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TECHNICAL ARTICLE

Revegetation to slow buckthorn reinvasion: strengths and limits of evaluating management techniques retrospectively

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Understanding the long-term success of ecosystem restoration following invasive plant removal is challenging. Long-term experiments are costly and slow to yield results, while management decisions must often be made immediately. Alternatively, retrospective studies can leverage contrasting historical management strategies to provide insight into long-term vegetation responses. We used a retrospective approach to evaluate how management techniques and site characteristics affected re-establishment of an invasive shrub, *Rhamnus cathartica* (common buckthorn), in midwestern North America. Following removal, buckthorn re-establishes rapidly from resprouts and seeds, so follow-up control is required but often lacking. We hypothesized that revegetating using native herbaceous seed after removing buckthorn increases herbaceous cover that competitively suppresses buckthorn regeneration, to a degree. We surveyed 46 management units at 24 sites. Revegetated units had higher herbaceous cover, lower buckthorn cover, and half the ratio of buckthorn:herbaceous cover compared with unseeded units. These effects, although considerable on average, were detected against a background of high variance. Seeding increased herbaceous cover and reduced buckthorn relative abundance more strongly on less acidic, more clayey soils and where follow-up herbicide was not applied. Additional variability in revegetation impacts may have arisen from buckthorn resprouts having a head-start on planted seeds. Only one site had both seeded and unseeded management units. This lack of blocking—a common challenge in retrospective studies—reduced statistical power. This investigation illustrates how retrospective studies can offer relatively inexpensive first assessments of long-term effects of management techniques; for more rigorous inference, researchers can partner with managers to conduct long-term experiments.

Key words: buckthorn, experimental design, invasive plant management, researcher-manager partnerships, retrospective survey, revegetation

Implications for Practice

- After removing the invasive shrub *Rhamnus cathartica* (common buckthorn), revegetating with native species may help to reduce the rate and extent of reinvasion. This result likely also applies to other non-native invasive shrubs.
- Follow-up control of vigorous buckthorn resprouts using methods such as foliar herbicide is likely a necessary complement to re-seeding, but further research is needed on how to prevent follow-up control from hampering establishment of seeded native plants.
- Revegetation may be more useful for suppressing buckthorn regeneration on less acidic, more clayey soils.

Introduction

Managing invasive plant species and restoring native plant communities is a central goal for many land managers. Understanding the long-term success of invasive plant removal and ecosystem restoration is limited by the short duration of much research because successional changes following invasive plant removal can take many years (Kettenring & Adams 2011). Long-term experiments may be precluded by logistics and funding, or because management is needed before newly initiated long-term experiments yield results. One alternative is a retrospective approach, which we define as using a consistent methodology to survey areas previously subjected to contrasting

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management techniques. "Retrospective" has been used in this way by studies of long-term vegetation response to management treatments (e.g. Grady & Hart 2006; Harms & Hiebert 2006); it has also been used to refer to longer-term paleoecological studies beyond our scope (Davis 1989).

Retrospective studies can leverage contrasts in historical management to provide timely and cost-effective insights into long-term processes (Grady & Hart 2006), although they also present challenges. Retrospective studies can be less costly than manipulative experiments because they do not require establishing or maintaining experimental units. Accordingly, retrospective studies can sample a wider range of environmental conditions. However, retrospective studies are limited from an experimental design viewpoint because they rely on uncoordinated efforts at different times, using different methods, and in diverse systems; when this precludes blocking and randomization, unmeasured variables can confound the effects of the management strategy of interest. Such confounding may either create apparent effects of the management strategy that are in fact spurious or obscure its real effects. We can reduce the likelihood of confounding by measuring and analyzing relevant covariates. These covariates may also help us to understand variation among sites in the management strategy's effects.

To illustrate some of the strengths and shortcomings of the retrospective approach and highlight opportunities for collaboration between researchers and managers, we present a retrospective survey evaluating the impacts of native plant revegetation on re-establishment of the invasive shrub *Rhamnus cathartica* L. (common buckthorn, hereafter "buckthorn"). Buckthorn is widely distributed and invasive throughout eastern North America, where it fundamentally alters ecosystem structure and function (Kurylo et al. 2007). By forming dense monospecific stands, it shades out native understory plants, inhibits canopy regeneration, reduces forest value to wildlife, and impedes forest use by humans; it is also an intermediate host for agricultural pests (Knight et al. 2007). Therefore, buckthorn removal is a common goal for land managers.

Mechanical and chemical methods of buckthorn removal are costly yet often ineffective in the long run (Delanoy & Archibold 2007). Following removal, buckthorn re-establishes in two ways. First, stumps can resprout vigorously, often resulting in a denser stand within a few years than before removal (Delanoy & Archibold 2007; Larson et al. 2011). Second, buckthorn invasion typically leaves a prolific seed bank that can germinate for up to 5 years (Archibold et al. 1997); even after this, birds deposit buckthorn seeds from neighboring areas. Therefore, follow-up control of resprouts and seedlings is needed, especially in the early years following removal, but continuing indefinitely. Such follow-up control using herbicide is impeded by high costs and concern about non-target impacts on native vegetation, insects, and water quality. Follow-up control using burning is often impeded by lack of fuel or by regulations. Accordingly, there is a need for restoration methods that require less follow-up control after buckthorn is removed.

Buckthorn re-establishment is accelerated by high resource availability and low competition conditions created by the removal of dense buckthorn stands (Heneghan et al. 2009). Seed banks often lack other species to compete with re-establishing buckthorn (Archibold et al. 1997; Knight et al. 2007). The low biotic resistance of invaded systems following removal favors both buckthorn resprouts and buckthorn seedlings. This is exacerbated by buckthorn's interaction with non-native earthworms, which results in bare soil and accelerated nitrogen cycling that favor buckthorn reinvasion (Heneghan et al. 2009; Roth et al. 2015). In grassland restorations, native species are commonly seeded after removing invasive species which effectively elevates native biodiversity and competitive biotic resistance to invader re-establishment (Larson et al. 2011). However, revegetation following invasive species removal is rarely used or tested in woodlands (Schuster et al. 2018).

After removing dense buckthorn stands from woodlands, some managers revegetate using mixes of native grass, sedge, and forb seed to increase the abundance of native herbs and potentially competitively suppress buckthorn regeneration. However, this practice is relatively uncommon, partly because we do not know (1) whether the high cost of revegetation is repaid by reduced need for follow-up control, and (2) the conditions in which revegetation is most impactful. This information is urgently needed to inform ongoing management, yet long-term experiments will take several years to yield definitive results. Therefore, we conducted a retrospective study by surveying 46 management units to evaluate the efficacy of revegetation for suppressing buckthorn re-establishment and how this depends on site characteristics and other management. We hypothesized that revegetating using herb seed after removing buckthorn increases herb cover and consequently suppresses regenerating buckthorn cover and reduces our focal response metric, the ratio of buckthorn:herb cover.

Methods

Survey Design and Measurements

We considered sites within 25 miles of Minneapolis/Saint Paul, Minnesota, USA, where buckthorn had been removed within 6 years preceding our survey (2010–2016) and where managers had maintained records of management activities over that period. We identified 24 properties meeting these criteria and surveyed them June–August 2016. At each property, we surveyed 1–9 management units (total 46 units, Fig. S1 and Table S1). We defined management units as contiguous areas that were subject to a single, consistent management regime and were relatively similar abiotically (slope, aspect, soil) and biotically (canopy and understory cover and composition). We identified management units in the field based on management history and our observations of abiotic and biotic factors. To independently assess heterogeneity within management units, we later located each management unit on a soil map (Soil Survey Staff 2020). Soil map units—each typically a phase (e.g. slope) subdivision of a soil series—"have similar use and management requirements" (Soil Survey Staff 2020). Of the 46 management units, all fell within single soil map units, except for three management units which each straddled two map units. In each of the latter three cases, the two map units were of the same soil series and differed only in slope (e.g. Mahtomedi loamy sand, 0–6% slopes bordering on Mahtomedi loamy sand, 6–12% slopes; Table S1). Overall, these soil map results broadly support the homogeneity of our management units.

We consulted managers to characterize each management unit's history including when buckthorn was removed; the removal method; whether and when it was seeded after removal; the timing and composition of seeding; whether and when follow-up foliar herbicide was applied; and whether and when follow-up prescribed burns were used. We characterized management units seeded at least 1 year prior to our survey as seeded, because units seeded the same season as our survey did not yet have measurable establishment of seeded species.

In each management unit, we surveyed three 2 m × 2 m plots. To place plots, we spaced three positions evenly along a line spanning the management unit's longest dimension and then established plots at random distances (within 10 m) and directions from each position. Plots were at least 10 m apart and 10 m from the unit edge; to meet this criterion, we surveyed two instead of three plots in the 6 smallest management units (total 132 plots). The distance between plots within a management unit (between the two plots furthest from each other, where there were 3 plots) averaged 104 m (standard deviation 89 m; range 10–544 m; Table S1); this indicates the range of management unit sizes. In each plot, we measured buckthorn abundance using percent cover (visual estimate) and the height of the tallest buckthorn. We characterized the understory (plants less than 2 m tall) by estimating percent cover of graminoids, forbs, ferns, and woody plants. Non-native species besides buckthorn were uncommon and were not separated from the more abundant native vegetation. Cover estimates were independent to account for vegetation layering, so they need not sum to 100%. We also identified the dominant understory species (native or non-native) in each plot, or the pair of co-dominant species where two species had similarly high cover. We characterized each plot's canopy light penetration by averaging four densiometer estimates, one per each cardinal direction, of the percent of sky not blocked by tree canopy. We took two clinometer slope measurements per plot and averaged them to yield a single estimate of slope for each plot. We characterized texture (hygrometer method) and pH (using a Corning pH meter 240 with soils suspended in water; a $CaCl_2$ solution gave the same trends) of soil samples. We collected 3 soil samples per plot, 10 cm deep; we aggregated soil samples by management unit before lab analysis because—given the way we defined management units (above)—we expected them to be fairly homogeneous in soil properties.

Analyses

First, we analyzed the effects of seeding on four response variables—cover of herbs (the sum of graminoids and forbs), cover of buckthorn, the ratio of buckthorn:herb cover, and maximum buckthorn height—using linear mixed models. To account for the hierarchical structure of our data (plots nested within management units nested within properties), we included random intercepts for property and management unit nested within property. We $\log_{10}$-transformed herb cover+1%, buckthorn cover+1%, and the cover ratio + 0.01 to improve homoscedasticity of residuals. The ratio of buckthorn:herb cover, a measure of buckthorn relative abundance, is more meaningful than either buckthorn or herb cover alone if the management goal is an understory where buckthorn is relatively uncommon, so this ratio is our focal response variable.

Similarly, we tested whether each of 11 covariates (listed in Table 1) differed between seeded and unseeded plots to assess their potential to confound the effects of seeding on our response variables. We used statistical models appropriate to each covariate as follows; in all cases, seeding treatment was the sole fixed effect. We analyzed both light penetration through the tree canopy and slope at the plot level using linear mixed models with the same random effects described above for the response variables. We analyzed soil pH and texture variables at the management unit level, using linear mixed models with property as a random intercept. We analyzed mean years since buckthorn removal and since follow-up herbicide using generalized linear models with Poisson error distributions and log link functions. We analyzed the proportions of management units where buckthorn was removed by forestry mower (versus by another method), which were burned since removal, and which received follow-up herbicide since removal using generalized linear models with binomial error distributions and logit link functions. For both Poisson and binomial models, management units were the data points and *p*values were corrected for overdispersion. Table S2 provides the number of management units receiving each combination of seeding treatment and post-removal management type.

Second, to characterize the percentage of variation in each of the response and site characteristic variables listed in Table 1 that was associated with each of the plot, management unit, and property levels of the hierarchy, we repeated the analyses above without the seeding treatment (i.e. including only the random effects) to calculate variance components (Table S3).

Third, to assess whether covariates either created spurious apparent effects of seeding on relative buckthorn abundance or could explain variation in the effects of seeding on relative buckthorn abundance, we analyzed the main and interactive effects of seeding and each covariate in turn on the ratio of buckthorn:herb cover ($\log_{10}$-transformed, as described above) (Table S4). We $\log_e$-transformed canopy light penetration to linearize its relationships with the response variables. We used linear mixed models. For plot-level covariates (canopy light penetration and slope), we included random intercepts for property and management unit nested within property. For the other covariates, measured per management unit, we included random intercepts for property. Predictor variables were centered to aid interpretation. We interpret these regression models as follows. If the interaction term has a relatively low *p*value, we infer that a covariate explained variation in the effect of seeding on the ratio of buckthorn:herb cover. Otherwise, if the interaction term *p*value is high and the estimate of the main effect of seeding is markedly closer to zero in the multiple regression model that includes the covariate than in the regression model that includes only

Table 1. Comparison of response variables and covariates between unseeded and seeded plots. Measurements are mean values unless otherwise specified. For the cover ratio, we report back-transformed means of the $\log_{10}$-transformed values used in the statistical analyses to reduce the influence of extreme outliers. Scale indicates whether each variable was measured at the plot ("plot") or management unit ("unit") level. *p*values for tests of the null hypothesis that unseeded and seeded plots do not differ are reported from statistical models that are described in Methods. Correlations between seeded/unseeded and each covariate are Spearman's ρ; for plot-level variables, these correlations were calculated using management unit means.

	Scale	*Unseeded*	*Seeded*	p*Value for Test of Equality*	*Correlation Between Seeding and Covariate (ρ)*
Plots (sample size)		92	40		
Management units (sample size)		32	14		
Response variables:					
Herb cover (%)	Plot	40	63	0.029	0.35
Buckthorn cover (%)	Plot	11	6	0.431	−0.04
Ratio of buckthorn:herb cover	Plot	0.18	0.09	0.148	−0.16
Maximum buckthorn height per plot (cm)	Plot	55.0	53.1	0.917	0.01
Covariates: Site characteristics:					
Light penetration through tree canopy (%)	Plot	19.6	25.9	0.096	0.22
Slope (degrees)	Plot	12.4	8.5	0.543	−0.17
Soil pH	Unit	6.3	6.4	0.682	0.08
Sand (%)	Unit	66.0	73.3	0.555	0.29
Silt (%)	Unit	27.2	21.9	0.532	−0.27
Clay (%)	Unit	6.2	4.9	0.267	−0.25
Covariates: Management history:					
Years since buckthorn removed	Unit	1.3	1.5	0.890	0.18
Buckthorn removal by forestry mower, as opposed to other methods (% of management units)	Unit	41	55	0.655	0.07
Burned since removal (% of management units)	Unit	23	15	0.294	−0.15
Follow-up herbicide applied (% of management units)	Unit	27	73	0.019	0.34
Years since follow-up herbicide (for those sites where follow-up herbicide was applied)	Unit	1.6	0.9	0.569	−0.14

seeding, then we infer that a covariate spuriously contributed to the apparent effect of seeding.

We follow recent publications that argue against treating *p*values as cut-offs of significance versus non-significance and instead interpret them as indicators of likelihood of effects (Amrhein et al. 2019; Wasserstein et al. 2019). We used JMP Pro 13 for all analyses.

Results

Plots revegetated with herb seed had 58% higher herb cover (mean 63% with seeding vs. 40% without seeding, $p = 0.029$), 45% lower buckthorn cover (mean 6% with seeding vs. 11% without seeding, $p = 0.431$), 50% lower relative abundance of buckthorn compared to herbs (mean ratio of buckthorn:herb cover 0.09 with seeding vs. 0.18 without seeding, $p = 0.148$), and similar maximum buckthorn height (mean 53.1 cm with seeding vs. 55.0 cm without seeding, $p = 0.917$) (Table 1). Although the first three effect sizes are large and roughly similar (≈50%), our confidence that these are not due to chance ranges from very high for herb cover (97% likely) to modest for buckthorn:herb cover ratio (85% likely) to weak for buckthorn cover (almost as likely due to chance as to revegetation; these percentages are the complements of the above *p*values).

Some of the 11 covariates were moderately correlated with seeding (absolute non-parametric correlations with seeding up to 0.34, Table 1) and some explained variation in the effects of seeding on buckthorn relative abundance (Fig. 1, Table S4).

The first set of covariates measured site characteristics. Plots with higher tree canopy light penetration had higher herb cover (Fig. 1A) and also higher buckthorn cover (Fig. 1B); hence, the ratio of buckthorn:herb cover was unrelated with light penetration (Fig. 1C; light penetration main effect $p = 0.200$, Table S4). Canopy light penetration was 32% higher in seeded than unseeded plots ($p = 0.096$, $\rho = 0.22$, Table 1), but there is no indication that this spuriously contributed to the apparent effects of seeding (i.e., adding canopy light penetration as a covariate did not markedly alter the effect of seeding on the ratio of buckthorn:herb cover, Tables 1 & S4).

Seeding reduced buckthorn:herb ratios more strongly in management units with less acidic soils (Fig. 1F; seeding * pH interaction −0.96, $p = 0.088$, Table S4). Underlying this pattern in buckthorn:herb ratios, seeding appeared to increase herb cover (Fig. 1D) and reduce buckthorn cover (Fig. 1E) more strongly on less acidic soils. There was a similar seeding * clay interaction (−0.20, $p = 0.084$, Table S4), such that seeding increased herb cover and reduced buckthorn:herb ratios more strongly on more clayey soils; pH and clay were correlated ($\rho = 0.33$).

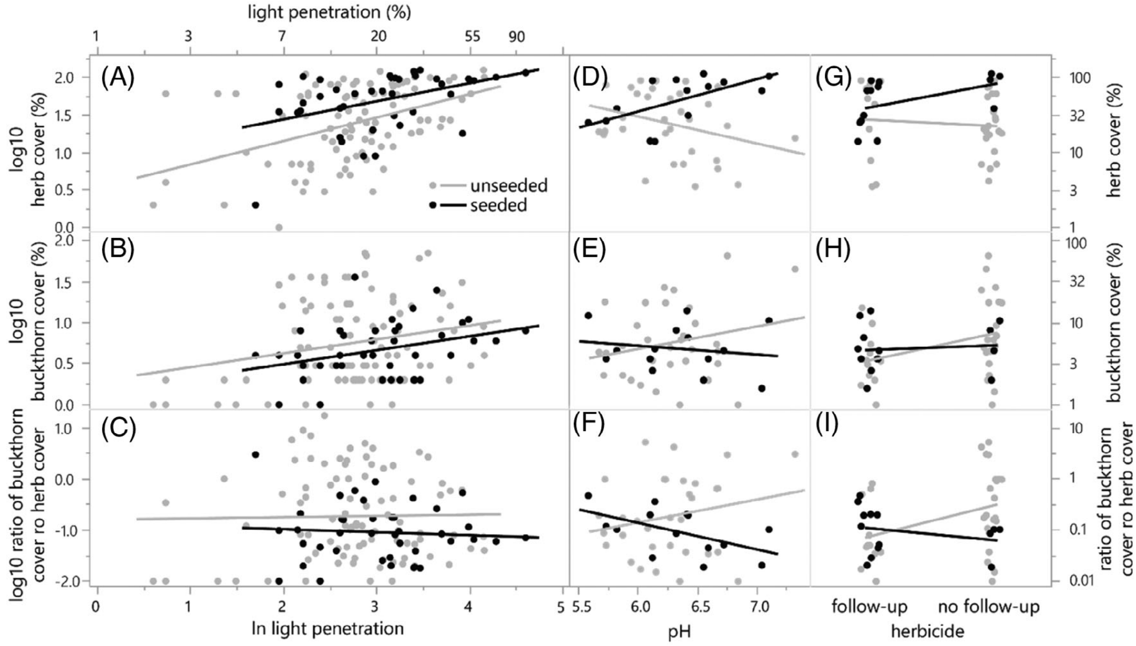

Figure 1. Effects of seeding and its interactions with $\log_e$ canopy light penetration (left column, A–C), soil pH (middle column, D–F), or whether follow-up herbicide was applied (right column, G–I) on $\log_{10}$ (herb cover+1%) (top row), $\log_{10}$ (buckthorn cover+1%) (middle row), and $\log_{10}$ ([buckthorn cover/herb cover] + 0.01) (bottom row). Horizontal values are jittered for visibility (G–I). Gray dots represent unseeded sampling units and black dots represent seeded sampling units. Canopy light penetration was measured at the plot level (in each of 3 plots per management unit), so each dot in the left column is a plot. pH and herbicide follow-up were measured at the management unit level so for those columns each dot is a management unit, and the vertical values are management unit means of the $\log_{10}$-transformed response variables. Secondary axis labels for light penetration (top; A–C) and the responses (right) show back-transformed values of the axis *labels* to aid interpretation of these log-transformed variables; note that these are not different axis *scales* from those presented at left and bottom of the graph.

The second set of covariates characterized management history. Removal method (forestry mowing vs. another method) and burning since removal did not explain variation in the effect of seeding on buckthorn:herb ratios (interaction effects $p \geq 0.780$, Table S4). In contrast, seeding reduced buckthorn: herb ratios far more strongly in management units that did not receive follow-up herbicide after buckthorn was removed (where seeding reduced the ratio 4-fold, from 0.30 to 0.07) than in units that did receive follow-up herbicide (where the ratio was 0.10 with or without seeding; Fig. 1I; interaction effect 0.37, $p = 0.158$, Table S4). This arose primarily because seeding increased herb cover 8 times more strongly without follow-up herbicide (from 36 to 86%) than with follow-up herbicide (from 46 to 54%) (Fig. 1G). Seeding also reduced buckthorn cover three times more strongly without follow-up herbicide (from 14 to 6%) than with follow-up herbicide (from 6 to 5%). (The average values in this paragraph are management unit means; the ratios were $\log_{10}$-transformed, averaged, and then back-transformed.) Of the covariates, follow-up herbicide was the most strongly correlated with seeding. Buckthorn was treated with follow-up herbicide in 73% of seeded management units but only 27% of unseeded management units ($p = 0.019$, $\rho = 0.34$, Table 1).

Common buckthorn is only one of several invasive plant species with which woodland managers in this region contend. Seventeen percent of the 46 management units we surveyed had another invasive species dominant or co-dominant in at least one of its plots: garlic mustard (*Alliaria petiolata*, in 3 units), glossy buckthorn (*Frangula alnus*, in 2 units), bush honeysuckle (*Lonicera* spp., in 1 unit), butter and eggs (*Linaria vulgaris*, in 1 unit), and Canada thistle (*Cirsium arvense*, in 1 unit). However, these plots (co-)dominated by other invasive species were just 8% of our 132 plots, so these other invasive species had little influence on our buckthorn results and we did not have statistical power to assess the effect of seeding on these other invasive species (Fig. 2).

Discussion

Implications of Case Study Results

This study provides some support for common seeding techniques as a tool to suppress buckthorn regeneration. Overall, the ratio of buckthorn:herb cover was halved in seeded management units, consistent with empirical support for revegetation suppressing invasion in other systems (Schuster et al. 2018). Covariate analyses suggest environmental conditions that may favor seeding success. Specifically, there were trends for management units with higher (more neutral) soil pH and clay content to have stronger increases in herb cover with seeding, and correspondingly stronger decreases in buckthorn cover with seeding, plausibly due to increased competition with herbs. Clay

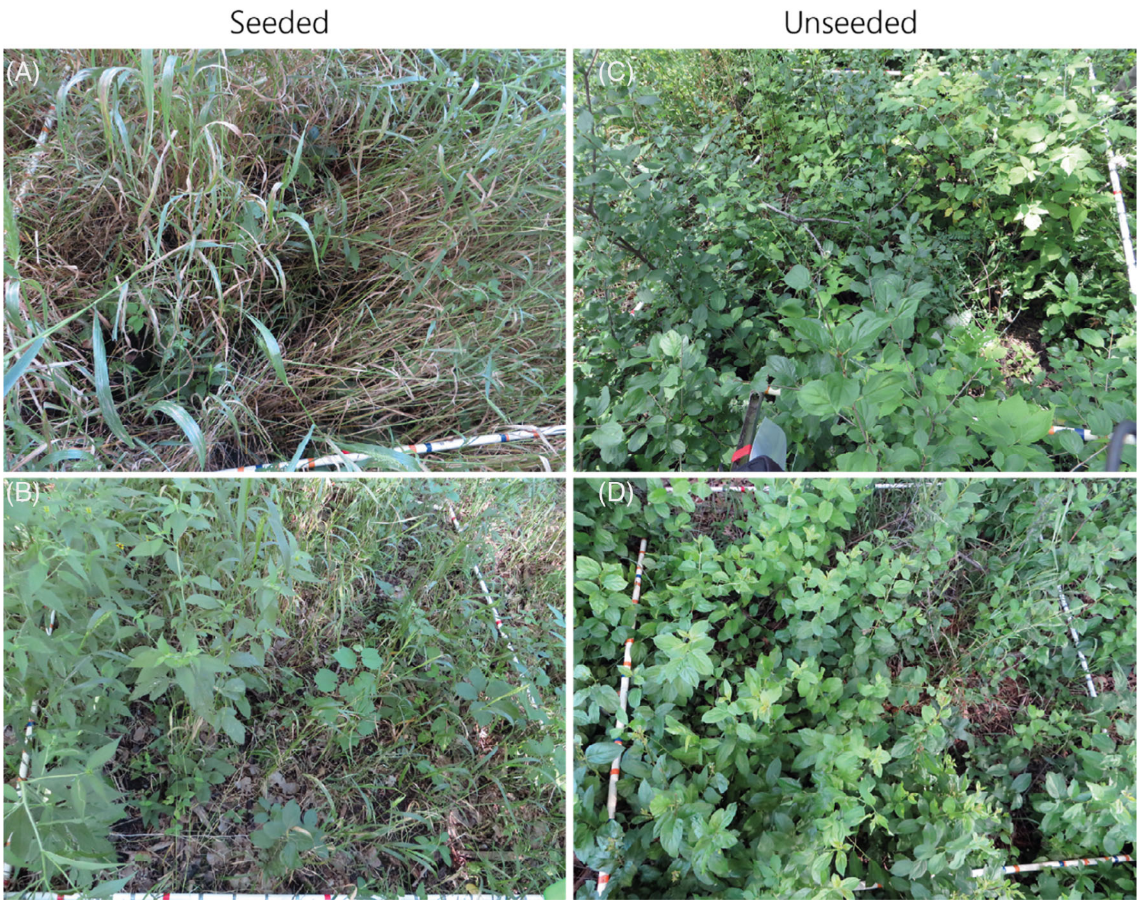

Figure 2. Photos of 2 m × 2 m survey plots in four different management units from which buckthorn had been removed. Following buckthorn removal, two of these units were seeded (A–B) and two were not seeded (C–D). As far as possible, these units were matched for removal date, canopy light penetration, follow-up herbicide, burning, and removal method. All four units had buckthorn removed before the start of the 2015 growing season (and after the 2014 growing season). All of these units were surveyed between mid-July and mid-August 2016. Average canopy light penetration in each unit was A = 23%, B = 29%, C = 33%, D = 19%. None of these units had follow-up herbicide (except B, where herbicide was applied in 2016 shortly before our survey and is unlikely to have been impactful). None of these units was burned since buckthorn was removed. Buckthorn was removed from A and C by cut-and-treat, and from B and D by shredding (a form of forestry mowing in which a drum-style head with planar teeth grinds buckthorn stumps close to the ground). Average buckthorn|herb cover in each unit was A = 1%|112%; B = 3%|77%; C = 65%|22%; D = 28%|28%. (Each management unit had 3 of these 2 m × 2 m survey plots.) Seeded wild rye grasses (*Elymus* spp., A and B) and brown-eyed susan forbs (*Rudbeckia triloba*, B) are prominent in the seeded units; common buckthorn is prominent in the unseeded units (C–D). Further details on each management unit are in Table S1 (A = "arboretum cut+seed"; B = "arboretum shred"; C = "Villa Park"; D = "Battle Creek Hilltop").

provides binding sites for cations associated with higher soil pH, explaining their correlation. Soils that are both more clayey and have higher pH typically have higher cation nutrient availability and greater water holding capacity, which could explain the greater success of herb seeding in these conditions. If borne out by further research, these trends will inform which site conditions to target for seeding.

The efficacy of seeding was highly variable. Only some of that variability is explained by our covariates. Site conditions and legacy effects of invasion may mean that native propagules alone cannot prevent buckthorn from re-establishing at many sites (Heneghan et al. 2009). Low woodland light availability combined with buckthorn's shade tolerance and fast growth rate—particularly of resprouts with extensive stored reserves—may enable buckthorn to win in competition for light over any herbaceous seed mix at many sites. This highlights the need to discover how to most effectively combine seeding with follow-up treatments of buckthorn resprouts and seedlings. Besides herbicide, fire can be used to control buckthorn resprouts and seedlings in some contexts; revegetation—particularly with graminoid cover—provides additional herbaceous fuel and may make fire a more viable management tool in these woodlands where fuel is otherwise sparse after buckthorn removal, although we did not have statistical power to assess that in this study because only two seeded management units were burned. Landscape context (e.g. the size of each management unit and the land cover/land use surrounding it) likely influence propagule pressure of buckthorn and native plants, which could affect the outcome of restoration. For example, Whitfeld et al. (2014) found that buckthorn abundance in other forests in Minnesota was positively associated with reproductive buckthorn abundance in the surrounding landscape, although it was difficult to separate this influence of landscape factors from biotic factors such as canopy shade and understory cover and diversity. Within the duration of this study (buckthorn removed up to 6 years previously; buckthorn removed within the last 3 years at 91% of sites), dynamics appeared to be governed primarily by propagules present at the time of removal (buckthorn resprouts and seed banks; native plant seed banks) so any influence of landscape context likely occurred through its impact on these unmeasured initial propagule pools.

Case Study Illustrates Opportunities and Caveats of Retrospective Studies

The high uncertainty of differences between seeded and unseeded management units is likely also due in part to high variability in our response metrics. For example, the coefficient of variation of the $\log_{10}$ ratio of buckthorn:herb cover was 95%. The influence of this variation on statistical tests could be reduced with a larger sample size, which was precluded by funding and a lack of management records for many properties, or with experiments that control for sources of variation unknowable in our current study. In an experimental context, we could have characterized suppressive capability of vegetation by monitoring a single cohort of buckthorn throughout their life cycle to provide consistent comparisons across sites and isolate the ability of seeding to suppress buckthorn seedling establishment, which is more likely than suppressing resprouting. Only at one of our 24 properties could we compare the effects of seeding against an unseeded control within the same property. This lack of blocking reduced power and may have confounded unmeasured property characteristics (e.g. moisture status, deer abundance, native plant seed banks and other seed sources, pre-removal buckthorn abundance) and aspects of management history with seeding. We assessed the effects of seeding while statistically controlling for each measured covariate in turn but could not simultaneously control for other covariates given our sample size. Although this potential for confounding challenges robust inference of seeding effects, it underscores the lesson that research on management techniques and resulting recommendations depend on site and management conditions.

Some covariates that affect plant growth were moderately correlated with seeding treatments, but they did not spuriously contribute to the apparent effects of seeding on buckthorn relative abundance with the possible exception of follow-up foliar herbicide. Seeded management units were considerably more likely than unseeded management units to have had follow-up herbicide applied to buckthorn resprouts and seedlings, presumably because buckthorn removals that included follow-up seeding were better funded—and therefore more likely to have an integrated long-term management plan including follow-up herbicide—than those that did not, or because managers applied both seeding and follow-up herbicide to management units more favorable to rapid reinvasion. This raises the possibility that some of the apparent effect of seeding on buckthorn regeneration is instead due to seeded units being more likely to have received follow-up herbicide. The positive seeding * follow-up herbicide interaction effect on buckthorn:herb ratio implies that—as currently implemented—managers are better off either using follow-up herbicide *or* seeding, because they are not receiving benefits from combining the two (by this response metric, on this timescale). Follow-up herbicide may be having non-target effects on newly seeded plants. Exploring ways to reduce non-target effects, such as waiting to seed until after the first year or two of follow-up herbicide, using more woody-selective herbicides such as bud inhibitors (Schuster et al. 2020), and using graminoid-only revegetation mixes that are less affected by broadleaf-selective herbicides may reveal how to combine seeding and follow-up herbicide for greater benefit than either alone. This underlines the value of covariates in retrospective studies for generating new hypotheses and research directions.

Limited historical records of site conditions (particularly pre-removal buckthorn abundance) and management constrained our retrospective study. Records were sometimes limited to the tenure of the current manager and often only coarsely categorized management methods. Categorizations such as cut-and-treat likely obscured variability in the timing and thoroughness of the treatment as well as the types and application rates of herbicides, which can affect the outcome of management (Enloe et al. 2018). This highlights a fundamental challenge: we cannot know in advance all the variables that will be needed for a future retrospective study.

An Experimental Alternative: Researcher-Manager Partnerships

Long-term designed experiments provide stronger causal inference than retrospective analyses, but are more costly. For example, a multi-decade, multi-acre savanna burning frequency experiment at Cedar Creek Ecosystem Science Reserve (Peterson & Reich 2001) has been possible only through a sequence of National Science Foundation Long-Term Ecological Research grants and sustained institutional support. Long-term researcher-manager partnerships promise to blend some of the cost advantages of retrospective studies with the rigor of experiments. These can range from researchers imposing treatments on land managed by partners, thus splitting management costs (e.g. the "Cover It Up" experiment that is a follow-up to this study, in which researchers replicate seeded and unseeded plots at several sites), to managers imposing treatments according to an experimental design developed with researchers (e.g. harvesting forest to create a fragmentation gradient [Haddad et al. 2015]).

Such partnerships between researchers and managers begin with developing a research agenda of mutual interest and hearing and respecting each other's goals, constraints, and knowledge (Dockry et al. 2017). In our experience, ongoing communication and accommodation, including researchers sharing preliminary findings and consulting managers on changes to protocols, and managers consulting researchers on changes to management plans, are key. Funding remains a challenge. Researchers need to acknowledge that dividing a land management unit into replicated, controlled plots decreases management efficiency and increases the cost of management.

Untreated control plots may be propagule sources for reinvasion. Accordingly, researchers may need to adapt their experimental designs (e.g. reduce replication) or contribute funds, materials, 2020 or labor to land management. For example, we budget research funds to remove invasive species from untreated control plots when the "Cover It Up" experiment concludes. Grants may be too short to span initiating an experiment and getting definitive results; funding agencies can assist by allowing extensions on funding and publication of results from long-term experiments and encouraging proposals that build on already-initiated experiments.

Retrospective studies such as the one described herein provide a relatively inexpensive first assessment of the effects of management options when experimental studies would take multiple years. They also allow sampling across a wider range of environmental and management conditions than could be studied using experiments at equivalent cost. For more rigorous inference, researchers can work with managers to initiate long-term experiments relatively cost-effectively.

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LITERATURE CITED

Amrhein V, Greenland S, Mcshane B (2019) Scientists rise up against statistical significance. Nature 567:305–307

Archibold O, Brooks D, Delanoy L (1997) An investigation of the invasive shrub European buckthorn, (*Rhamnus cathartica* L.) near Saskatoon, Saskatchewan. *Canadian Field-Naturalist* 111:617–621.

Davis MB (1989) Retrospective studies. Pages 71–89. In: Likens GE (ed) Long-term studies in ecology: approaches and alternatives. Springer, New York, New York, NY

Delanoy L, Archibold OW (2007) Efficacy of control measures for European buckthorn (*Rhamnus cathartica* L.) in Saskatchewan. Environmental Management 40:709–718

Dockry MJ, Gutterman SA, Davenport MA (2017) Building bridges: perspectives on partnership and collaboration from the US Forest Service tribal relations program. Journal of Forestry 116:123–132

Enloe SF, O'sullivan SE, Loewenstein NJ, Brantley E, Lauer DK (2018) The influence of treatment timing and shrub size on Chinese privet (*Ligustrum sinense*) control with cut stump herbicide treatments in the southeastern United States. Invasive Plant Science and Management 11:49–55

Grady KC, Hart SC (2006) Influences of thinning, prescribed burning, and wildfire on soil processes and properties in southwestern ponderosa pine forests: a retrospective study. Forest Ecology and Management 234:123–135

Haddad NM, Brudvig LA, Clobert J, et al. (2015) Habitat fragmentation and its lasting impact on Earth's ecosystems. Science Advances 1:e1500052

Harms RS, Hiebert RD (2006) Vegetation response following invasive tamarisk (*Tamarix* spp.) removal and implications for riparian restoration. Restoration Ecology 14:461–472

Heneghan L, Umek L, Bernau B, et al. (2009) Ecological research can augment restoration practice in urban areas degraded by invasive species—examples from Chicago wilderness. Urban Ecosystem 12:63–77

Kettenring KM, Adams CR (2011) Lessons learned from invasive plant control experiments: a systematic review and meta-analysis. Journal of Applied Ecology 48:970–979

Knight KS, Kurylo JS, Endress AG, Stewart JR, Reich PB (2007) Ecology and ecosystem impacts of common buckthorn (*Rhamnus cathartica*): a review. Biological Invasions 9:925–937

Kurylo J, Knight K, Stewart J, Endress A (2007) *Rhamnus cathartica*: native and naturalized distribution and habitat preferences. The Journal of the Torrey Botanical Society 134:420–431

Larson DL, Bright J, Drobney P, et al. (2011) Effects of planting method and seed mix richness on the early stages of tallgrass prairie restoration. Biological Conservation 144:3127–3139

Peterson DW, Reich PB (2001) Prescribed fire in oak savanna: fire frequency effects on stand structure and dynamics. Ecological Applications 11: 914–927

Roth AM, Whitfeld TJ, Lodge AG, Eisenhauer N, Frelich LE, Reich PB (2015) Invasive earthworms interact with abiotic conditions to influence the invasion of common buckthorn (*Rhamnus cathartica*). Oecologia 178:219–230

Schuster MJ, Wragg PD, Reich PB (2018) Using revegetation to suppress invasive plants in grasslands and forests. Journal of Applied Ecology 55: 2362–2373

Schuster M, Bockenstedt P, Wragg P, Reich P (2020) Fosamine ammonium impacts on the targeted invasive shrub Rhamnus cathartica and non-target herbs. Invasive Plant Science and Management, 1–6. https://doi.org/10.1038/gim.2015.30

Soil Survey Staff, Natural Resources Conservation Service, United States Department of Agriculture (2020) Web Soil Survey. https://websoilsurvey.nrcs.usda.gov/app/WebSoilSurvey.aspx. (accessed 6 March 2020).

Wasserstein RL, Schirm AL, Lazar NA (2019) Moving to a world beyond "$p < 0.05$". The American Statistician 73:1–19

Whitfeld TJS, Lodge AG, Roth AM, Reich PB (2014) Community phylogenetic diversity and abiotic site characteristics influence abundance of the invasive plant *Rhamnus cathartica* L. Journal of Plant Ecology 7:202–209

Supporting Information

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

Table S1. Management unit mean values for variables relating to a) management history, b) site characteristics, and c) vegetation responses.
Table S2. Number of sampled management units receiving each combination of seeding treatment and post-removal management type.
Table S3. Variance components analyses of each response variable and each site characteristic.
Table S4. Results of statistical models.
Figure S1. Map of study sites around Minneapolis-Saint Paul, Minnesota, USA.

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