, $w < 0.001$). Seedling height growth was most strongly related to GLI, change in basal area, and percent cover of groundlayer and this model had a much higher weighting ($w = 0.47$) relative to the other top models and relatively strong predictive power ($R^2 = 0.43$). Each variable in the top model had a weak, indirect relationship suggesting that as light increases, both seedling growth and groundlayer cover increase. For seedling basal diameter growth three highly supported models (<2 ΔAIC) accounted for >77% of the weight of the set and the null model had very little support (ΔAIC = 7.68, $w < 0.006$). The most highly supported model indicated that seedling diameter growth was positively related to GLI and percent cover of groundlayer. This model had a higher weighting ($w = 0.29$) than the other most supported models, but had relatively low predictive power ($R^2 = 0.24$).

Groundlayer and Shrublayer Vegetation

Groundlayer cover differed significantly among treatments ($F_{4,110} = 2.71$, $p = 0.03$, Table 1), and understory-only treatments had the lowest overall post-treatment groundlayer cover. Groundlayer cover increased substantially from pre- to post-treatment in all treatments (60–114% mean increase), but the magnitude of change did not differ significantly among treatments (H = 3.55, $p = 0.471$; Table 1). There was a significant difference among treatments in both species richness ($F_{4,110} = 11.76$, $p < 0.01$) and Shannon's diversity index ($F_{4,110} = 2.906$, $p = 0.03$), with both metrics of diversity generally increasing with intensity of removal, and subcanopy removal treatments differing from overstory removal treatments

Table 2. Mean values (with standard errors) of light and canopy conditions for each treatment across all three study areas in the post-treatment sampling (2016/2017). Results of ANOVA test comparing treatments are indicated and superscript letters indicate significant differences among treatment means based on the Tukey pairwise comparison test.

Treatment	*Canopy Openness (%)*	*Gap Light Index (%)*	*Leaf Area Index*	*Transmitted PAR (proportion)*
Understory	17.4 ± 0.3	24.6 ± 0.6^{a}	1.86 ± 0.02	0.11 ± 0.01^{a}
Light	19.8 ± 0.5	28.8 ± 1^{b}	1.68 ± 0.03	0.18 ± 0.02^{ab}
Group	20.2 ± 0.7	29.5 ± 1.2^{b}	1.64 ± 0.05	0.23 ± 0.03^{bc}
Moderate	19.3 ± 0.4	27.6 ± 0.9^{b}	1.74 ± 0.03	0.23 ± 0.02^{bc}
Woodland	22.2 ± 0.7	32.5 ± 1.4^{c}	1.55 ± 0.04	0.28 ± 0.03^{c}
ANOVA result	$F_{4,110} = 1.59$ $p = 0.18$	$F_{4,110} = 8.35$ $p < 0.01$	$F_{4,110} = 1.51$ $p = 0.21$	$F_{4,110} = 9.04$ $p < 0.01$

(Table 4). Shrublayer stem density did not differ significantly across the five treatments (which all received equivalent invasive shrub removal treatments; $F_{4,110} = 0.59$, $p = 0.667$; Table 1) and percent change in shrub stem density was negative in all overstory treatments, except for group shelterwood. Density of naturally regenerated oak seedlings differed among the treatments in the post-treatment sampling ($F_{4,110} = 16.78$, $p < 0.01$), but was universally low across all treatments (Data S1; Table S1). However, relative density and change in relative stem density of naturally regenerated oak seedlings did not differ significantly among the treatments 5 years after management implementation ($F_{4,110} = 0.91$, $p = 0.46$ and $F_{4,110} = 0.407$, $p = 0.802$, respectively; Data S1; Table S1). Understory removal only (−39.96%) and group shelterwood (−24.8%) treatments both had negative mean percent change in relative stem density of oak seedlings, while relative stem density increased by 12.3% in the light thinning, 34.3% in moderate thinning, and 34.9% in woodland treatments.

NMS ordinations for groundlayer community composition across all sites had a three-dimensional solution explaining 71% of the variation in the original data matrix. The ordination solution was significant based on Monte Carlo tests (Stress = 5.67, $p = 0.004$). The two strongest axes were axis 1 (explaining 28% of the variation) and axis 2 (explaining 24% of the variation) with the third axis explaining an additional 20% of the variance. Based on MRPP analysis, composition differed significantly, but not especially strongly, across sites (A = 0.036, $p < 0.001$), which is supported by the presence of some clustering of plots by site in the ordination space (Data S1; Fig. S2). MRPP analysis comparing species composition among treatments was also significant, but did not support strong clustering based on treatment (A = 0.011, $p = 0.012$; Fig. 2). The ordination was overlaid with bi-plots of GLI, fPAR, and canopy openness, but none were highly correlated with the axes (all $r < 0.30$).

Discussion

Canopy structure and availability of light in the understory were strongly affected by restoration-focused silvicultural treatments, but did not translate into variation among treatments in near-term seedling survival and growth or substantial differentiation in groundlayer plant communities. Canopy density and light transmission are relatively easily manipulated through silvicultural treatments and alteration of these factors can promote oak regeneration success and groundlayer diversity (Larsen & Johnson 1998; Dey 2014). In the SDPR project, levels of canopy openness and light availability were increased by low-intensity canopy removal treatments (relative to understory-removal-only treatments and pre-treatment baseline conditions) and generally aligned with the intensity of the treatment in terms of total basal area removal. From the perspective of light requirements for successful oak regeneration, 23% of plots that received overstory treatments exhibited >30% transmitted PAR, the minimum often cited for oak survival (Wuenscher & Kozlowski 1971; Dey & Parker 1997; Brose & Rebbeck 2016), and only 8% had >50% light transmittance, the lower limit for high growth rates for seedlings/saplings of most oak species (Dey 2002). Overall, our results suggest that sub-canopy removal alone is not sufficient to alter the sub-canopy light environment (no plots reaching even 30% light transmittance), but also indicate that low-intensity canopy removals may not be vastly superior (only increasing light

Table 3. Mean values (with standard errors) of planted seedling characteristics for each treatment across all three study areas. Results of ANOVA test comparing treatments are indicated and superscript letters indicate significant differences among treatment means based on the Tukey pairwise comparison test.

Treatment	*Survival (%)*	*Height Growth (cm)*	*Diameter Growth (mm)*	*Basal Area Growth (m^2)*	*Leaf Count*
Understory	43.2 ± 5.5	21.9 ± 3.4	4.3 ± 0.4	0.007 ± 0.0007	17.3 ± 3.1
Light	52.8 ± 4.1	22.1 ± 2.4	4.6 ± 0.4	0.008 ± 0.0008	24.2 ± 3.8
Group	45.1 ± 5.4	29.2 ± 2.7	5.0 ± 0.5	0.008 ± 0.0009	27.0 ± 2.8
Moderate	45.1 ± 5.4	26.1 ± 3.2	4.0 ± 0.3	0.007 ± 0.0006	24.1 ± 3.6
Woodland	50.1 ± 3.8	25.7 ± 2.5	4.1 ± 0.3	0.007 ± 0.0006	27.2 ± 3.1
ANOVA result	$F_{4,109} = 0.46$ $p = 0.77$	$F_{4,107} = 1.26$ $p = 0.30$	$F_{4,110} = 0.80$ $p = 0.53$	$F_{4,110} = 0.70$ $p = 0.60$	$F_{4,110} = 1.77$ $p = 0.14$

Table 4. Mean values (with standard errors) of groundlayer community characteristics for each treatment across all three study areas in the post-treatment sampling (2016/2017). Results of ANOVA test comparing treatments are indicated and superscript letters indicate significant differences among treatment means based on the Tukey pairwise comparison test.

Treatment	*Richness*	*Evenness*	*Shannon's Diversity*	*Simpson's Diversity*
Understory	20.0 ± 0.9^{a}	0.79 ± 0.18	2.36 ± 0.07	0.86 ± 0.01
Light	24.9 ± 1.1^{b}	0.77 ± 0.02	2.46 ± 0.08	0.86 ± 0.01
Group	26.6 ± 0.8^{b}	0.80 ± 0.01	2.62 ± 0.04	0.90 ± 0.005
Moderate	26.8 ± 0.8^{b}	0.78 ± 0.13	2.57 ± 0.05	0.86 ± 0.01
Woodland	27.1 ± 0.9^{b}	0.78 ± 0.01	2.56 ± 0.06	0.87 ± 0.01
ANOVA result	$F_{4,110} = 11.76$ $p < 0.01$	$F_{4,110} = 0.63$ $p = 0.64$	$F_{4,110} = 2.91$ $p = 0.03$	$F_{4,110} = 1.02$ $p = 0.40$

availability by 7–17%), and may rarely create canopy conditions associated with successful oak regeneration (i.e. 30–50% light availability; Brose & Rebbeck 2016).

One key factor in restoring functioning oak ecosystems is encouraging oak seedling survival and growth, to promote development of a sustainable, competitive advance regeneration layer from which canopy accession can occur (Sander 1971; Lorimer 1993; Dey 2014). In this study, underplanted seedling survival was moderate in comparison to other investigations of oak underplanting (Lorimer et al. 1994; Paquette et al. 2006). Across all treatments, seedlings had an overall survival rate for all treatments of ~45% and over 50% of plots exhibiting more than half of seedlings surviving despite the lack of browse protection or directed mechanical or chemical release (Dey et al. 2012). However, despite the variation among treatments in sub-canopy light environment noted above, there was no statistically significant difference among treatments in seedling survival. Growth of planted seedlings, both in terms of height and diameter growth, also did not vary significantly among treatments, but was generally low relative to prior studies (Spetich et al. 2002; Dey et al. 2008; Dey et al. 2012; Brose & Rebbeck 2016). Growth rates were relatively low even in the most intensive thinning treatment ("Woodland"), where percent PAR transmitted to the understory commonly reached >30%, (Berg 2004; Parker & Dey 2008), but were not outside the range of other underplanting studies focused on oaks (Paquette et al. 2006). The lack of a treatment effect on aboveground growth is somewhat surprising given the substantial differences in shading among the treatments (Gottschalk 1985), but other authors have found similar lack of near term aboveground seedling growth responses to varying canopy removal treatments (Paquette et al. 2006; Dillaway et al. 2007). Canopy removal and associated increased understory light availability also did not appear to encourage natural oak regeneration; although there were some differences among treatments in seedling densities, these occurred at low densities and the relative density of oaks in comparison to the overall seedling pool did not differ among treatments. These results suggest that conditions in these sites were generally amenable to oak seedling survival, but not substantially different from each other in their effects on the understory growing environment and outcomes for seedling survival and growth. This findings may be related to the nature of the treatments (i.e. thinning treatments were all meant as a low-intensity alternative to traditional silvicultural approaches), or the relatively short timeframe between planting and remeasurement, which may not have allowed for differentiation in growth.

Although canopy light transmittance is often a limiting factor to oak regeneration success, many other factors could be highly influential. Seedling survival was strongly predicted by a combination of light availability and groundlayer cover, with greater groundlayer cover related to lower seedling survival rate. Groundlayer vegetation often represents direct competition for young seedlings (Lorimer et al. 1994), can limit light availability at the groundlayer (Miller et al. 2016), but can also mediate environmental conditions in the understory (López-Marcos et al. 2020). The response of shrub and herbaceous layer to overstory removal, therefore, can limit the positive effect of canopy thinning on seedling survival and growth (Montgomery 2004; Kern et al. 2006), but may also facilitate establishment under some conditions (Torroba-Balmori et al. 2015; Alday

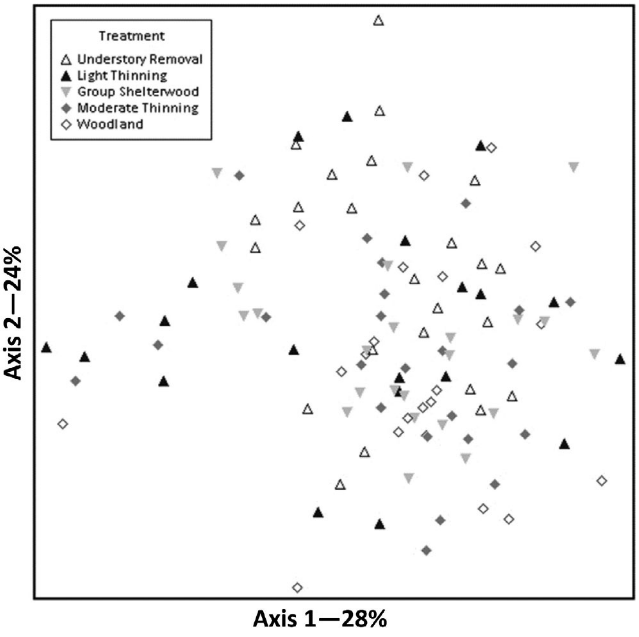

Figure 2. Non-metric multidimensional scaling ordination of plot-level groundlayer plant species cover for all 120 plots across all three sites in the post-treatment sampling (2016/17). Each point represents a single plot and symbols represent treatments.

et al. 2016). Groundlayer cover increased greatly following canopy removal in all treatments (which was also potentially related to the temporary cessation of prescribed burning during the study period), which appears to have had a negative effect on seedling survival, and likely was associated with the lack of a strong relationship between light and seedling growth because high light environments also had greater direct competition (Pubanz et al. 1989; Kaelke et al. 2001). However, in early development stages seedlings can be influenced by a number of abiotic and biotic influences beyond light availability and direct groundlayer competition, including drought, herbivory, and soil nutrient availability (Larsen & Johnson 1998; Miller et al. 2016; Lopez-Marcos et al. 2019). For example, browsing damage is a common biotic factor that influences seedlings in their first 5 years of growth and establishment (Ward et al. 2000; Torroba-Balmori et al. 2015). Seedling monitoring indicated that around 15% of live seedlings demonstrated signs of animal browse, and some component of seedling mortality was likely related to browsing damage, despite the history of deer population management at the sites. The lack of a natural regeneration response may also be related to seedling browse, acorn consumption and lack of mast years, or competition with understory species for newly available light resources (Aldrich et al. 2005; Brudvig & Asbjornsen 2009a; Dey & Kabrick 2015; Alday et al. 2016).

Although promoting oak seedling survival and eventual canopy accession is an essential component of maintaining oak-dominated ecosystems, groundlayer plant communities are an extremely important component of the biodiversity of the system and a common target of restoration activities (Abella et al. 2004; Bowles et al. 2007; Brudvig & Mabry 2008). With oak ecosystems transitioning toward shade-tolerant mesophytic dominance and high canopy density, there have been corresponding declines in understory diversity (Abella et al. 2001; Bowles et al. 2007). Therefore, the response of groundlayer cover to the overstory treatments in the SDPR project could be seen as a positive development despite the potential for competition with oak regeneration. This may be especially true as the increase in cover appeared to be largely related to native species and was associated with attendant increases in groundlayer plant richness and diversity (Bowles et al. 2000). Positive effects on groundlayer diversity suggest that increasing light availability in the understory may have promoted the establishment or increased relative dominance of formerly rare species adapted to a greater light availability (Bowles et al. 2007). Importantly, our findings do not suggest increased dominance of non-native invasive shrub species in the sites following treatment (Knight et al. 2007; Iannone III et al. 2014), which likely reflects the long history of invasive species control on these sites (D. Maurer, personal observation). Species composition of the groundlayer did not show a consistent treatment response and was highly variable spatially within and across the three study sites. The lack of a response in composition likely reflects the dominance of pre-disturbance plant community composition in systems such as this, where disturbance of the ground surface was relatively limited (Kern et al. 2006; Fahey & Puettmann 2007).

The SDPR project provides an example of the potential for adaptation of silvicultural practices to urban ecosystems where socio-ecological conditions could limit silvicultural options (Knoot et al. 2010; Johnson et al. 2020), and provides a basis for development of adaptive management strategies for oak ecosystem restoration in urban–exurban areas. Managers may be able to utilize low-intensity canopy removals as an initial treatment in an adaptive management program, paired with planting and more intensive understory management in years following thinning implementation (Albrecht & McCarthy 2006; Iverson et al. 2008). Multiple canopy interventions may be beneficial, with initial low-intensity canopy and subcanopy removal allowing increased light in the understory to promote early establishment of underplanted oaks and increased cover and diversity of groundlayer plants, followed by additional (potentially heavier) thinning to release advance regeneration of oak seedlings/saplings once they have reached a stage at which groundlayer competition would no longer provide as substantial a barrier to recruitment (Povak et al. 2008; Miller et al. 2016). Multi-cohort management techniques, such as shelterwood with reserves systems, are likely to be an important tool in management for oaks in urban–exurban landscapes. Prescribed burning following the first thinning would be beneficial to the regeneration of oaks by removing some groundlayer competition (Brose et al. 1999; Brose et al. 2001), and creating a more open understory for seedling growth and development (Albrecht & McCarthy 2006). Where use of fire is not feasible for ecological or sociological reasons, fire-surrogate treatments such as understory thinning and removal of invasive shrubs may be highly beneficial (Iverson et al. 2004). Fire or fire-surrogate treatments could then be followed by underplanting of a substantial number of oak seedlings or broadcast seeding of acorns to allow development of a robust advance regeneration layer (Dey et al. 2012). Alternatively, treatments could be timed to coincide with mast years, although such flexibility may rarely be possible in practice (Miller et al. 2016). From the perspective of oak regeneration, the somewhat high survival rate for planted seedlings in this study suggests that high-intensity or even-aged methods may not be immediately necessary to promote the development of a seedling regeneration layer in oak forests and woodlands where intensive underplanting is a possibility (Dey et al. 2012; Brose & Rebbeck 2016). However, the “bottleneck” in oak regeneration is often the accession of oak saplings into the canopy layer (Lorimer 1993; Povak et al. 2008; Alday et al. 2016), and longer-term monitoring will be needed to evaluate this essential transition.

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Supporting Information

The following information may be found in the online version of this article:

Figure S1. Pearson correlation matrix for all response and predictor variables.
Figure S2. Non-metric multidimensional scaling ordination of groundlayer cover by plot for all 120 plots across all three sites.
Table S1. Pre- and post-treatment natural oak seedling population and change from pre to post treatment condition for each treatment across all three study areas with standard errors.
Table S2. Results of linear mixed effects modeling relating survival and growth of planted seedlings to environmental conditions.
Data S1. Past restoration and management in the SDPR project areas.

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