

RESEARCH ARTICLE

Active restoration after three decades: Seed addition increases native dominance compared to landscape-scale secondary succession

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Abstract

1. Active restoration often aims to accelerate ecosystem recovery. However, active restoration may not be worthwhile if its effects are overwhelmed by changes that occur passively. Moreover, it can be challenging to separate the effects of passive processes, such as dispersal and natural succession, from active restoration efforts.
2. We assess the 24-year impact of actively restoring a Minnesota old-field grassland via seed addition of native tallgrass prairie species. We compared the abundance of four functional plant groups in actively restored plots against abundances in three reference classes: (1) unrestored plots undergoing passive recovery within the same old field, (2) passively recovering plots in two nearby old fields of similar age and (3) a chronosequence of 21 old fields within the same landscape.
3. Active restoration led to a higher abundance of native grasses and forbs in the 36m² treatment plots. Seed addition was more effective if the original vegetation was first removed using herbicide, burning and tilling. However, long-term conclusions about the efficacy of active restoration varied widely depending on the choice of reference class.
4. In our small-scale restoration experiment, native abundance was similarly high in both the actively restored and reference plots after 24 years, suggesting either (1) passive recovery or (2) local dispersal of native species from nearby treatment plots (i.e. cross-contamination). In contrast, a comparison with two nearby reference fields suggested active restoration resulted in much higher native abundance relative to passive recovery. A smaller, positive effect was detected when we compared actively restored plots to the chronosequence of old fields. In the chronosequence, many passively recovering old fields had transitioned to native grass dominance naturally, although active restoration appeared to increase native forb abundance.
5. *Synthesis and applications:* Our findings highlight the importance of using scale-appropriate references for assessing the efficacy and need for active restoration.

Comparing actively restored plots with the surrounding landscape, we found that active restoration and passive recovery led to similar plant communities after 24 years. Because local dispersal from actively restored sites can nearby references, caution should be exercised when evaluating long-term restoration projects using only small-scale experiments.

KEYWORDS

degraded grasslands, ecological restoration, seed addition, succession

1 | INTRODUCTION

Plant communities typically recover through secondary succession following major disturbances or perturbations. However, various factors can hinder recovery and prevent the ecosystem from reaching a desired state. For example, legacies of past land use can lead to novel ecosystem states with no historical analogue (Hobbs et al., 2009). Agricultural activities, such as ploughing or fertiliser addition, can create conditions that are unfavourable to native species (Isbell et al., 2013). Furthermore, the introduction of non-native plants can alter the trajectory of vegetation change through mechanisms such as competition, priority effects or altered plant–soil feedbacks (Fukami, 2015). Large-scale environmental drivers, including changes in nitrogen deposition, climate or fire regimes, may also fundamentally alter the direction of successional change (MacDougall et al., 2004; Williams & Jackson, 2007).

Ecological restoration aims to overcome the drivers preventing system recovery and re-establish desired plant species, thereby shifting successional trajectories towards desirable ecosystem states (Gann et al., 2019). Worldwide, agricultural activities such as grazing and fertiliser addition have resulted in many grasslands being transformed into non-native-dominated pastures (Cramer et al., 2008). When agricultural disturbances cease and no active restoration is attempted, these grasslands will undergo passive recovery. In some cases, old-field grasslands appear to stably persist in undesirable non-native-dominated states (Buisson et al., 2022). In such cases, active restoration may be required to reduce non-native dominance and promote native species establishment.

Nevertheless, the long-term benefits of active restoration in grasslands are unclear. While active restoration that re-introduces native species can have positive outcomes within 2–5 years (e.g. Kiehl et al., 2010; Kiehl & Pfadenhauer, 2006; Pywell et al., 2002, 2006), these effects may diminish over time (Shackelford et al., 2021). Although active restoration can speed up ecosystem recovery, passive recovery may achieve similar outcomes over decades to centuries (Jones et al., 2018). Unless rapid recovery is needed, active restoration may be unnecessary and a misallocation of resources if actively and passively restored sites follow the same successional trajectory albeit at different rates.

Evaluating the impact of active restoration requires estimating what would have occurred at the actively restored site if it had been allowed to recover passively. This is usually achieved by comparing

actively restored sites with comparable, unrestored reference sites. However, identifying appropriate reference sites can be challenging. Many studies use local reference plots nested within an actively restored site (Christie et al., 2019). While local reference plots share similar environmental conditions and plant composition with actively restored plots, small-scale experiments are prone to cross-contamination through local propagule dispersal, particularly when sowing or planting in new species. Keeping local reference plots independent from active restoration treatments over long time periods can be difficult (Furey et al., 2022). Some studies overcome this problem by using reference plots from sites with a similar land use history as the restoration plots but located further away (Ribas et al., 2021). However, finding closely matched reference sites may be challenging if there is spatial variation in the successional trajectories of recovering plant communities due to differences in site history, soil type, topography or herbivore pressure (Woods, 2007). A third approach is to consider a chronosequence of sites with similar land use history but differing in successional age. Chronosequences may better capture the likely range of long-term successional trajectories within a landscape (Foster & Tilman, 2000), irrespective of localised differences in factors such as site history and soil type. However, chronosequences require a more intensive sampling effort and may not always be available.

Here, we aimed to (1) assess whether active restoration facilitates grassland recovery relative to passive background successional change and (2) determine whether the choice of reference sites affects assessment of restoration success. We report results from a 24-year-old active restoration experiment at Cedar Creek Ecosystem Science Reserve (henceforth Cedar Creek) in Minnesota, United States, which aimed to restore native dominance in a degraded old field undergoing secondary succession. Old fields at Cedar Creek transition from non-native dominance to native dominance with increasing time since abandonment (Catford et al., 2023). Although this transition is relatively predictable (Clark et al., 2018), some fields have divergent trajectories and remain in non-native-dominated states (Isbell et al., 2019).

We examined the effect of adding seed of native grasses and forbs in a single old field, in combination with other treatments designed to remove non-native vegetation that established following agricultural abandonment. We compared outcomes in actively restored plots with outcomes in three different sets of passively recovering reference plots that are no longer used for agriculture but

have not been actively restored: (1) at a local scale, using untreated plots within the actively restored field, (2) using local reference plots plus two passively recovering fields matched by time since abandonment and (3) using local reference plots plus a chronosequence of 21 old fields within the same landscape, including the two fields of similar age. Each set of references provided different information on landscape-level trajectories of recovery, which affected our conclusions regarding the long-term effectiveness of active restoration. Our findings have important implications for the design and evaluation of long-term restoration projects, as well as for understanding the factors influencing the success of active restoration in grassland ecosystems.

2 | MATERIALS AND METHODS

2.1 | Study location and design

The study was conducted at Cedar Creek Ecosystem Science Reserve (hereafter Cedar Creek) in East Bethel, Minnesota (45.4086° N, 93.2008° W), which is a ~2200 ha area that includes a mosaic of ex-agricultural, prairie and oak savanna communities, as well as woodlands and wetlands. ([Supporting Information](#): About the study site). No permits were required.

The active restoration experiment was carried out in a single field (F0), which was abandoned in 1965 (Svenson, 1995). In May 1993, 35 plots were established in F0. Plots were 6 m × 6 m in size and arrayed in a 36 m × 48 m grid with 1 m buffers between plots. The experiment followed a pseudoreplication design wherein six treatments were compared against a single non-intervention [C]ontrol treatment. Treatments were randomly assigned to individual plots, resulting in five replicates for each treatment ([Table 1](#)). Six combinations of active restoration activities included [S]eed addition of 18 native grassland species (5 grasses and 13 forbs; [Table S1](#)). Five treatments included additional site preparation: [B]urning, [H]erbicide, [T]illing or seeding of a [N]urse crop species. These treatments were intended to increase the success of native seed addition by inhibiting or removing the resident non-native species and/or remediating local nutrient cycles. Species cover was visually surveyed in four 1 m² quadrats in each plot, 5 months after treatment in September 1993 and again in August 1994 (hereafter both surveys together referred to as 'Survey 1'; see also [Supporting Information](#): Detailed survey methods). In 1995, all plots in the field were burned as part of standard management of the field. Fifteen plots corresponding to treatments C, S and SBT were resurveyed in 1999 and 2000 ('Survey 2'). Survey 2 measured species biomass, rather than cover. Quadrats within these plots were disturbed and had non-native seed added, but quadrat level effects did not persist long term (Blumenthal et al., 2005; [Supporting Information](#): Disturbance and re-invasion sub-experiment). All 35 restoration plots were then resurveyed in

TABLE 1 Summary of six restoration treatments and one control applied to field F0 in 1993.

Code	Treatments
C	Control (passively recovering)
S	Seed only
SB	Seed, Burned
SBH	Seed, Burned, Herbicide
SBT	Seed, Burned, Tilled
SBTN	Seed, Burned, Tilled, Nurse crop
SBTH	Seed, Burned, Tilled, Herbicide

Note: Seed addition aimed to establish persistent populations of native species, additional treatments were intended to increasing the success of native seed addition. Herbicide-treated plots were sprayed with glyphosate (Roundup®; 110 mL/m²) on the 15 May 1993. Burning occurred on the 15 June 1993. Tilled plots were rototilled to ~8 cm, raked and packed on 17–18 June 1993. Native species seed composition is described in [Table S1](#).

June 2017 ('Survey 3'), visually recording cover in the same four quadrats.

We analysed the change in native species dominance over time in the active restoration plots, then compared these to non-intervention reference plots, two passively recovering old fields matched by time since abandonment and a chronosequence of 21 old fields. All fields are distributed within a ~3.5 km radius, often separated by roads, waterways or forest fragments, and therefore treated as spatially independent units. The two age-matched old fields (F1 and F2) are included in the larger chronosequence and were measured using the same sampling protocol. F1 and F2 were initially similar to the actively restored F0 in terms of successional age and ex-agricultural plant communities. The fields (F1–F21) form a 70-year successional chronosequence with the earliest year of field abandonment in 1927 and the most recent in 1997 (Inouye et al., 1987). The fields previously produced corn, oats, potato, rye and soybeans but otherwise share similar post-abandonment histories. In each of the 21 old fields, four 40 m transects were established in 1983: Two transects are regularly burned, and two transects are unmanaged. Burning was not conducted in one field, and burned plots are not included in our analyses. All fields are disturbed by herbivores (e.g. insects, deer and gophers). Species cover was visually surveyed along the four 40 m transects in each field (1 m × 0.5 m plots, 1 m between plots; 25 m between transects; [Supporting Information](#): Detailed survey methods). Surveys were conducted in 1983, 1989, 1994, 1997, 2002, 2006, 2011 and 2016 (Clark et al., 2018). We address differences in survey protocol, observer perception and plot size between the restoration experiment and the chronosequence. Cover or biomass observations are standardised to represent functional group abundances normalising raw observations by the standard deviations of each group, in each survey ([Supporting Information](#): Data compilation). We do not address differences in plot layout between fields.

2.2 | Statistical analyses

We represent the successional trajectory of passive recovery as a saturating growth curve fitted to the standardised abundance of four functional groups: native grasses, native forbs, non-native grasses and non-native forbs. Woody species were rare and are excluded from our analyses. If passive restoration leads to the recovery of native vegetation dominance, we expect that the growth curve will trend upward (from a low starting abundance) for native species and trend downwards (from a high starting abundance) for non-native species. However, due to natural variability, we also expect to observe fluctuations in abundance between surveys. For each functional group, we accounted for stochastic fluctuations by estimating autocorrelated noise with a 'mixing' parameter that estimated the degree to which abundance in one time survey was correlated with abundance in the previous survey. This approach is flexible enough to allow functional groups with strong autocorrelation to have divergent trajectories, and for 'flat' but fluctuating successional trajectories if the changes in abundance are entirely stochastic (i.e. no long-term, unidirectional outcomes).

Within each plot, we modelled patterns of vegetation change as a function of time, with the abundance of each functional group increasing or decreasing monotonically. We modelled the relationship between functional group abundance λ and time since abandonment t in each plot using a type IIa parameterisation of the Gompertz curve (Tjørve & Tjørve, 2017), with three parameters:

$$\lambda(t)_{[ijk]} = \alpha_{K[ijk]} \cdot \left(\frac{\alpha_{0[ijk]}}{\alpha_{K[ijk]}} \right)^{\exp(-r_{[ik]} \cdot t)} \quad (1)$$

where α_0 is the initial functional group abundance at the time of abandonment ($t=0$), α_K is the expected long-term asymptotic abundance, and r is the intrinsic rate of increase in abundance of functional group i in plot j in field k given restoration treatment l . All parameters were constrained to be positive. Our parameterisation has several desirable characteristics. It has a positive intercept (meaning we can model non-zero starting abundances), and the rate of change in abundance will increase or decrease given higher or lower values for the asymptotic abundance, α_K . Changes in long-term asymptotic abundance will also alter the point of inflection between initial and asymptotic abundances across a wide range of realistic trajectories (increasing, stable and declining). In this parameterisation, α_0 and α_K are independent and the greater the difference between abundances at the start and end, the longer succession would take for a given r . Restoration treatments affected the trajectory of vegetation change by increasing or decreasing α_K , the expected asymptotic abundance within a given plot. Alternative curves or co-dependencies between functional groups are not explored.

We did not observe α_0 and α_K directly but modelled them as latent parameters. Parameter estimates were drawn from hierarchical normal distributions, with functional group-level means and plot-level random effects. Distributions for α_0 and α_K shared a common standard deviation parameter for each functional group to

constrain the initial and asymptotic abundances to the same scale. We estimated our model parameters in a Bayesian framework using Hamiltonian Monte Carlo. Our model structure and priors are described more fully in an appendix (Supporting Information: Model fitting). We include a left-censored lognormal observation component to describe the probabilistic distribution of our data and observations of zero abundance. From the fitted models, we generated 1200 samples of the posterior predictive distribution of expected abundance for each functional group, in each plot at a fixed age, $t=52$, which was the successional age of F0 in 2017. These samples represent possible unobserved values conditional on the data, capturing our uncertainty in the underlying successional trajectory of each field, but ignore plot-level random effects and autocorrelation between observations. We use these posterior samples to evaluate whether native dominance is expected in a field, both asymptotically and 52 years after abandonment (coinciding with the age of F0 in Survey 3).

We calculated response ratios (RR) to compare the effects of active restoration treatments on functional group abundance relative to passively recovering control plots. For each treatment and functional group combination, we calculated the log response ratio as $RR = \log(\bar{y}_T / \bar{y}_C)$, where $\bar{y}_T$ and $\bar{y}_C$ are the mean abundances in treatment and control plots, respectively. We repeated this analysis using three sets of data each with a different reference group: (1) standardised abundance data from field F0 in 2017, with five replicates for each of the seven treatments, with the control plots as the reference group; (2) posterior samples of the expected standardised abundance in each treated F0 plot 52 years after abandonment, comparing treatment plots to 105 control plots from fields F0–F2; and (3) posterior samples from treated plots in F0, but comparing these with 1105 control plots from fields F0–F21. We calculated the standard deviation σ_{RR} of the aggregate response ratio, pooling the RR from all six restoration treatments to account for potential bias in using a single set of controls for repeated comparisons (Lajeunesse, 2011). Significant effects were determined by examining whether the credible interval of each response ratio ($CI_{RR} = RR \pm 1.96 \cdot \sigma_{RR}$) included zero. A positive RR indicates higher functional group abundance in treatment plots compared with control plots, while negative RR indicates the opposite.

3 | RESULTS

Twenty-four years after seed addition, actively restored plots in field F0 had transitioned to native dominance (Figure 1; Table S1). Although native grasses had low abundance in Survey 1 (1993–94), they had exceeded their non-native counterparts in all plots by Survey 3 (2017). Native forbs recruited best in plots where the extant community was removed by tilling or herbicide application and became moderately abundant in all plots by Survey 3. Non-native grasses had high abundance in Survey 1 and decreased to low levels in all plots by Survey 3. Non-native forbs remained in low abundance throughout.

FIGURE 1 Abundance of native and non-native grasses and forbs in field F0 in each survey. Active restoration treatments (light blue) are ordered, from left to right: Seed addition only, seeding + burning, herbicide and burning, burning, and tilling, burning, tilling and a nurse crop, and herbicide, burning and tilling in Surveys 1 and 3. Only reference plots and those that received seed addition only, or seed addition plus herbicide, burning and tilling were measured in Survey 2. $n=5$ for each combination of treatment and year.

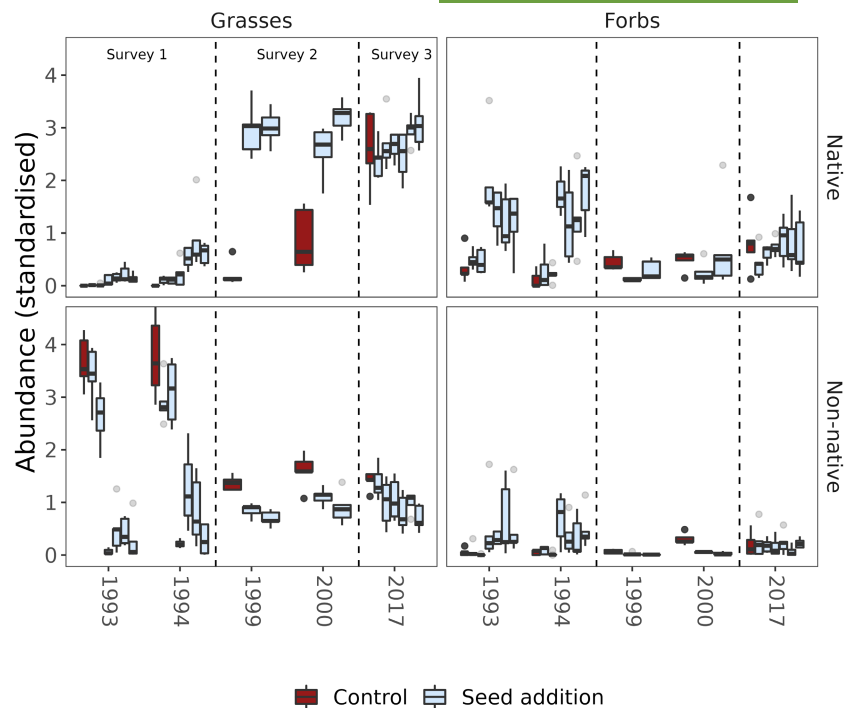


TABLE 2 Response ratios (RR) and associated uncertainties of restoration treatments compared with unrestored plots [C], calculated using the expected abundance of each functional group at $t=52$ (equivalent to the age of the restored field in 2017).

Treatment	σ_{RR}	RR_S	RR_{SB}	RR_{SBH}	RR_{SBT}	RR_{SBTN}	RR_{SBTH}
Single field (F0; # control plots = 5)							
Non-native grasses	0.076	-0.02	-0.35	-0.28	-0.57	-0.35	-0.69
Native grasses	0.127	-0.08	0.03	0.02	-0.05	0.13	0.18
Non-native forbs	0.541	0.23	-0.11	-0.22	0.17	-0.99	0.12
Native forbs	0.313	-0.65	-0.28	-0.11	0.06	0.02	-0.11
Age comparable old fields (F0-F2; # control plots = 105)							
Non-native grasses	0.115	-0.03	0.18	-1.52	-0.51	-0.51	-1.09
Native grasses	0.518	3.98	3.90	3.85	4.21	4.28	4.35
Non-native forbs	0.167	-0.86	-1.50	-0.02	-0.04	-0.35	-0.53
Native forbs	0.346	1.96	2.42	2.91	2.83	2.80	2.68
Landscape chronosequence (F0-F21; # control plots = 1105)							
Non-native grasses	0.047	0.16	0.22	-0.61	-0.17	-0.09	-0.36
Native grasses	0.058	0.41	0.35	0.42	0.45	0.51	0.58
Non-native forbs	0.051	-0.01	-0.24	0.26	0.32	0.10	0.09
Native forbs	0.041	0.49	0.63	0.94	0.90	0.89	0.75

Note: σ_{RR} is the aggregate standard deviation across the response ratios of all six treatments. Positive values indicate greater abundance after restoration compared with controls. **RR** where the 95% credible interval does not span zero are italicised and underlined.

3.1 | Active restoration compared with passively recovering reference plots in the same field (F0)

Relative to the reference plots in field F0, native grass abundance was higher in the active restoration plots for the first 7 years, but by 24 years native grass abundance was similarly high in both active restoration and reference plots (Figure 1). Native forb abundance

peaked in the restoration plots 1 year after the restoration treatments but then declined such that native forb abundance was similar in the restoration and reference plots after 24 years. Response ratios (RR; logarithm of the ratio of abundance in restored relative to reference plots, 52 years after field abandonment) revealed little difference in native grass and forb abundance between passive recovery and active restoration treatments, but non-native grass

abundance was consistently lower in active restoration plots where the ex-agricultural plant community was removed before seed addition (Table 2). Based on comparisons with unrestored reference plots in the same field, functional group composition was similar between passively recovering and actively restored plots 24 years after intervention. Beyond the first few years, natural succession or local dispersal from the actively restored plots achieved the same outcome as active restoration.

3.2 | Comparison with passively recovering old fields of a similar age (F0 vs. F1 and F2)

The increase in native abundance of passively recovering plots in F0 was not evident in similarly aged nearby old fields (F1 and F2; Figure 2). While there were pronounced fluctuations in abundance between surveys within plots, and all functional groups had strong autocorrelation between observations (estimates of δ , a measure of autocorrelation, were all greater than 0.5, see Supporting Information: Model Fitting), reference plots in F1 and F2 showed little change over time and remained dominated by non-native grasses. In reference plots in F0, native grasses were the only functional group that increased over time.

After controlling for autocorrelated stochastic variation, some treatment effects were detectable when comparing restored and reference plots in F0, F1 and F2 (Table 2). The most pronounced effect of active restoration was the uniform increase in native grass (RR between 3.98 and 4.35) and native forb abundance (RR between 1.96 and 2.91). Restoration treatments that combined the application of herbicide with burning and/or tilling (SBH and SBTH) were more effective at reducing the abundance of non-native grasses in F0 than other treatments (e.g. $RR_{SBH} = -1.52$; $CI = [-1.74, -1.29]$). In this comparison, active restoration appeared to substantially increase the abundance of native grasses and forbs.

3.3 | Comparison with a landscape chronosequence of passively recovering old fields (F0 vs. F1–F21)

We detected some effect of active restoration when we compared the active restoration plots in F0 with reference plots across multiple fields that spanned a range of successional ages (i.e. our chronosequence; Figure 3). Trends across all 21 fields in the chronosequence showed that native grasses often dominated secondary grassland communities ($\alpha_K[\text{Native grasses}] = 4.09$, $CI = [3.53, 4.65]$; Figure S1). Non-native grasses and non-native forbs were predicted to have greater asymptotic abundance (α_K) than natives in less than half (27% and 37%, respectively) of passively recovering fields.

Using an expanded set of fields dramatically increased the statistical power of our study to detect differences between the active restoration plots in F0 and reference plots (Table 2). With

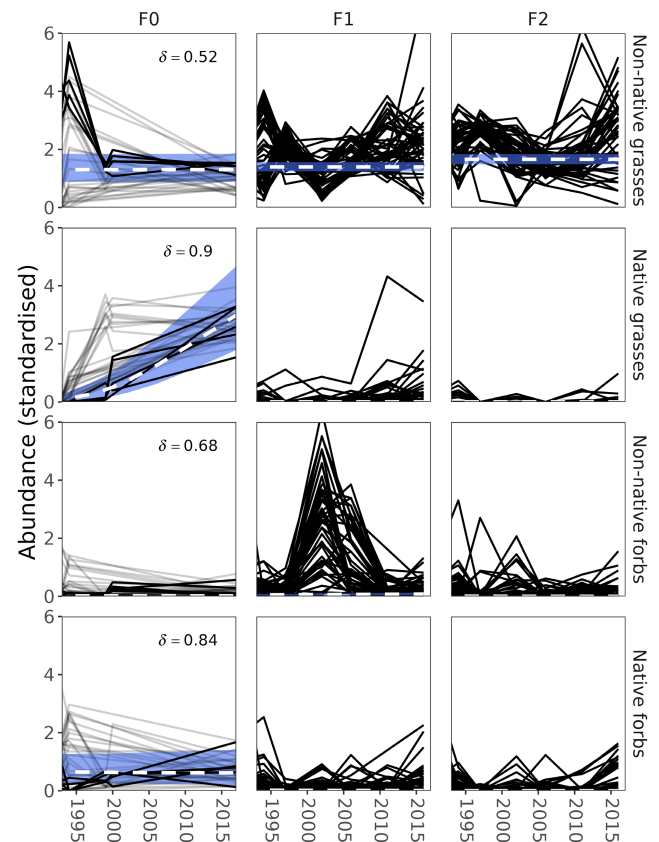


FIGURE 2 Change in abundance over time of native and non-native grasses and forbs in F0 relative to similarly aged old fields (F1 and F2; 56 years since abandonment). Functional group abundances in passively recovering reference plots [C] are shown for each field (dark black lines) and compared with actively restored plots in F0 (light grey lines). White dashed lines show the modelled trajectory of passive recovery in each field (95% credible intervals in blue). Estimates of δ (our estimate of the level of autocorrelation) that are >0.5 suggest functional group abundance is highly correlated between measurements.

increased power, we observed small but clear positive effects of seed addition on the abundance of native grasses (RR between 0.41 and 0.58) compared with 1105 unrestored reference plots across all 22 fields. Non-native grasses decreased in plots that received herbicide (e.g. $RR_{SBH} = -0.61$; $CI = [-0.70, -0.52]$), but there was no clear pattern of effects on non-native forb abundance in restored plots. The most striking effect of active restoration was the greater abundance of native forbs after 27 years, especially in plots that had seed addition plus disturbance: RR values in some disturbed plots were almost double those in plots that received seed addition only (between 0.63 and 0.94 in disturbed plots relative to 0.49 in seed addition only plots), and up to double that of grasses undergoing the same treatments. Our comparison with a broader grassland chronosequence indicated that active restoration enhanced ecosystem recovery more than we would expect from natural succession alone. However, the estimated effect sizes were up to 10 times lower than estimated by comparison with old fields of a similar age (Table 2).

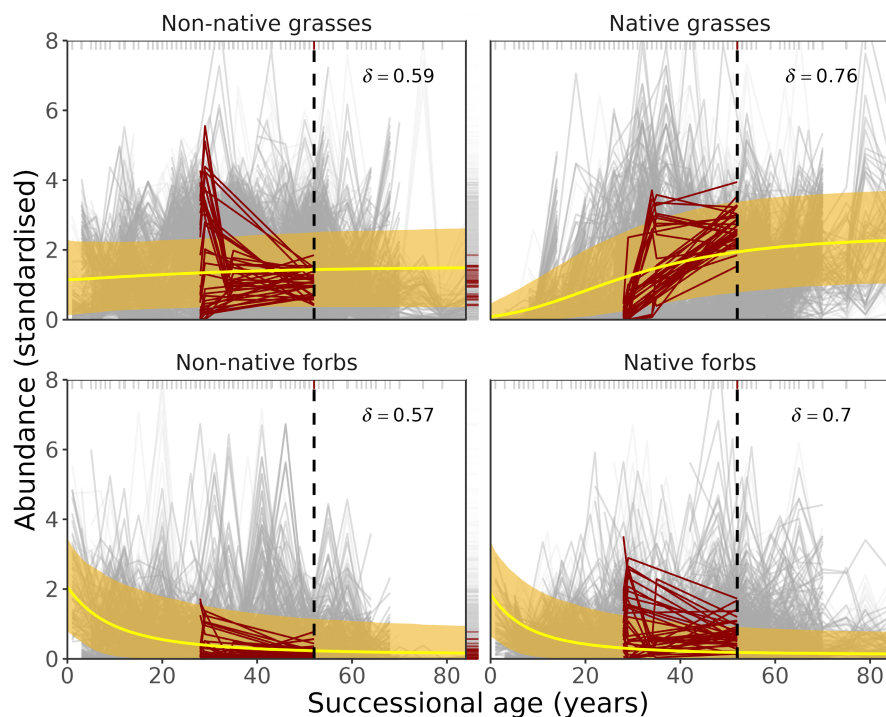


FIGURE 3 Functional group abundance in the field F0 set against a successional background of 21 passively recovering old fields. Red lines show abundances in actively restored plots in F0; grey lines show passively recovering plots from fields F0–F21. The modal (most common) trajectory for each group is shown by the yellow line, with shading representing 95% posterior credible intervals. Tick marks on the right of each panel show the distribution of standardised abundances in F0 at successional age 52 (red), compared with the distribution of abundances observed across all fields (grey). Tick marks at the top of each panel show the ages are represented by 34 years of surveys. Actively restored plots had lower non-native abundance than the predicted long-run outcome of natural succession (α_K), and higher abundance for native grasses and forbs.

4 | DISCUSSION

When populations of native species are present in the surrounding landscape (i.e. seed sources), secondary grasslands dominated by non-native species can sometimes recover to native dominance passively via species dispersal and colonisation (Buisson et al., 2022; Fensham et al., 2015). In such situations, active restoration may be required only when native species pools are absent or depauperate (Li et al., 2015, 2016). We compared three decades of plant community change in actively restored plots with the successional trajectory of reference plots undergoing passive recovery at three different scales. Within the same field, passively recovering plots achieved the same recovery outcome as actively restored plots. However, the abundance of native grasses and forbs in the actively restored plots was higher than in two nearby old fields and, to a lesser degree, than the mean successional trend in a chronosequence of 21 passively recovering old fields.

Nevertheless, our results revealed that the ability to detect a successful outcome of active restoration depends on the choice of reference. Small-scale restoration experiments could produce misleading results in the long term if seed addition to restored plots also reduces dispersal limitation in local control plots. Compared with untreated reference plots within the actively restored field, active restoration was clearly effective in the first 7 years, but

after 24 years active and passively restored plots had similar vegetation composition. However, passively recovering plots in nearby similar aged old fields (F1 and F2) showed little signs of recovery. This suggests that passively recovering plots in the same field (F0) as the actively restored plots may have benefited either from the restoration efforts, for example through local dispersal of native propagules present in actively restored plots, or because all plots in the field were on a long-term successional trajectory toward native dominance, independent of active restoration. Indeed, our comparison with the chronosequence of 21 passively recovering old fields revealed that natural succession often led to native dominance. Other studies have shown that studies grassland experiments may be confounded by dispersal from plots receiving interventions to non-intervention reference plots (Furey et al., 2022), and our study shows that only a few matched references were insufficient to detect landscape-scale trends.

Previous work has recommended restoration study designs should use one or two matched reference sites (Ruiz-Jaen & Mitchell Aide, 2005). However, leveraging the large amount of data from the full Cedar Creek chronosequence highlighted the range of natural successional trajectories old fields followed and demonstrated that remaining in a non-native-dominated state was atypical at the landscape scale. Moreover, the two old fields chosen as our closely matched reference sites (F1 and F2) performed

worse than expected given their age in comparison with old-field successional trajectories sampled more widely across the landscape. We thus caution that only one or two matched reference sites may be insufficient to judge restoration outcomes if there is variation in successional trajectories. We identified a stronger positive effect of active restoration when restored plots were compared with the two matched old fields relative to the range of outcomes across the full chronosequence.

For restoration of tallgrass prairie in these Minnesota old fields, our results suggest that active restoration is primarily important for reducing dispersal limitation, particularly for native forbs. The fact that both native grasses and native forbs recovered in disturbed and undisturbed plots in F0 suggests that establishment limitation was relatively unimportant. Our estimate of the long-term effects of seed addition through comparison with the full Cedar Creek chronosequence, suggests dispersal limitation commonly limits forb recovery, even over many decades. Native grasses appear to be dispersal limited in some old fields but not others given the variation in recovery among fields. This difference between grasses and forbs may not have been detected in the comparison with local reference plots (within F0) if local seed dispersal overcame long-term establishment limitation.

4.1 | Implications for management

While short-term, experimental studies have repeatedly confirmed the positive effects of active restoration via seed addition (Kiehl et al., 2010; Kiehl & Pfadenhauer, 2006; Pywell et al., 2002, 2006), global meta-analyses have found limited long-term efficacy of active restoration in natural ecosystems (Jones et al., 2018; Shackelford et al., 2021). These conflicting results might reflect that the benefits of active restoration are limited in the long term. This can be due to the failure of restored species to establish or persist (Shackelford et al., 2021) or, alternatively, due to passive ecosystem recovery without intervention. Where passively recovering ecosystems transition to native dominance anyway, then the long-term impact of active restoration may only be to achieve native dominance more quickly. The present study provides an example of an ecosystem in which passive restoration often yields native dominance, but active restoration can both speed recovery and improve long-term recovery of native forbs.

The availability of an existing dataset on the Cedar Creek chronosequence allowed us to identify the range of natural successional pathways that old fields follow. Our fitted models indicated that around one-third of the old fields are not expected to increase in native dominance following agricultural abandonment (Figure S1). These non-recovering fields may occupy apparently stable, non-native-dominated states (Shriver et al., 2019; Suding et al., 2004) and are likely to be good candidates for active restoration. This finding suggests that there is considerable opportunity to accelerate the transition to native dominance even if the long-term outcomes of passive and active restoration are similar.

Nevertheless, we required data from multiple old fields and many years of surveys to make this assessment and identify sites most likely to benefit from active restoration. Covariates related to ecosystem recovery processes, such as early compositional indicators, may also be predictive of restoration outcomes (Holl et al., 2018), but landscape-scale monitoring is necessary to identify the range and likelihood of possible successional outcomes. We propose that good practice in the design of long-term restoration experiments should include: (1) using extensive assessments created by, for example, spreading out randomised restored and control plots over large areas to increase spatial independence (Record et al., 2021); (2) revisiting permanently marked plots (Lindermayer et al., 2022); and (3) sharing of data and survey protocols in openly accessible repositories to enable the harmonisation of long-term collections (Sutter et al., 2015). The increasing availability of long-term reference datasets can provide opportunities for practitioners to assess likely successional trends while planning active restoration interventions.

AUTHOR CONTRIBUTIONS

Andrew O'Reilly-Nugent, Jane A. Catford and Dana M. Blumenthal conceived the study. Andrew O'Reilly-Nugent and Dana M. Blumenthal collected and harmonised the data. Andrew O'Reilly-Nugent developed the dynamic panel model, and analysed the data and model output. Andrew O'Reilly-Nugent wrote the first draft of the manuscript, and Dana M. Blumenthal, Elizabeth M. Wandrag, Richard P. Duncan and Jane A. Catford all contributed substantially to revisions.

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CONFLICT OF INTEREST STATEMENT

Elizabeth Wandrag is an associate editor of the *Journal of Applied Ecology* but took no part in the peer review and decision-making processes for this paper.

DATA AVAILABILITY STATEMENT

Data, models, and code are available at: <https://doi.org/10.5281/zenodo.7878670> (O'Reilly-Nugent et al., 2023).

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REFERENCES

- Blumenthal, D. M., Jordan, N. R., & Svenson, E. L. (2005). Effects of prairie restoration on weed invasions. *Agriculture, Ecosystems & Environment*, 107(2–3), 221–230. <https://doi.org/10.1016/j.agee.2004.11.008>
- Buisson, E., Archibald, S., Fidelis, A., & Suding, K. N. (2022). Ancient grasslands guide ambitious goals in grassland restoration. *Science*, 377(6606), 594–598. <https://doi.org/10.1126/science.abo4605>
- Catford, J. A., Shepherd, H. E. R., Tennant, P., & Tilman, D. (2023). Higher plant colonisation and lower resident diversity in grasslands more recently abandoned from agriculture. *Journal of Ecology*, 111(11), 2424–2440. <https://doi.org/10.1111/1365-2745.14192>
- Christie, A. P., Amano, T., Martin, P. A., Shackelford, G. E., Simmons, B. I., & Sutherland, W. J. (2019). Simple study designs in ecology produce inaccurate estimates of biodiversity responses. *Journal of Applied Ecology*, 56(12), 2742–2754. <https://doi.org/10.1111/1365-2664.13499>
- Clark, A. T., Knops, J. M. H., & Tilman, D. (2018). Contingent factors explain average divergence in functional composition over 88 years of old field succession. *Journal of Ecology*, 107(2), 545–558. <https://doi.org/10.1111/1365-2745.13070>
- Cramer, V., Hobbs, R., & Standish, R. (2008). What's new about old fields? Land abandonment and ecosystem assembly. *Trends in Ecology & Evolution*, 23(2), 104–112. <https://doi.org/10.1016/j.tree.2007.10.005>
- Fensham, R. J., Butler, D. W., Fairfax, R. J., Quintin, A. R., & Dwyer, J. M. (2015). Passive restoration of subtropical grassland after abandonment of cultivation. *Journal of Applied Ecology*, 53(1), 274–283. <https://doi.org/10.1111/1365-2664.12551>
- Foster, B. L., & Tilman, D. (2000). Dynamic and static views of succession: Testing the descriptive power of the chronosequence approach. *Plant Ecology*, 146(1), 1–10. <https://doi.org/10.1023/A:1009895103017>
- Fukami, T. (2015). Historical contingency in community assembly: Integrating niches, species pools, and priority effects. *Annual Review of Ecology, Evolution, and Systematics*, 46(1), 1–23. <https://doi.org/10.1146/annurev-ecolsys-110411-160340>
- Furey, G. N., Hawthorne, P. L., & Tilman, D. (2022). Might field experiments also be inadvertent metacommunities? *Ecology*, 103(7), e3694. <https://doi.org/10.1002/ecy.3694>
- Gann, G. D., McDonald, T., Walder, B., Aronson, J., Nelson, C. R., Jonson, J., Hallett, J. G., Eisenberg, C., Guariguata, M. R., Liu, J., Hua, F., Echeverría, C., Gonzales, E., Shaw, N., Decler, K., & Dixon, K. W. (2019). International principles and standards for the practice of ecological restoration. *Restoration Ecology*, 27(S1), S1–S46. <https://doi.org/10.1111/rec.13035>
- Hobbs, R. J., Higgs, E., & Harris, J. A. (2009). Novel ecosystems: Implications for conservation and restoration. *Trends in Ecology & Evolution*, 24(11), 599–605. <https://doi.org/10.1016/j.tree.2009.05.012>
- Holl, K. D., Reid, J. L., Oviedo-Brenes, F., Kulikowski, A. J., & Zahawi, R. A. (2018). Rules of thumb for predicting tropical forest recovery. *Applied Vegetation Science*, 21(4), 669–677. <https://doi.org/10.1111/avsc.12394>
- Inouye, R. S., Huntly, N. J., Tilman, D., Tester, J. R., Stillwell, M., & Zinnel, K. C. (1987). Old-field succession on a Minnesota sand plain. *Ecology*, 68(1), 12–26. <https://doi.org/10.2307/1938801>
- Isbell, F., Tilman, D., Polasky, S., Binder, S., & Hawthorne, P. (2013). Low biodiversity state persists two decades after cessation of nutrient enrichment. *Ecology Letters*, 16(4), 454–460. <https://doi.org/10.1111/ele.12066>
- Isbell, F., Tilman, D., Reich, P. B., & Clark, A. T. (2019). Deficits of biodiversity and productivity linger a century after agricultural abandonment. *Nature Ecology & Evolution*, 3(11), 1533–1538. <https://doi.org/10.1038/s41559-019-1012-1>
- Jones, H. P., Jones, P. C., Barbier, E. B., Blackburn, R. C., Rey Benayas, J. M., Holl, K. D., McCrackin, M., Meli, P., Montoya, D., & Mateos, D. M. (2018). Restoration and repair of Earth's damaged ecosystems. *Proceedings of the Royal Society B: Biological Sciences*, 285(1873), 20172577. <https://doi.org/10.1098/rspb.2017.2577>
- Kiehl, K., Kirmer, A., Donath, T. W., Rasran, L., & Hölzel, N. (2010). Species introduction in restoration projects—Evaluation of different techniques for the establishment of semi-natural grasslands in Central and Northwestern Europe. *Basic and Applied Ecology*, 11(4), 285–299. <https://doi.org/10.1016/j.baae.2009.12.004>
- Kiehl, K., & Pfadenhauer, J. (2006). Establishment and persistence of target species in newly created calcareous grasslands on former arable fields. *Plant Ecology*, 189(1), 31–48. <https://doi.org/10.1007/s11258-006-9164-x>
- Lajeunesse, M. J. (2011). On the meta-analysis of response ratios for studies with correlated and multi-group designs. *Ecology*, 92(11), 2049–2055. <https://doi.org/10.1890/11-0423.1>
- Li, S., Cadotte, M. W., Meiners, S. J., Hua, Z., Jiang, L., & Shu, W. (2015). Species colonisation, not competitive exclusion, drives community overdispersion over long-term succession. *Ecology Letters*, 18(9), 964–973. <https://doi.org/10.1111/ele.12476>
- Li, S., Cadotte, M. W., Meiners, S. J., Pu, Z., Fukami, T., & Jiang, L. (2016). Convergence and divergence in a long-term old-field succession: The importance of spatial scale and species abundance. *Ecology Letters*, 19(9), 1101–1109. <https://doi.org/10.1111/ele.12647>
- Lindenmayer, D. B., Lavery, T., & Scheele, B. C. (2022). Why we need to invest in large-scale, long-term monitoring programs in landscape ecology and conservation biology. *Current Landscape Ecology Reports*, 7(4), 137–146. <https://doi.org/10.1007/s40823-022-00079-2>
- MacDougall, A. S., Beckwith, B. R., & Maslovat, C. Y. (2004). Defining conservation strategies with historical perspectives: A case study from a degraded oak grassland ecosystem. *Conservation Biology*, 18(2), 455–465. <https://doi.org/10.1111/j.1523-1739.2004.00483.x>
- O'Reilly-Nugent, A., Blumenthal, D. M., Wandrag, E. M., Duncan, R. P., & Catford, J. A. (2023). Data from: Active restoration after three decades: Seed addition increases native dominance compared to landscape-scale secondary succession. *Zenodo*. <https://doi.org/10.5281/zenodo.7878670>
- Pywell, R. F., Bullock, J. M., Hopkins, A., Walker, K. J., Sparks, T. H., Burke, M. J. W., & Peel, S. (2002). Restoration of species-rich grassland on arable land: Assessing the limiting processes using a multi-site experiment. *Journal of Applied Ecology*, 39(2), 294–309. <https://doi.org/10.1046/j.1365-2664.2002.00718.x>
- Pywell, R. F., Bullock, J. M., Tallowin, J. B., Walker, K. J., Warman, E. A., & Masters, G. (2006). Enhancing diversity of species-poor grasslands: An experimental assessment of multiple constraints. *Journal of Applied Ecology*, 44(1), 81–94. <https://doi.org/10.1111/j.1365-2664.2006.01260.x>
- Record, S., Voelker, N. M., Zarnetske, P. L., Wisnoski, N. I., Tonkin, J. D., Swan, C., Marazzi, L., Lany, N., Lamy, T., Compagnoni, A., Castorani, M. C. N., Andrade, R., & Sokol, E. R. (2021). Novel insights to be gained from applying metacommunity theory to long-term, spatially replicated biodiversity data. *Frontiers in Ecology and Evolution*, 8, 612794. <https://doi.org/10.3389/fevo.2020.612794>
- Ribas, L. G. S., Pressey, R. L., & Bini, L. M. (2021). Estimating counterfactuals for evaluation of ecological and conservation impact: An introduction to matching methods. *Biological Reviews*, 96(4), 1186–1204. <https://doi.org/10.1111/brv.12697>
- Ruiz-Jaen, M. C., & Mitchell Aide, T. (2005). Restoration success: How is it being measured? *Restoration Ecology*, 13(3), 569–577. <https://doi.org/10.1111/j.1526-100x.2005.00072.x>
- Shackelford, N., Paterno, G. B., Winkler, D. E., Erickson, T. E., Leger, E. A., Svejcar, L. N., Breed, M. F., Faist, A. M., Harrison, P. A., Curran, M. F., Guo, Q., Kirmer, A., Law, D. J., Mganga, K. Z., Munson, S. M., Porensky, L. M., Quiroga, R. E., Török, P., Wainwright, C. E., ...

- Suding, K. L. (2021). Drivers of seedling establishment success in dryland restoration efforts. *Nature Ecology & Evolution*, 5(9), 1283–1290. <https://doi.org/10.1038/s41559-021-01510-3>
- Shriver, R. K., Andrews, C. M., Arkle, R. S., Barnard, D. M., Duniway, M. C., Germino, M. J., Pilliod, D. S., Pyke, D. A., Welty, J. L., & Bradford, J. B. (2019). Transient population dynamics impede restoration and may promote ecosystem transformation after disturbance. *Ecology Letters*, 22(9), 1357–1366. <https://doi.org/10.1111/ele.13291>
- Suding, K. N., Gross, K. L., & Houseman, G. R. (2004). Alternative states and positive feedbacks in restoration ecology. *Trends in Ecology & Evolution*, 19(1), 46–53. <https://doi.org/10.1016/j.tree.2003.10.005>
- Sutter, R. D., Wainwright, S. B., Boetsch, J. R., Palmer, C. J., & Rugg, D. J. (2015). Practical guidance for integrating data management into long-term ecological monitoring projects. *Wildlife Society Bulletin*, 39(3), 451–463. <https://doi.org/10.1002/wsb.548>
- Svenson, E. L. (1995). *Response of prairie species and old-field vegetation in an experimental restoration from seed*. University of Minnesota.
- Tjørve, K. M. C., & Tjørve, E. (2017). The use of Gompertz models in growth analyses, and new Gompertz-model approach: An addition to the unified-Richards family. *PLoS One*, 12(6), e0178691. <https://doi.org/10.1371/journal.pone.0178691>
- Williams, J. W., & Jackson, S. T. (2007). Novel climates, no-analog communities, and ecological surprises. *Frontiers in Ecology and the Environment*, 5(9), 475–482. <https://doi.org/10.1890/070037>
- Woods, K. D. (2007). Predictability, contingency, and convergence in late succession: Slow systems and complex data-sets. *Journal of*

Vegetation Science, 18(4), 543. [https://doi.org/10.1658/1100-9233\(2007\)18\[543:pcacil\]2.0.co;2](https://doi.org/10.1658/1100-9233(2007)18[543:pcacil]2.0.co;2)

SUPPORTING INFORMATION

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

Figure S1. Some fields are predicted to remain in non-native dominated states.

Table S1. List of extant and added species in the restored experiment (field F0).

Table S2. Non-native forb species seeded in Disturbance and invasion sub-experiment (Blumenthal et al., 2005).

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