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RESEARCH ARTICLE

Suppression of reed canarygrass by assisted succession: A sixteen-year restoration experiment

Kattia Palacio-Lopez[1,2] | Stephen M. Hovick[1] | Kali Z. Mattingly[1,3] | Leah M. Weston[1] | Nathaniel P. Hofford[1] | Logan Finley[1] | Aaron Tayal[1] | James A. Reinartz[4]

[1]Department of Evolution, Ecology, and Organismal Biology, The Ohio State University, Columbus, Ohio, USA

[2]Department of Natural Sciences, University of Houston-Downtown, Houston, Texas, USA

[3]SpecPro Professional Services Contract to the U.S. Environmental Protection Agency, Duluth, Minnesota, USA

[4]Department of Biological Sciences, University of Wisconsin-Milwaukee, Milwaukee, Wisconsin, USA

Correspondence
Kattia Palacio-Lopez
Email: palaciolopezk@uhd.edu

Stephen M. Hovick
Email: hovick.2@osu.edu

Funding information
The Ohio State University

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Abstract

1. Assisted succession could enable long-term restoration where successional trajectories stall due to competition from invasive plants. Many invasives are shade-intolerant; therefore, interventions reducing light availability should suppress invasion and re-establish successional processes. However, given how ubiquitous nonlinearities are in ecology, restoration success also depends on identifying critical system thresholds, for example invader abundances below which regeneration of desired species is possible. We report the successful use of assisted succession to restore a swamp forest invaded by *Phalaris arundinacea* (reed canarygrass; hereafter *Phalaris*), initiated by a high-density planting of woody species to outcompete *Phalaris* by reducing light availability.
2. We established five pre-planting treatments in a *Phalaris* near-monoculture in Wisconsin, USA: herbicide-only, herbicide+plough, herbicide+burn, mow+herbicide and control. In 2003 we planted 22 tree and shrub species at high densities, then in 2019 we censused the site to: (1) screen for long-term differences among treatments, (2) evaluate long-term effects of our interventions on community composition and (3) characterize the critical thresholds that enable invader suppression and restoration success.
3. Vegetation responses and light availability across our four pre-planting invader removal treatments did not differ. Late fall glyphosate application suppressed *Phalaris* long enough that a dense canopy of native woody species could establish and eventually out-shade it. Overstory tree and shrub densities of 0.071/m^2 suppressed *Phalaris* to 50% cover, but, due to nonlinearities, much higher densities were needed to reduce light availability and thus *Phalaris* cover enough to shift the system from being invader-dominated. Compositional similarities between juvenile woody species and the overstory suggest a long-term restoration success.
4. *Synthesis and applications*. Invasive species management and the restoration of target plant communities can be aided by assisting successional trajectories that have stalled. We document a restoration strategy for forests invaded by

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shade-intolerant invaders that is both effective and economical, as only a simple site preparation and single planting effort is required. Establishing a dense canopy of woody species in this way can break the feedbacks maintaining invader dominance and re-introduce feedbacks enabling long-term ecosystem recovery. We also illustrate the value of identifying critical thresholds influencing the abundance and impact of key invasive species.

KEYWORDS
forest regeneration, long-term study, nonlinear relationships, reed canarygrass, succession, swamp forest, wetland restoration

1 | INTRODUCTION

Many restoration projects fail, and those that succeed are often costly, involving recurring interventions. Principles of ecological succession may help alleviate those challenges (Bourgeois et al., 2016; Suding & Hobbs, 2009), especially when conditions lead to arrested or truncated succession, the suppression of later-successional species by early and mid-successional species (Young & Peffer, 2010). In such cases, interventions re-establishing a desired successional trajectory will help achieve restoration goals. This approach, referred to here as assisted succession, entails seeding or planting later-successional species to jump-start their population establishment and thus a stalled successional trajectory (Palomeque et al., 2017).

A common context in which arrested succession occurs is suppressed forest regeneration by established stands of invasive species (Langmaier & Lapin, 2020; Lázaro-Lobo et al., 2021; Miller et al., 2023), many of which are invasive grasses (Canavan et al., 2019; Flory & Clay, 2010; Kerns et al., 2020). Forest regeneration in many regions is imperilled, thus improved restoration strategies are urgently needed. When competition from invasive species hinders forest regeneration, assisted succession interventions would ideally transition that system to one in which later-successional species can establish (Krueger-Mangold et al., 2006). Over the long-term, re-establishing feedbacks that would allow restored communities to persist might then restore lost ecosystem services such as biodiversity provisioning or floodwater infiltration (Galatowitsch & Bohnen, 2021; Zedler, 2005). Swamp forests and other lowland forest communities disproportionately support these ecosystem services, relative to their area (Galatowitsch & Bohnen, 2021; Zedler, 2005), plus their low-elevation position on the landscape makes them especially prone to downstream movements of invasive propagules (Zedler & Kercher, 2004). Thus, the need for improved restoration strategies in invaded lowland forests experiencing arrested succession is especially great.

Understanding exactly how intervention intensity, invader abundance and invader impact co-vary is important for restoration success (Bourgeois et al., 2016; González et al., 2017). For example, if intervention intensity is linearly related to invader abundance, then we might expect a 50% change in limiting conditions (e.g. decreased light availability for a shade-intolerant invader) to yield a 50% (or otherwise proportional) decrease in invader abundance. But, if invader abundance responds nonlinearly to limiting conditions, then outcomes following a 50% change in condition will depend on the critical threshold at which abundance drops rapidly in response to condition change (Figure 1, graphs i and ii). Such nonlinearities, if unknown, can lead to either over- or underestimating the expected efficacy of an intervention (Figure 1). Similarly, if an invasive species' impacts are nonlinearly related to its abundance, then a seemingly substantial reduction in invader abundance may yield native biodiversity increases that are negligible, substantial or something in between (Figure 1, graph iii). Characterizing these nonlinearities will enable more accurate expectations for restoration outcomes. Such nonlinearities are commonplace in restoration contexts (Bourgeois et al., 2016; Lennox et al., 2011), yet their exact nature is usually unknown (Bestelmeyer, 2006). The prevalence of threshold effects in ecological systems generally has long been appreciated (Barbier et al., 2008; Dodds et al., 2010; Ficetola & Denoël, 2009), as well as the importance of characterizing them accurately in an era of rapid global change (Spake et al., 2022). Within invasion biology specifically, there is a clear and urgent need to understand such nonlinear and threshold effects (e.g. Bradley et al., 2019; Pearse et al., 2019), especially as they pertain to our most widespread invaders and the systems they impact.

Across temperate North America, reed canarygrass (*Phalaris arundinacea*, hereafter *Phalaris*) is a highly competitive and persistent invasive species (Barnes, 1999) that can establish in and degrade formerly forested wetlands. *Phalaris* is a cool-season perennial with native Eurasian and North American genotypes; however, most North American populations where *Phalaris* is dominant are non-native (Jakubowski et al., 2014; Lavergne & Molofsky, 2004). Invasive *Phalaris* tolerates a wide range of abiotic conditions (Martina & von Ende, 2013; Nelson & Anderson, 2015; Winikoff et al., 2020), but it does not tolerate shade (Perry & Galatowitsch, 2003). Thus, particularly where the restoration goal is forest (re-) establishment in *Phalaris*-invaded areas, a strategy facilitating the establishment of closed canopy should also suppress *Phalaris* and enable forest community recovery (Figure 1).

Here, we characterize nonlinear relationships among factors that drive positive long-term outcomes from an experiment designed to

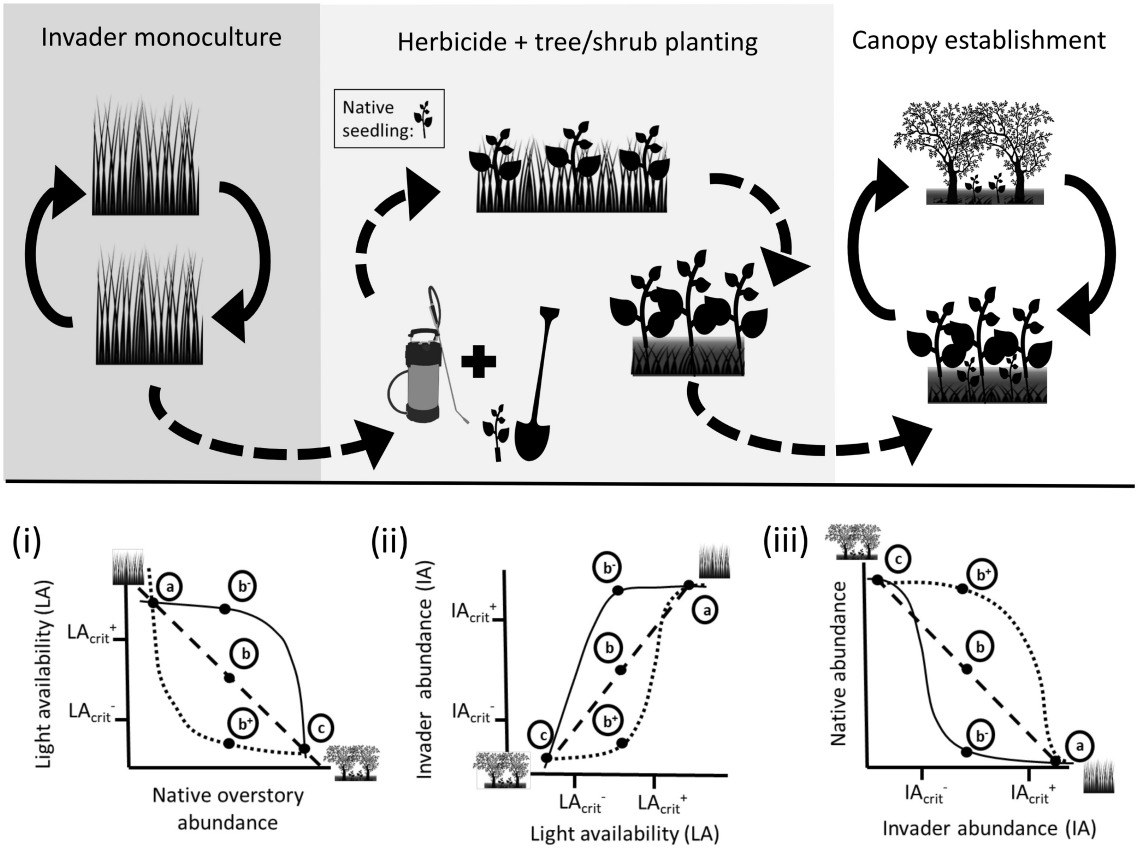


FIGURE 1 (Top panel) Conceptual diagram illustrating the intended restoration pathway (dashed arrows) via assisted succession from monoculture of a shade-intolerant invader such as *Phalaris* to restored forest (presumed to be maintained via positive feedbacks, indicated by solid arrows). (Bottom panel) Theoretical implications of linear versus nonlinear relationships among key indicators of restoration success. In plots i, ii and iii, Scenario (a) represents an invaded monoculture and scenario (c) represents negligible invader abundance due to canopy light limitation (thus negligible invader impacts). Scenario (b) is intermediate between scenarios (a) and (c), with the dashed line reflecting linear relationships in each plot. Solid lines (and the point b^-) indicate nonlinearities that would result in underperformance of management activities relative to expectations under assumptions of linearity; critical thresholds of invader abundance (IA_{crit}^-) or light availability (LA_{crit}^-) needed to achieve restoration success are thus quite low and more difficult to achieve. Dotted lines (and the point b^+) indicate nonlinearities that would lead to overperformance of management activities relative to linearity assumptions; here, critical thresholds of invader abundance (IA_{crit}^+) or light availability (LA_{crit}^+) needed to achieve restoration success are higher and thus easier to achieve relative to the linear scenario.

test whether establishment of a closed canopy suppresses *Phalaris* and allows for assisted succession in a swamp forest restoration. Hovick and Reinartz (2007) reported initial survival of 23 tree and shrub species 2 years after planting at high densities into *Phalaris* monocultures exposed to various pre-planting treatments. For this study, we report outcomes 16 years post-planting. We evaluate the suppressive effect of reduced light availability on *Phalaris* as a function of canopy establishment, as well as subsequent recruitment of native woody species as an indicator of long-term restoration success. Assessing whether the feedback cycles maintaining *Phalaris* dominance have been broken and the system has shifted to an alternative state (Figure 1) is critical for designing effective long-term restoration strategies. We, therefore, ask the following questions: (1) Have our different strategies for *Phalaris* removal yielded long-term differences in restoration outcomes? (2) How have our assisted succession interventions (*Phalaris* removal and planting) changed community composition over time? (3) What are the critical thresholds of light availability, overstory density and *Phalaris* density that enable restoration success?

2 | MATERIALS AND METHODS

2.1 | Study area and treatments

This study was conducted in southeastern Wisconsin, USA at the Huiras Lake State Natural Area (Lat: 43.5136095, Lon: −87.9828698); all required permissions to do this work were obtained from the land trust property owners before the experiment began. In 2002, 0.50 ha of a near-monoculture field of *Phalaris* was divided into 50 plots ranging from 30.3 to 154 m^2. Except for two large blocks left as eight untreated control plots, the entire site was sprayed with 0.7% active ingredient glyphosate solution in early November 2002; such late-season herbicide application is recommended for *Phalaris*

(Adams & Galatowitsch, 2006). Four pre-planting invader removal treatments were established in sprayed plots between fall 2002 and spring 2003 (Hovick & Reinartz, 2007): (1) herbicide-only (H)—no additional pre-planting treatment; (2) mow+herbicide (MH)—*Phalaris* biomass mowed in early fall 2002, before herbicide application; (3) herbicide+burn (HB)—herbicide application followed by burning *Phalaris* litter in spring 2003; and (4) herbicide+plough (HP)—herbicide application followed by ploughing in spring 2003 (Figure S1).

In spring 2003, 22 tree and shrub species were planted by hand at a density of 9500/ha (0.95/m^2) across all plots (4668 individual plants; 29–146 per plot, depending on plot size). Most species were bareroot stock, although American elm, yellow birch and basswood were small, rooted plugs and willows were live stakes. Initial planting numbers varied widely among species, due to availability (Table 1). No additional *Phalaris* management occurred post-planting.

2.2 | Sampling design

We surveyed vegetation in July 2019, complementing this data set with survival data from summer 2003 and 2004 (Hovick & Reinartz, 2007). The 2019 survey had three main components:

2.2.1 | Groundcover

We quantified *Phalaris* cover and that of any non-*Phalaris* herbaceous species, recording visual estimates of each group in two 1 m^2 quadrats per plot. We used modified Daubenmire cover classes: <5%, 5%–24%, 25%–49%, 50%–74% and 75%–100% (Daubenmire, 1959), allowing the sum of *Phalaris* and non-*Phalaris* cover to exceed 100%. For each quadrat, we also estimated cover of litter, vegetation or bare soil, constraining the summed estimates of these components to equal 100%. Prior to analysis, cover estimates were transformed to the midpoint of each cover class (restricting midpoints to minimum 2.5%, maximum 87.5%) and averaged to yield a single estimate per plot.

2.2.2 | Tree and shrub abundance

To characterize the woody plant community, we separately quantified species-specific abundances in the overstory, sapling layer and seedling layer. In the overstory, we recorded all woody species in the plot ≥2.5 cm diameter at breast height (DBH). Due to widespread mortality in some species (most notably green and black ash

TABLE 1 Per-species abundance change over time.

Scientific name	Common name	*n*, planted	*n*, 2003	*n*, 2004	*n*, 2019
Trees					
Acer rubrum	Red maple	488	199	60	2
Acer saccharinum	Silver maple	108	50	13	4
Betula alleghaniensis	Yellow birch	93	3	0	0
Betula papyrifera	Paper birch	125	53	8	1
Fraxinus spp.	Ash	874	554	543	785
Larix laricina	Tamarack	576	245	242	136
Populus tremuloides	Aspen	70	44	47	18
Thuja occidentalis	White cedar	576	238	115	2
Tilia americana	Basswood	52	22	7	2
Ulmus americana	American elm	49	13	12	12
Shrubs					
Cornus spp.	Dogwood	778	461	430	82
Lonicera spp.	Honeysuckle	0	0	0	3
Rhamnus cathartica	Buckthorn	0	0	0	1
Ribes americanum	Black currant	49	32	38	0
Rubus occidentalis	Black raspberry	49	21	11	0
Salix bebbiana	Bebb's willow	26	1	14	9
Salix discolor	Pussy willow	238	22	48	7
Salix petiolaris	Slender willow	245	15	104	30
Sambucus canadensis	Elderberry	70	40	40	36
Viburnum lentago	Nannyberry	129	58	65	30
Viburnum opulus	Highbush cranberry	73	22	39	6

Note: For 2019, only individuals from the overstory are shown (note that zero abundances in 2019 for the understory species black currant and black raspberry reflect this sampling strategy). Saplings and seedlings are reported in Figure 2.

[*Fraxinus americana* and *F. nigra*]), we noted whether overstory individuals were alive (foliage green), dead (no green foliage) or resprouting (most foliage dead, but some recent growth with green leaves). We sampled saplings within two 2 × 2 m sampling quadrats per plot (each of which contained a groundcover sampling plot at one corner), counting as saplings all woody species >1 m tall and <2.5 cm DBH. We sampled seedlings using four 1 m^2 quadrats per plot, positioning two quadrats at opposite corners within each sapling quadrat. We counted as seedlings all woody species <1 m but >30 cm in height. Individuals in each stratum were identified to species whenever possible, except for lumping together ashes (as *Fraxinus* spp.) and dogwoods (*Cornus sericea* and *C. stolonifera* as *Cornus* spp.).

2.2.3 | Light availability

Total light availability above the herbaceous level was estimated as percent canopy openness using hemispherical photos. We took two pictures per plot, centred in each sapling quadrat and analysed with Gap Light Analyser, Version 2.0 (Frazer et al., 1999). Data were averaged to yield a single estimate per plot.

2.3 | Statistical analysis

Using census data from 3 years (2003, 2004, 2019), we quantified density and survival trajectory. Density is per-plot abundance of a given species divided by plot area (overstory) or sampling area (saplings, seedlings). Survival trajectory is per-species density, relative to the number of planted individuals (2003) or relative to density in the preceding survey (2004, 2019). Survival trajectory in 2019 was divided by 15 to compare all density changes on a per-year basis.

As preliminary tests of differences among removal treatment types, we compared light availability, *Phalaris* cover and overstory density across treatments using linear mixed models (R Core Team, 2021) lme4::lmer, (Bates et al., 2015); car::Anova, (Fox & Weisberg, 2019) with random effects, included to account for spatial non-independence among plots within blocks and among blocks themselves (Figure S1). All pairwise comparisons among removal treatments and controls were then contrasted with Tukey's post-hoc tests. Seeing negligible differences among removal treatments themselves, as expected, we shifted our focus to be on *Phalaris* removal vs. control differences in density, survival trajectory and groundcover percentages. We present linear mixed models followed by Dunnett's post-hoc tests comparing each treatment to control (emmeans, Lenth et al., 2020). Most response variables were non-normal, but model residuals were largely normally distributed, supporting model fits.

We estimated nonlinear relationships at the plot scale (n = 50), combining data from all pre-planting treatments to describe (1) the ability of increased overstory densities to decrease light availability and (by extension) *Phalaris* cover, (2) the ability of decreased light to suppress *Phalaris* and (3) the impact of *Phalaris* cover in suppressing sapling density. These models allowed us to estimate, for example, the overstory density or reduction in light availability required to suppress *Phalaris* to a target percent cover. Preliminary analyses indicated no support for treatment-specific models and that these relationships were best characterized using log-logistic curves (drc::drm, Ritz et al., 2015), with slope and inflection point the estimated parameters. We fixed lower and upper limits to realistic ranges of y: 0 to 100 for *Phalaris* percent cover or light availability, and 0 to 3.125 saplings/m^2 (the maximum observed value) for sapling density. We used these curves to estimate predictor values required to suppress *Phalaris* to 50%, 25% and 10% cover. For the three models with *Phalaris* cover as a variable, we achieved estimates directly by substituting the target percentage and solving for the corresponding value. We used model-estimated light availability corresponding to 50%, 25% and 10% *Phalaris* cover to predict overstory densities required to achieve those light levels. These estimated nonlinear relationships imply causal direction, but to examine other relationships lacking clear causality we calculated Pearson correlations (stats::cor, stats::cor.test, R Core Team, 2021).

3 | RESULTS

3.1 | Differences among *Phalaris* removal treatments

Comparisons of key habitat variables among treatments showed that any type of invader removal treatment lowered light levels and *Phalaris* cover relative to control, but that there were no significant differences among removal treatments (Table S1). Overstory density was increased by all treatment types but did not differ significantly from each other or controls (Table S1).

3.2 | Community dynamics over time

3.2.1 | Post-planting survival and recruitment

Across treatments, all species surviving the first 2 years post-planting were present in 2019 (Table 1; Figure 2). However, the abundance of some species declined precipitously over that time (e.g. white cedar, 98% decline; red maple, 97%; dogwoods, 81%; and willows, 35%–85%). Survival trajectories indicated that mortality occurred mostly in the first growing season (Figure S2a), with some additional mortality between 2003 and 2004 (Figure S2b). Net annual losses between 2004 and 2019 were near zero (Figure S2c).

3.2.2 | Contemporary overstory composition

In 2019, the highest density trees in the overstory were ash, tamarack and aspen (Figure 2a). The highest density shrubs were

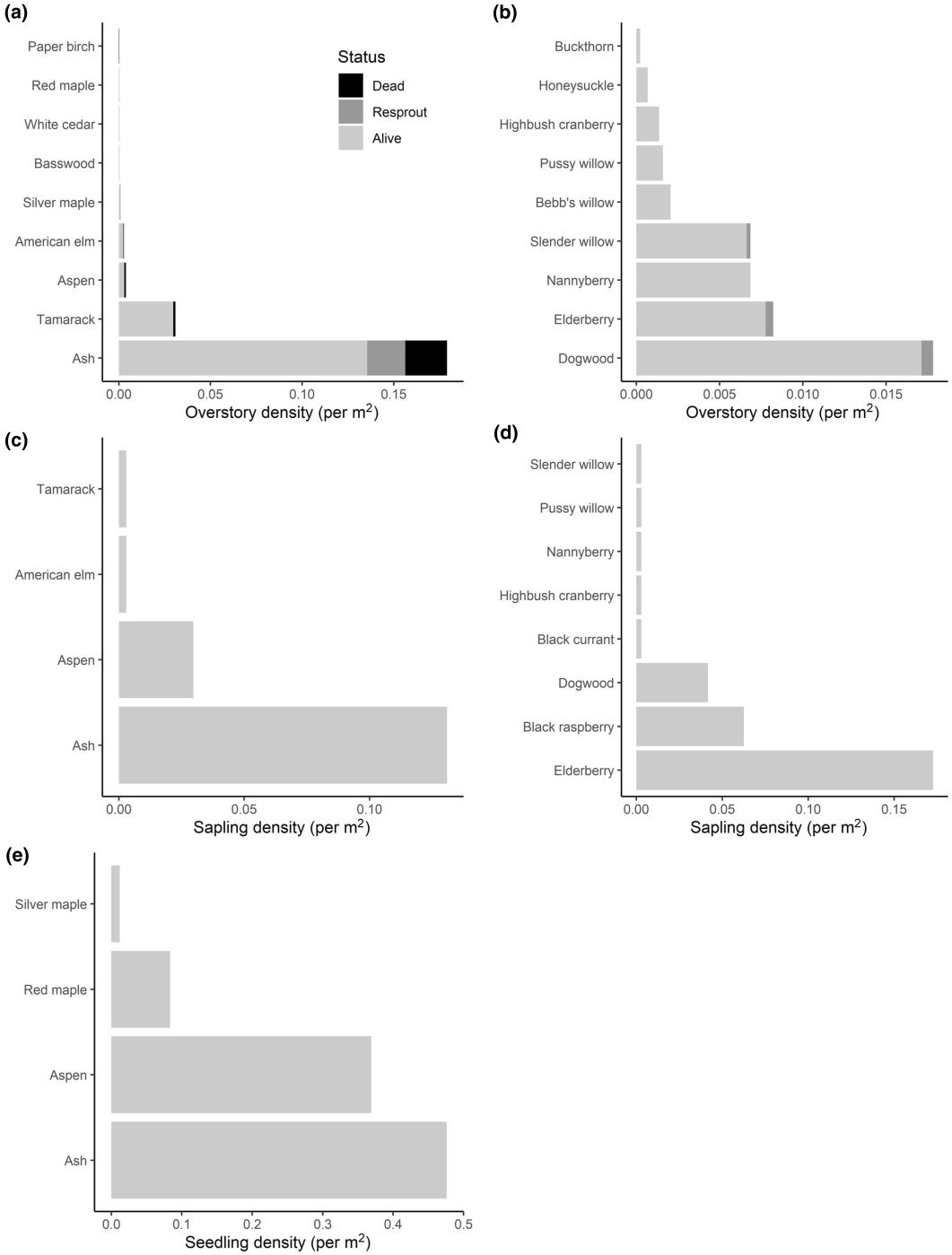


FIGURE 2 Density of tree and shrub species at the current overstory (a and b), sapling (c and d) and seedling layers (e) across all treatment plots (control omitted). Species status (alive, dead or resprouting) as defined in Section 2.

dogwoods, elderberry, nannyberry and slender willow (Figure 2b). Despite substantial mortality, including from emerald ash borer (EAB) (*Agrilus planipennis*), most overstory individuals were alive (Figure 2). Of the currently high abundance species, aspen and elderberry were planted in low numbers ($n < 100$) but had high survival (>50%), and slender willow had relatively low survival (15%; Table 1). Greater overstory densities were nonlinearly associated with reduced *Phalaris* cover (Hill slope = −0.719 ± 0.174 SE, $p < 0.001$, Figure 3b). *Phalaris* reductions likewise corresponded with increased overstory richness and diversity (Figures S3a–d and S4a–d).

Tree and shrub abundance in 2019 was lower than both the initial number planted and abundances at the end of the second growing season (Table 1). This latter pattern did not hold for American elm, which exhibited no change from 2004 to 2019, nor for ash, which exhibited a 45% increase in that period (Table 1). For ash this shift largely reflected a doubling in density from 2004 to 2019 under the herbicide-only treatment (Figure S5). Overall, abundance changes

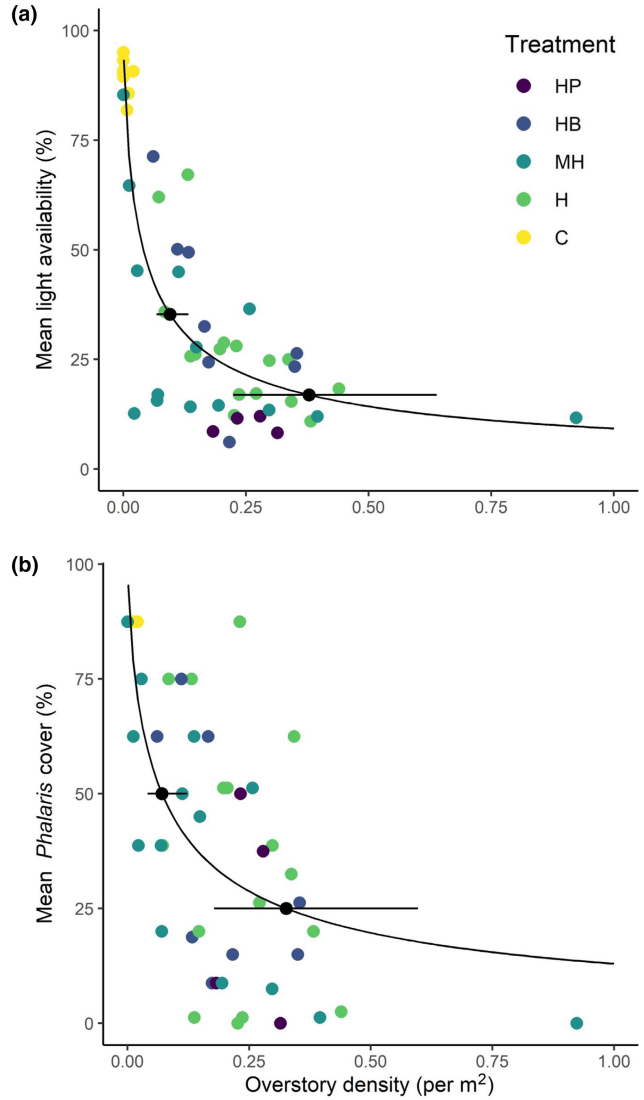


FIGURE 3 The influence of overstory density on: (a) light availability, (b) *Phalaris* groundcover, with threshold responses ±95% CI indicated for 50% and 25% *Phalaris* cover. The five treatments are: (HP)—herbicide+plough; (HB)—herbicide+burn; (MH)—mow+herbicide; (H)—herbicide-only; and (C)—control.

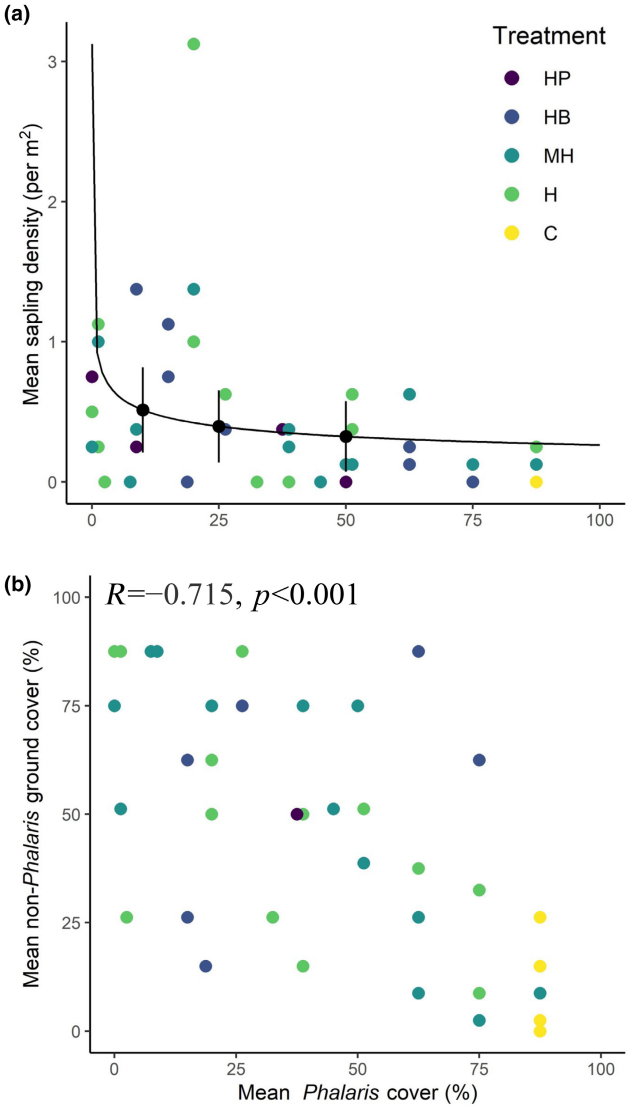


FIGURE 4 Influence of *Phalaris* groundcover on: (a) sapling density, with threshold *Phalaris* percent predictions ±95% CI; (b) non-*Phalaris* groundcover, with Pearson correlations shown. Treatment abbreviations as in Figure 3.

through 2004 reflected mortality of planted individuals only (SMH, pers. obs.), whereas changes from 2004 to 2019 reflect some unknown combination of mortality and colonization by new individuals.

3.2.3 | Prospective woody species recruitment and understory regeneration

The composition of juvenile woody species in the sapling layer was similar to that in the overstory, with ash, tamarack, aspen and American elm the most abundant trees (Figure 2a,c) and dogwood and elderberry among the most abundant shrubs (Figure 2b,d). Despite being common in the overstory, nannyberry and slender willow saplings were relatively uncommon (Figure 2b,d). Black raspberry saplings also occurred at high densities (Figure 2d), although its small stature prevented inclusion in the overstory census. Overall, shrubs were more abundant than trees, making up 64% of saplings. Sapling densities were apparently constrained nonlinearly by higher *Phalaris* cover (Hill slope = −0.330 ± 0.189 SE, $p = 0.088$, Figure 4a), as was sapling richness and diversity (Figure S3e–h).

In control plots covered mainly by *Phalaris*, we found no recruitment of woody seedlings. Across the remaining 168 quadrats we found 158 tree seedlings (0.940 seedlings/m^2), composed of ash (50%), aspen (39%), red maple (9%) and silver maple (1%) (Figure 2e).

Average groundcover across all plots was mostly vegetation (85%), with smaller proportions litter (10%) or bare ground (5%). These proportions were similar across treatments, although controls had higher *Phalaris* cover and lower non-*Phalaris* cover than all invader removal plots (Table 2). *Phalaris* cover and non-*Phalaris* cover were negatively correlated (Figure 4b).

TABLE 2 Groundcover reported as means and standard errors (SE) across quadrats.

	Bare		Litter		Vegetation		*Phalaris* cover		Non-*Phalaris* cover	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Herbicide + Plough	7.50[a]	4.33	12.50[a]	3.23	80.00[a]	4.56	24.06[b]	8.16	71.88[b]	6.58
Herbicide + Burn	9.06[a]	5.98	10.31[a]	4.13	80.63[a]	6.66	35.47[b]	6.84	55.31[b]	7.93
Mow + Herbicide	5.71[a]	2.10	7.50[a]	2.21	86.79[a]	3.59	39.20[b]	6.48	52.68[b]	6.58
Herbicide	5.63[a]	1.62	13.28[a]	1.93	80.94[a]	2.63	36.48[b]	6.03	48.44[b]	5.40
Control	0.00[a]	0.00	4.69[a]	2.03	95.31[a]	2.03	87.50[a]	0.00	6.88[a]	2.57

Note: Treatment means sharing a superscript letter with control means do not differ from control (Dunnett's post-hoc comparisons).

3.3 | Critical thresholds of light availability, overstory density and *Phalaris* cover

Invader removals and the subsequent planting of woody species successfully decreased light availability, which reduced *Phalaris* cover. We estimate reductions in light availability would need to reach ~35% to achieve 50% *Phalaris* cover, ~17% to achieve 25% *Phalaris*, and ~8% to achieve 10% *Phalaris* (Figure 5). This causal relationship can also be approximated by characterizing *Phalaris* abundance reductions via woody overstory establishment (Figure 3b) that decreases light availability (Figure 3a). On this basis, and at this early stage of forest development, achieving 50% *Phalaris* cover requires an estimated 0.071 ± 0.019 overstory trees and shrubs/m^2 (=710/ha; Figure 3b). Similar estimates are obtained by using 35% light availability as a proxy for achieving 50% *Phalaris* cover (Figure 5), yielding a target overstory density of 0.095 ± 0.016/m^2 (Figure 3a). Due to nonlinearities, a target of 25% *Phalaris* cover requires overstory density over 3.5 times higher (0.326 ± 0.098/m^2), while a 10% *Phalaris* target requires 1.502 ± 0.927/m^2, a potentially unrealistic density falling above any observed at our site (Figure 3b). Using 17% light availability as a proxy for 25% *Phalaris* cover (Figure 5) yields a similar estimate (0.379 ± 0.099/m^2; Figure 3a), as does the 10% *Phalaris* proxy of 8% light (1.224 ± 0.516/m^2; Figure 3a).

The final nonlinear relationship we characterized examined the impact of *Phalaris* cover on tree and shrub sapling densities (Figure 4a). Based on this, we expect 0.324 ± 0.128 saplings/m^2 with 50% *Phalaris* cover, 0.396 ± 0.131 saplings/m^2 with 25% *Phalaris* cover and 0.513 ± 0.155 saplings/m^2 with 10% *Phalaris* (Figure 4a).

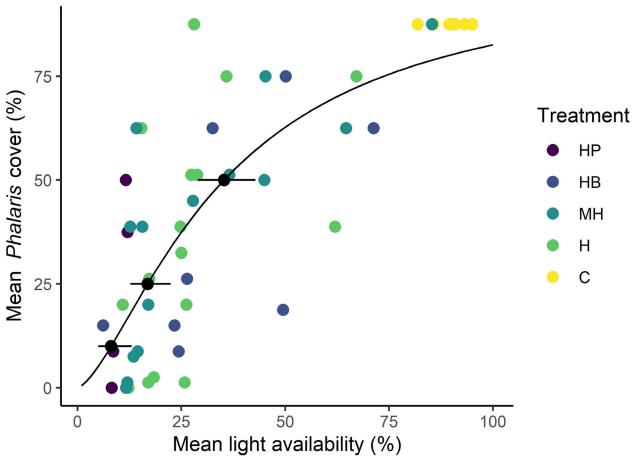


FIGURE 5 Relationship of *Phalaris* groundcover with light availability. Threshold *Phalaris* percent responses with ±95% CI. Treatment abbreviations as in Figure 3.

4 | DISCUSSION

We used assisted succession to restore swamp forest from a near-monoculture of *Phalaris*, demonstrating long-term effectiveness of a single pre-planting intervention, followed by high-density planting of woody natives. Even without follow-up treatments *Phalaris* declined, enabling overstory establishment and regeneration within 16 years. Long-term restoration success is often limited by seedling establishment, which is subject to climate variability (Orrock et al., 2023), deer herbivory (Cogger et al., 2014; Miller-Adamany et al., 2019; Thomsen et al., 2012) or competition from invasive species (Fierke & Kauffman, 2005; Langmaier & Lapin, 2020; Lázaro-Lobo et al., 2021; Matthews et al., 2019; Miller et al., 2023). The presence of overstory species in the sapling and seedling layers at our site, therefore, suggests *Phalaris* will continue to be suppressed via light limitation (Figure 1) as this forest matures (Flory & Clay, 2010; Young et al., 2017).

4.1 | The effect of different pre-planting treatments

Relative to controls, herbicide treatments complemented by burning, mowing or ploughing had similar effects in our study to herbicide treatments alone. This result supports two key inferences: (1) our herbicide treatment was effective and (2) additional pre-planting treatments yielded no measurable effectiveness gains. Although a single glyphosate treatment rarely kills *Phalaris* outright (Adams & Galatowitsch, 2006; Apfelbaum & Sams, 1987; Kilbride & Paveglio, 1999), herbicide is an important tool for impeding its growth temporarily. However, the *timing* of herbicide application matters greatly, with late-season applications more effective at reducing *Phalaris* biomass than early season applications. Late-season applications can also reduce non-target impacts because applications

occur when *Phalaris* is still actively photosynthesizing but after most native species have senesced (Adams & Galatowitsch, 2006; Miller-Adamany et al., 2019; Thomsen et al., 2012). A single well-timed treatment can thus create enough of an opportunity window for planted species to establish and grow above *Phalaris* before it fully recovers (Hovick & Reinartz, 2007). The second inference, that our other pre-planting treatments added little to the herbicide treatment, aligns with other studies reporting that without herbicide these treatments do not reduce *Phalaris* (Clark & Thomsen, 2020; Foster & Wetzel, 2005; Sinks et al., 2021). Burning can reduce seed density (Adams & Galatowitsch, 2006), and ploughing can increase herbicide effectiveness by damaging rhizomes (Thomsen et al., 2012), but these methods are rarely successful when used alone. Our earlier recommendation (Hovick & Reinartz, 2007) favoured the herbicide-only treatment over those with additional manipulations due to simpler logistics and thus lower costs. Based on data 16 years post-planting, that same recommendation still holds.

One adjustment that could increase restoration success would be re-applying herbicide post-planting to lengthen the establishment window for planted stock. This could either be done with grass selective herbicides (applying even when planted stock is actively growing) or with glyphosate in late fall once planted stock has senesced for winter. At Huiras Lake a single glyphosate application was effective, but at a neighbouring site with similar conditions where *Phalaris* was less affected by our herbicide treatment, mortality of planted stock from 2004 was nearly 100% by 2019 (SMH, pers. obs.). A follow-up herbicide application may have alleviated this restoration failure.

4.2 | Contemporary and future community composition

Species abundances decreased immediately following our initial planting but stabilized soon thereafter, indicating juvenile establishment was a critical bottleneck in the restoration process, as expected (Orrock et al., 2023). In 2019, seven species still occurred in numbers ≥20% of the original number planted: nannyberry (23%), tamarack (24%), aspen (25%), American elm (25%), Bebb's willow (35%), elderberry (51%) and green/black ash (90%). Elderberry and ash increased in at least some individual treatments, and both ash and aspen seedlings and saplings were common, indicating recruitment from the seed bank or surrounding areas (Flory & Clay, 2010). Overall, we recommend these eight species for similar restorations, updating our earlier 'top ten' list (Hovick & Reinartz, 2007). From that original list, highbush cranberry, red-osier dogwood and silky dogwood had high initial survival but substantial mortality between 2004 and 2019 (Table 1). Black currant was included initially, but its small stature limits its ability to out-shade *Phalaris*. Despite some uncertainty because they were planted in relatively small numbers, we add American elm and Bebb's willow to our original recommendations because of their high long-term survival rates.

Survival and recruitment dynamics of planted woody species, plus patterns in the herbaceous community, provide hints about future successional trajectories. First, the groundcover was predominantly herbaceous species other than *Phalaris*. Second, tree and shrub seedlings were abundant across invader removal treatments. Lastly, sapling densities suggest native tree and shrub abundances will continue to increase. Re-invasion by *Phalaris* thus seems unlikely because native species are recruiting into available niches, reflecting a system-wide shift from invader dominance to native dominance (Figure 1).

Two genera from our initial planting show particularly interesting dynamics with implications for restoration success. First, despite high ash abundance, invasive EAB drove widespread ash mortality at our site, as is common throughout northeastern North America (Cappaert et al., 2005). EAB impacts mostly larger trees (DBH ≥5 cm), but saplings and resprouting individuals ≥2.5 cm are also susceptible (Aubin et al., 2015; BenDor et al., 2006). The age structure of ash in our study aligns well with these thresholds, as our living trees were mostly ≤5 cm DBH. Mortality of larger ashes may limit future seed production, since flowering first occurs at 8–10 cm DBH (Kappler et al., 2019; Klooster et al., 2014). This will likely preclude long-term restoration benefits of shade from ash. Light gaps from dead ash trees additionally represent opportunities for *Phalaris* recolonization, so EAB-induced ash mortality is a management concern for the foreseeable future.

Maples also displayed intriguing dynamics over time: high mortality of the original cohort and absence in the sapling layer, coupled with abundant maple seedlings. Red and silver maple seeds often germinate immediately after dispersal (Gabriel, 1990; Walters & Yawney, 1990), so the seedlings we observed likely dispersed from the surrounding forest and may yet succumb to the unknown factors limiting maple establishment at our site. We speculate deer browsing may have contributed to these losses, given documented maple preferences by deer (De Jager et al., 2013; Miller-Adamany et al., 2019) and widespread deer impacts on forest regeneration (Frerker et al., 2014; Miller et al., 2023).

4.3 | Implications of nonlinearity for restoration outcomes

Nonlinear relationships between invader abundance and invader impact are common (reviewed by Bradley et al., 2019). Characterizing nonlinear and other mechanistic relationships underlying restoration outcomes is clearly important for matching expectations to reality. Following our conceptual diagram (Figure 1), some indicators of restoration success (i.e. sapling densities) require reductions in *Phalaris* cover to ≤10% (compare Figure 4a with Figure 1, graph ii); this result coincides with similar recommendations that *Phalaris* cover be reduced to ≤10%–15% to enable restoration success (Fierke & Kauffman, 2005; Jenkins et al., 2008; Thomsen et al., 2012). Knowing such thresholds exist can clarify management goals (Figure 1, graph iii) and enable better decision-making (e.g. deciding when to conduct follow-up herbicide treatments to reach critical overstory threshold densities; Figure 1, graph i). We speculate that other monoculture-forming invasive grasses will require suppression beyond similarly

low abundance thresholds to enable restoration success, thus the patterns we identify here may be broadly generalizable (even if the exact thresholds vary by invader).

Based on the relationship between light availability and *Phalaris* abundance (Figure 5), we predict a reduction in canopy openness to ≤8% is needed to suppress *Phalaris* to ≤10% cover. If these relationships had instead been estimated as linear with our data (Figure 1, graph ii), target light availability to yield 10% *Phalaris* cover would be near zero, setting potentially impossible management goals. To our knowledge, the only other assessment of *Phalaris* abundance in relation to a light availability continuum (Maurer & Zedler, 2002) found that *Phalaris* biomass declined linearly with decreasing light availability; however, their experiment was harvested after <1 month, so nonlinear patterns may have had insufficient time to develop. Additional published data are roughly consistent with our findings despite not fully characterizing this relationship, with reductions in *Phalaris* shoot biomass of 40% (Adams & Galatowitsch, 2006) and 52% (Perry & Galatowitsch, 2004) associated with approximately 40% light availability (cf. Figure 5). In both cases, such biomass reductions were insufficient to enable persistence of native competitors, as our models suggest. In field surveys across restoration sites in Canadian riparian forests, Bourgeois et al. (2016) identified 40% canopy cover as a critical threshold for forest succession to proceed. According to our data, greater canopy closure than this will be needed if *Phalaris* is limiting succession, but, of course, the critical threshold in any given site will depend on what factors limit restoration success there.

Light reductions in response to canopy densities at our site were also nonlinear, with light availability (and thus *Phalaris* abundance) declining rapidly as overstory density increased from low levels (Figure 3). Such reductions in light availability are more pronounced than expected based on linear assumptions (Figure 1, graph i). Unfortunately, we lacked enough sampling plots with overstory densities near the upper range to characterize light extinction and *Phalaris* suppression values most relevant to restoration. Overstory densities needed to yield *Phalaris* cover low enough to enable native plant establishment (10%) were estimated at 1.502/m^2, roughly an order of magnitude greater than target sapling densities in healthy regenerating forests of the Northeastern US (see tab. 2 in Miller et al., 2023). Even if this is an overestimate, our initial planting density of 0.950/m^2 may have been insufficient to shift our system from *Phalaris* monoculture to swamp forest, had it not been for additional natural recruitment. High-density plantings are clearly a requirement for this method's success; more work will be needed to characterize where exactly that threshold lies and how generalizable those patterns are.

AUTHOR CONTRIBUTIONS

Stephen M. Hovick and James A. Reinartz conceived the study and designed methodology. Kattia Palacio-Lopez, Stephen M. Hovick, Kali Z. Mattingly, Leah M. Weston, Nathaniel P. Hofford, Logan Finley, Aaron Tayal and James A. Reinartz collected data. Kattia Palacio-Lopez, Kali Z. Mattingly and Stephen M. Hovick analysed the data. Kattia Palacio-Lopez and Stephen M. Hovick led the writing. All authors contributed critically to the drafts and gave final approval.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data and code associated with this study are available via Dryad Digital Repository https://doi.org/10.5061/dryad.r7sqv9sks (Palacio-Lopez et al., 2024).

ORCID

Kattia Palacio-Lopez https://orcid.org/0000-0002-9475-270X
Stephen M. Hovick https://orcid.org/0000-0003-1774-9686
Kali Z. Mattingly https://orcid.org/0000-0001-7987-6061
Leah M. Weston https://orcid.org/0000-0002-8646-3190

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Figure S1: Experimental design as applied across the 1.2 h area at Huiras.

Figure S2: Per-year changes in woody density across surveys: (a) from planting to 2003, (b) 2003 to 2004, (c) 2004 to 2019.

Figure S3: Richness and diversity (mean ± SE across plots) among the different treatments for the current overstory layer trees (a, b) and shrubs (c, d) and sapling layer trees (e, f) and shrubs (g, h).

Figure S4: Relationship of Phalaris ground cover with richness and diversity for overstory layer trees (a, b) and shrubs (c, d), with Pearson correlations shown.

Figure S5: Density trajectory of ash across the different treatments since planting (0) throughout the different surveys (03: survey from 2003, 04: survey from 2004, 19: survey from 2019).

Table S1: Key habitat variables reported as means and standard errors (SE) across quadrats.

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