

RESEARCH ARTICLE

Multiple disturbances, multiple legacies: Fire, canopy gaps and deer jointly change the forest seed bank

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Abstract

1. Disturbance regimes, like low-intensity fire, canopy gaps and ungulate browsing, play a critical role in determining ecological composition and structure in temperate forests around the world.
2. Each disturbance (or lack thereof) can lead to unique plant communities, but we do not understand how combined disturbances change plant diversity and the resulting soil seed bank. Changes in the soil seed bank, which depend on the plants that survive post-disturbance, can then influence future biodiversity and succession.
3. We used a long-term experiment in West Virginia, USA, that factorially manipulated low-intensity fire, deer exclusion and canopy gaps. Thirteen years after disturbance initiation, we sampled the seed bank from each disturbance treatment.
4. We found that low-intensity fire led to increased seed bank density, with additional canopy gaps and deer exclusion each creating unique seed bank communities. Combined fire, canopy gaps and deer presence led to high seed bank diversity and the most unique seed communities, while canopy gaps and deer had no effect on seed banks unless the area was previously burned. In contrast, combined fire, canopy gaps and deer exclusion led to the lowest seed bank diversity of all treatments, reflecting the continued legacy of extant plants that grew immediately after disturbance. Seed communities were also distinct from extant understory species over 13 years, regardless of disturbance treatment.
5. Each reintroduced disturbance combination left a unique legacy in the seed bank that will likely influence future forest reorganization following disturbances,

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adding to our understanding of how multiple disturbances influence forest succession and organization.

6. *Synthesis.* Forest disturbance regimes have changed around the world and are being restored or manipulated to support biodiversity. Reintroduction of disturbance leads to unique plant communities, but we do not understand how combined disturbances change the soil seed bank. Using an experiment that manipulates low-intensity fire, canopy gaps and deer exclusion, we find that combinations of these experimental treatments leads to substantially different seed communities. These disturbance-altered seed banks will likely influence future biodiversity and successional patterns, highlighting how the restoration of disturbance can strongly and indirectly influence temperate forest community dynamics.

KEYWORDS

canopy gap, deer, disturbance legacy, fire, seed bank, temperate forest

1 | INTRODUCTION

Forests around the world have experienced substantial changes in their historic disturbance regimes with altered land use, climate change or forced removal of Indigenous peoples (Bowman et al., 2011; Gilliam, 2016; Götmark, 2013; Kelly et al., 2023). Many mesic temperate forests in North America, Europe and Asia have become more even aged, undergone severe fire suppression and experienced increased ungulate browsing (Carpio et al., 2021; Frelich, 2002; Hai et al., 2023; McDowell et al., 2020; Pascual-Rico et al., 2021). These altered conditions create adverse environments for the plant species that coevolved and depend on historic disturbance patterns, such as globally dispersed oak (*Quercus*) species (Carrero et al., 2020; Tinner et al., 2005). Changes in plant composition with altered disturbance regimes have led managers to restore or manipulate disturbance to support biodiversity and ecosystem function (Long, 2009; Stanturf et al., 2014). However, our understanding of how the reintroduction of multiple historic disturbances influences biodiversity is nascent and represents a key knowledge gap in our long-term management and restoration of temperate forest systems.

Mesic North American forests are expansive ecosystems that have experienced dramatic alterations in their disturbance regimes over the last century (Abrams, 2005; Hanberry & Nowacki, 2016; Vander Yacht et al., 2020; Webster et al., 2018). This scenario is particularly acute in Appalachian hardwood forests, which have lost oak (*Quercus* spp.) tree regeneration and are transitioning to wetter, maple-dominated (*Acer* spp.) systems (Nowacki & Abrams, 2008; Pile Knapp et al., 2024). This transition from oak to maple forests was initiated by the forced removal of Indigenous peoples and their use of cultural burning as a management tool (Abrams et al., 2021; Pile Knapp et al., 2024; Poulos, 2015). This was followed by mass deforestation and slash wildfires in the late 19th and early 20th century (Lafon et al., 2017). Negative perceptions of these wildfires

led to a century of state-sanctioned fire exclusion and suppression that favoured maple growth and wetter understories (Alexander et al., 2021; Arthur et al., 2021). As a result, Appalachian forests became dominated by even-aged stands with few mid-sized and large (>15-m diameter; >175 m²) canopy gaps and infrequent low-intensity fires (Clebsch & Busing, 1989; Nowacki & Abrams, 2008; Raymond et al., 2009). In regions of Appalachia, the fire return interval is now over 10,000 years, as opposed to the historic 1-to-2-decade fire return interval under Indigenous stewardship and with lightning-ignited fires (Lafon et al., 2017).

Concurrently, white-tailed deer (*Odocoileus virginianus*) populations have increased dramatically above historical baselines (above 4 to 8 deer/km²) in most of eastern North America, driving ecological change depending on their population density, similar to the effects of overabundant cervid populations in many other areas in Europe and Asia (Côté et al., 2004; Iijima et al., 2023; Reed et al., 2022; Valente et al., 2020). To reverse the long-tailed effects of historic management and sustain oak-dominated plant communities, forest managers are reintroducing disturbances like prescribed burns, canopy gap creation through tree harvesting and lowering deer densities through hunting or fencing off vulnerable areas (Nuttall et al., 2013; Raymond et al., 2009).

Reintroducing multiple disturbances can be a powerful tool in efforts to restore and direct change within ecological communities (Abrams et al., 1985; Batllori et al., 2019; Reed et al., 2023; Sasaki et al., 2015; Yantes et al., 2023). For instance, combined low-intensity fire and canopy gap creation can lead to greater oak growth in both North America and Europe, while these disturbances alone are less effective (Brose et al., 2013; Hutchinson et al., 2024; Izbicki et al., 2020; Petersson et al., 2020). In this example, the surviving oak trees represent a post-disturbance legacy, which is broadly characterized as the adaptations, individuals and biomass that remain on the landscape following a disturbance (Cuddington, 2011; Franklin et al., 2000). Disturbance legacies can be material (e.g. wood and

nutrient pools) and informational (e.g. species' adaptive responses and genetic material), although the categories are not mutually exclusive (Johnstone et al., 2016). Each disturbance that occurs in a given area modifies the legacy community of the previous disturbance, and in certain cases, the disturbance combination and timing may lead to unique communities depending on how the disturbances in question interact (Anoszko et al., 2022). Thus, in eastern US forests and in temperate forests around the world, the disturbance legacies of combined low-intensity fire, canopy gap creation and ungulate browsing may have a particularly influential role in determining how forests reorganize and develop into the future when compared to the legacies of these disturbances individually (Cuddington, 2011; Seidl et al., 2014; Turner & Seidl, 2023).

To this end, the soil seed bank represents an important, but understudied, entity that may be strongly influenced by the re-introduced disturbances and may influence future disturbance regimes (Archibold, 1979; Ferrandis et al., 1996; Morgan & Neuenschwander, 1988; Pakeman & Small, 2005; Sousa, 1984). Seed banking is a reproductive adaptation that allows plants to persist belowground as dormant seeds, wherein the soil serves as a buffer from aboveground disturbances (Baskin & Baskin, 2022; Thompson, 1987). The forest seed bank has been shown to be a reservoir of biodiversity in temperate forests around the world, holding many herbaceous and woody early successional species (Grubb et al., 2013; Plue et al., 2010; Yang et al., 2021). The seed bank is also a latent source of genetic diversity (Levin, 1990; McCauley, 2014), making the seed bank both a material and information legacy.

Germinated plants that survive a disturbance eventually mature and release seeds, reestablishing the seed banking process that allows for plant communities to reorganize with future disturbance, thereby setting another legacy depending on the seeds that are returned to the soil (Baltzer et al., 2021; Falińska, 1999; Grubb, 1988; Hyatt & Casper, 2000; Seidl & Turner, 2022). Hypothetically, more disturbance will lead to a seed bank that is more similar to aboveground vegetation, as the herbaceous layer is homogenized and a few ruderal species survive and reproduce (Ma et al., 2021). These changes in the seed bank with disturbance can have long-lasting ecological ramifications. For example, rampant timber harvesting and slash wildfires in the United States during the late 19th and early 20th centuries likely allowed the shrub *Rubus* to spread and saturate forest seed banks with its long-lived seeds, creating a century-old legacy of heavy *Rubus* regeneration following overstory disturbance throughout the eastern United States (Dunn et al., 1982; Peterson & Carson, 1996). *Rubus* can then survive as a recalcitrant understory for decades (Donoso & Nyland, 2006; Kern et al., 2012).

Prescribed burns, canopy gap creation and deer browsing each provide a unique and important opportunity for new vegetation to grow from the seed bank and for the seed bank to change (Gioria et al., 2022; Muscolo et al., 2014; Schuler, 2010). Prescribed fires clear plant material, catalysing seed germination with increased light, heat, smoke and nutrients (Keeley & Fotheringham, 2000; Ooi, 2012; Pausas et al., 2022). In fire-prone ecosystems throughout the world, Pausas and Lamont (2022) found that ≈42% of seed-banking species

are adapted to germinate with heat or smoke. Canopy gaps increase understory resources like light, soil temperature and soil moisture, which are critical for seeds to germinate (Dalling & Brown, 2009; Pakeman & Small, 2005). Both fire and canopy gaps result in a temporary depletion of seeds in the seed bank as plants germinate, but over time, newly established vegetation will grow, reproduce and replenish the seed bank (Auld & Denham, 2006; Shinoda & Akasaka, 2020). This replenishment process may be disrupted by ungulate herbivores, as chronic over-browsing can constrain seed set, reduce plant abundance and lower long-term understory plant diversity by shifting composition to browse tolerant species (Brody & Irwin, 2012; Pendergast et al., 2016). These direct consumptive effects may indirectly reduce the abundance and diversity of seed banking species (Beauchamp et al., 2013; Tamura, 2019). However, in regions where deer populations are low and similar to historic estimates, deer browsing has been shown to increase understory diversity by reducing the abundance of otherwise competitive ruderal species, which could then lead to a more diverse seed bank (Royo et al., 2010; Yacucci et al., 2024).

Despite the increasing prevalence and co-occurrence of experimental tests of reintroduced disturbances in the eastern United States and in temperate systems more broadly (Kleinman et al., 2019; Thom & Seidl, 2016), our understanding of how individual and combined low-intensity fires, canopy gaps and ungulate herbivores change long-term forest seed banks is minimal. This highlights a significant gap in our understanding of post-disturbance legacies, as seed banks are critical for maintaining forest biodiversity in light of disturbance. Therefore, the primary question guiding our research is: *Do multiple reintroduced disturbances cause more substantial long-term changes in the seed bank than each respective individual disturbance?* To test this question we used a unique, multi-disturbance forest experiment that factorially manipulated low-intensity fire via controlled burning, canopy gap creation via girdling and herbicide injection and deer density via fenced enclosures. Thirteen years after the experiment's initiation, we sampled the seed bank in each disturbance combination treatment and tested how seed composition varied by disturbance treatment and in comparison to extant vegetation at multiple time points.

We expected low-intensity fire to be the predominant driver of increased seed density and diversity, as the Appalachian ecosystem has historically experienced frequent low-intensity burns and many plant species are likely favoured by fire (H1). Similarly, we expected canopy gaps to lead to a modest increase in seed bank density and diversity, mirroring the increased aboveground plant diversity with canopy gaps noted by Royo et al. (2010) (H2). We hypothesized that fire combined with canopy gaps would cause the greatest increases in seed bank density and diversity, leading to concomitant changes in seed community composition (H3). Based on studies showing negative impacts of deer herbivory on aboveground plant growth and reproduction, we expected deer to have a negative effect on seed bank density and diversity, particularly when combined with fire (H4). Lastly, when comparing the seed bank to extant vegetation, we expected the seed bank community to be most similar to extant vegetation in highly disturbed

plots, as many seed banking species are favoured by disturbance and may have been able to saturate the seed bank (H5).

2 | MATERIALS AND METHODS

2.1 | Study site

To test how the forest seed bank responds to multiple reintroduced disturbances, we experimentally manipulated prescribed fire, deer presence and canopy gap creation in four replicate Appalachian hardwood stands in central West Virginia, USA (Figure 1). We established this experiment in 2000 in the Western Allegheny Mountain ecological subsection using two stands in the Monongahela National Forest (39°06'N, 79°43'W) and two stands in the Fernow Experimental Forest (39°01'N, 79°42'W). Each stand was 60–90 years old and between 670 and 800 m in elevation. All stands were dominated by oak (*Quercus rubra* L., *Q. alba* L. and *Q. montana* L.) with associated maple (*Acer saccharum* Marsh. and *A. rubrum* L.), cherry (*Prunus serotina* Ehrh.), beech (*Fagus grandifolia* Ehrh.) and birch (*Betula* spp.) (Royo et al., 2010). Mean annual max temperature is 15.1°C, mean annual min temperature is 3°C, with an average of 122 cm of precipitation (McNab et al., 2007). For further details about the pre-existing manipulative experiment and aboveground plant sampling, please see Royo et al. (2010).

2.2 | Disturbance treatments

Our experimental design was a split-plot factorial (Figure 1), with each stand split in half and randomly assigned a burn treatment

(burned or unburned). In each burned and unburned half stand, we established eight treatment plots (20 × 20 m, 400 m²) for a total of 64 plots with either deer exclusion (no deer) + closed canopy, deer exclusion + canopy gap, deer presence + closed canopy, or deer presence + canopy gap. Treatment plots were 20 m from one another, stand edges and burn lines to avoid nonindependence and edge effects.

In May and June of 2000, we established 2-m high fencing around treatment plots to prevent deer entry. Deer densities in this location are between 4 and 7 deer/km², which are slightly higher than historical estimates, but low relative to most eastern North American forests (Horsley et al., 2003). We created all canopy gaps in June 2000 by girdling multiple canopy-dominant trees. By summer 2001, all trees in canopy gaps were standing dead, fallen or near-dead. Canopy gaps were mid-sized (284 ± 16 m²) (Collins & Carson, 2003). We lit each understory fire between 27 April and 1 May 2001. Fire temperatures on the mineral soil surface were 245 ± 15.4°C, while temperatures at 1 m from the ground were 91.9 ± 1.7°C (Royo et al., 2010). Fires have been absent here for at least 100 years and took place during the historic peak spring fire season (Adams et al., 2012; Lafon et al., 2017; Nuttle et al., 2013), during understory bud-break but prior to canopy bud-break. Historically, fire return intervals in this region are between 25 and 30 years (Guyette et al., 2012; Lafon et al., 2017). While low-intensity fires were also started in the fall in this region, spring burns can benefit fire-adapted species such as oak (Knapp et al., 2009). Considering that there was a minimum of 20 m of space between burned and unburned regions, we assume that drifting smoke did not lead to a substantial germination event within unburned plots. Fire was only used once at each site.

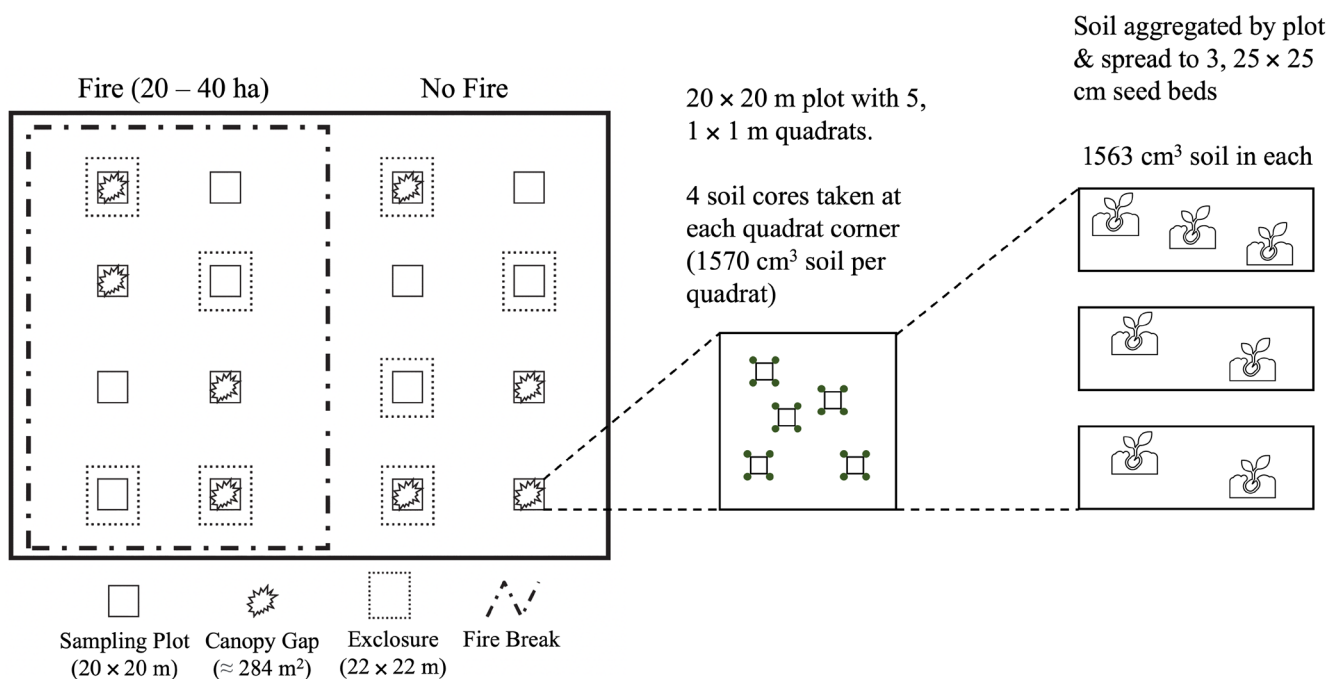


FIGURE 1 Diagram showing the organization of our replicated, factorial multi-disturbance study. Figure adapted from Thomas-Van Gundy et al. (2014).

2.3 | Seed sampling and germination

We placed five permanent 1-m² sampling quadrats within each treatment plot. Within these quadrats, we measured forb, graminoid, shrub and vine species abundances in 2000 (pre-treatment), 2001 (post-treatment), 2002, 2006 and 2013. Trees were measured within larger 10×10-m plots and were not included in comparative analyses between the extant understory and seed bank. One fire and canopy gap treatment plot could not be found in 2013, thus $n=63$. We sampled soil in early June 2013 and germinated seeds using a standard seedling emergence methodology (Brown, 1992; Gross, 1990). Following the recommendations of Plue and Hermy (2012), in June 2013 we sampled ca. 3% of the quadrat surface area to represent seed bank abundance and diversity. We collected seed bank samples at each corner of the five quadrats using a 5-cm deep by 10-cm diameter PVC pipe (soil volume: $392.5\text{ cm}^3 \times 4 = 1570\text{ cm}^3$). All 20 soil cores per treatment plot were then pooled, mixed and subsampled for use in emergence trials (7850 cm^3). Three subsamples were taken from each of the 63 treatment plot's pooled soils and placed in separate 25×25-cm trays in a greenhouse, with 2.5 cm of subsampled soil placed on top of 2 cm of sterile sand in each tray ($1563\text{ cm}^3 \times 3 = 4689\text{ cm}^3$ soil per plot; $625\text{ cm}^2 \times 3 = 1875\text{ cm}^2$ per plot). We watered all 189 trays (63 treatment plots × 3 subsamples) daily and occasionally rotated the trays to minimize any greenhouse positional effects (e.g. light and temperature). All germinants were identified to species or genera depending on life form, counted and removed from the tray (Table S1). After 5 months, we subjected trays to a 90-day, 5°C cold stratification period, after which they were returned to the greenhouse for another 5-month germination phase, which has been shown to be adequate by Gross (1990).

2.4 | Statistical analysis

For operational purposes, we define seed species density as the total number of species found across the three trays representing a single treatment plot. Seed species density is different from seed richness because it is not rarefied and does not represent an asymptotic estimate (Gotelli & Colwell, 2001). Similarly, seed abundance is a measure of density and is defined as the total number of germinants found across the three trays per plot.

We conducted analyses using R software (R v4.3.1). We tested differences in average species density and abundance using a generalized linear mixed effects model (GLMM) with either Poisson or quasi-Poisson distributions in the 'glmmTMB' package (Brooks et al., 2017). We calculated classic seed Shannon diversity within the 'vegan' package based on species abundances per plot (Oksanen et al., 2022) and modelled responses using a linear mixed effects model in the 'lme4' package (Bates et al., 2015). The use of classic Shannon diversity and species density in our linear models allowed us to more easily explore two-way interactions between treatments.

We also calculated Hill richness and Hill Shannon diversity based on total seed abundance using the 'iNEXT' package, which rarefies and extrapolates diversity metrics (Hsieh et al., 2016). The use of Hill richness and Hill Shannon diversity allowed us to calculate 'true' richness values and provides greater clarity regarding whether our sampling effort was sufficient, which is particularly important in seed bank studies, as the seed bank is often undersampled (Chao & Jost, 2012; Plue et al., 2021).

To explore life form-specific seed diversity metrics, we subset the data according to life form (forb, graminoid, shrub, tree and vine) and modelled life form abundance, species density and classic Shannon diversity response to treatments. Graminoid classic Shannon diversity was modelled using a GLMM with a Tweedie distribution due to the data being zero-inflated. Since *Rubus* is a critical species occupying the seed bank, particularly following disturbance, we tested how total *Rubus* seed abundance varied with disturbance treatments using a GLMM.

We constructed several hypothesis-derived models with individual disturbances and their interactions as fixed effects to align with experimental design and determine the best fit (Model Independent Variables: Fire; Deer Exclusion; Canopy Gap; Fire×Deer Exclusion; Fire×Canopy Gap; Canopy Gap×Deer Exclusion; Fire×Canopy Gap×Deer Exclusion). We used this set of models for every dependent variable and then compared these models using AICc as a means to reduce the likelihood of overfitting our models and to reduce Type I error due to there being many hypothesis-derived main and interactive effects (Burnham & Anderson, 2004; Johnson & Omland, 2004). We report the results from models with the lowest AICc. For our random effects, treatment plot was nested within the experimental site. If models failed to converge, we only used experimental site as a random effect. All model assumptions were tested using the 'DHARMA' package (Hartig, 2017), while post-hoc tests were done with the 'emmeans' package using a Bonferroni correction (Lenth, 2016).

We tested differences in community composition between treatments using seed species abundance data and the 'adonis2' PERMANOVA function, while checking community dispersion with the 'betadisper' function to meet the assumptions of PERMANOVA (Oksanen et al., 2022). Data was not transformed. We visualized differences among communities using three-dimensional NMDS to keep stress below 0.20. We identified indicator species using vegan's 'multipatt' function. When comparing extant plants (forbs, graminoids, shrubs and vines) and the seed bank at various time points, certain species were concatenated by genera as they could not be identified to species immediately after germination in 2013 (*Carex*, *Galium*, *Rubus*, *Solidago*, & *Viola*). We removed species that did not occur in at least three plots for multivariate analysis. When comparing the seed bank and annual plant cover, all data were converted to presence-absence format prior to analysis. Similar to Plue et al. (2021) we used Raup-Crick similarity within PERMANOVA to test for community differences between 2013 seeds and extant plants at each time point.

3 | RESULTS

A total of 3642 seeds germinated in our trials (across all trays there was an average of 309 germinants/m² and 12,329 germinants/m³), representing at least 59 different taxa, with 38 forb species, 8 shrub species, 7 graminoid species, 5 tree species and 1 vine species (Table S1). *Rubus* spp. accounted for 28% of total seeds, followed by *Betula* spp. (9%), *Ageratina altissima* (6%), *Aralia spinosa* (5%) and *Robinia pseudoacacia* (5%). Among all germinating taxa, nine species were non-native, accounting for 16% of all taxa (Table S1). However, non-native species' proportional abundance among all seeds was low, with non-native species representing 1% of total seeds germinated.

3.1 | Seed abundance and species density

Fire under a closed canopy led to a 63% increase in mean seed abundance in comparison to unburned plots under a closed canopy ($z=2.5$, $p=0.07$), but when fire and canopy gaps were combined, there was a 205% increase in seed abundance in comparison to unburned plots with a closed canopy ($z=6.8$, $p<0.001$; Figure 2; Table 1). This increase in seed abundance was driven by a 478% increase in forb seed abundance with fire and canopy gaps in comparison to unburned plots with a closed canopy ($z=6.7$, $p<0.001$; Figure 2; Table 2). In addition, canopy gaps in burned areas decreased vine seed abundance by 93% in comparison to unburned plots with a canopy gap overhead ($z=-4.6$, $p<0.001$), whereas canopy gaps in unburned plots had no influence on vine seed abundance. Lastly, fire alone decreased tree seed abundance by 33% in comparison to unburned plots ($\chi^2=5.3$, $df=1$, $p=0.02$).

We found that fire increased average seed species density from an average of 57.2 ± 2.7 species/m² to 68.8 ± 3.3 species/m² in comparison to unburned plots ($\chi^2=6.4$, $df=1$, $p=0.01$; Table 1). Fire and deer presence increased forb seed species density to 39.2 ± 4.1 species/m² in comparison to 18.7 ± 3.1 forb species/m² in unburned

plots with deer exclusion ($z=-4.2$, $p<0.001$). The combination of fire and deer exclusion had a strong influence on life-form specific seed abundance as well. Burned and deer excluded plots led to 750% greater shrub seed abundance in comparison to unburned plots with deer presence ($z=6.1$, $p<0.001$; Figure 2; Table 2). Fire and deer exclusion had an interactive effect on graminoid abundance ($\chi^2=3.2$, $df=1$, $p=0.07$), wherein deer exclusion in burned plots decreased graminoid seed abundance by 62% in comparison to burned plots with deer presence ($z=-2.2$, $p=0.03$). There was a three-way interaction among fire, canopy gaps and deer exclusion on *Rubus* abundance, the most common germinant in our trials ($\chi^2=3.0$, $df=1$, $p=0.08$). Burning only increased *Rubus* seed abundance with a canopy gap or deer exclusion. Fire, deer exclusion and canopy gaps together caused a 1432% increase in *Rubus* seed abundance in comparison to unburned plots with deer presence and a closed canopy ($z=6.1$, $p<0.0001$).

3.2 | Seed diversity

Deer exclusion decreased the classic Shannon diversity of the seed bank by 8% in comparison to plots with deer present ($F_{1,58.1}=9.1$, $p=0.004$; Table 1). Fire increased the classic Shannon diversity of forb seeds by 45% in comparison to unburned plots ($F_{1,56.1}=7.9$, $p=0.003$). In contrast, fire led to a 40% decrease in classic Shannon diversity of shrub seeds in comparison to unburned plots ($F_{1,58.1}=9.5$, $p=0.007$). However, the results from our linear models differed from rarefied and extrapolated Hill richness and diversity. When extrapolating seed species richness across all treatments in the iNEXT package, Hill richness was highly variable and there were no substantial differences between treatments (Figure 3; Table S2). In contrast, Hill Shannon diversity varied substantially depending on whether the plot had been burned. We found that fire with deer exclusion and a canopy gap led to the lowest Hill Shannon diversity of all the treatments (6.7 species; 95% CI [6.0–7.5]; Figure 3;

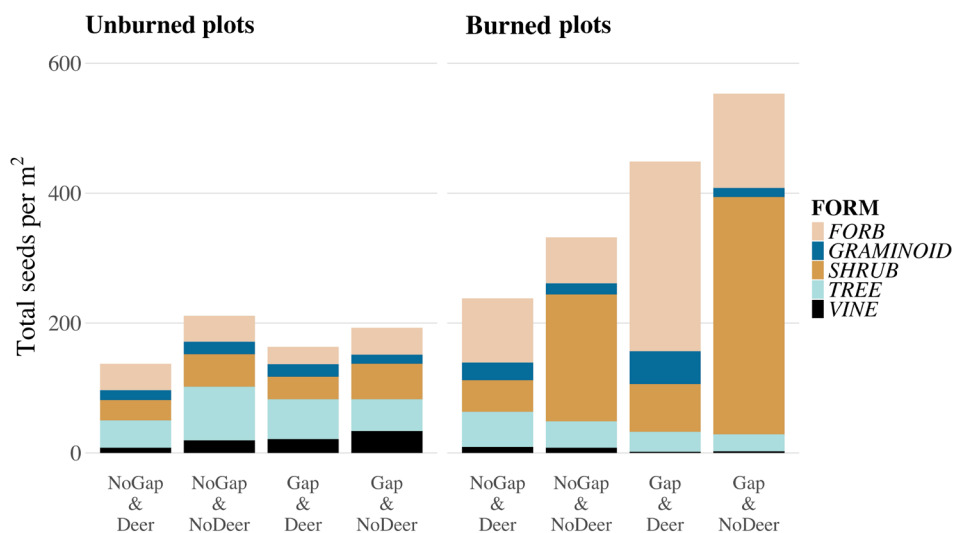


FIGURE 2 Bar charts that represent the relative proportion of seeds for each plant life form in disturbance treatments.

TABLE 1 Seed abundance, species density and classic Shannon diversity (H') response to individual disturbance and their combinations. Each variable corresponds to a single model.

Treatments	Seed abundance				Seed species density				Classic seed H'			
	χ^2	df	p	AICc	χ^2	df	p	AICc	F	df	p	AICc
Fire		1		603	6.4	1	0.01	329		1,58		-10
Deer		1		621		1		334	9.1	1,58	0.004	-18
Gap		1		615		1		334		1,58		-10
Fire \times Deer		1		605		1		332		1,56		-9
Fire \times Gap	4.9	1	0.03	591		1		332		1,56		1
Deer \times Gap		1		618		1		337		1,56		-8
Fire \times Deer \times Gap		1		597		1		339		1,52		10.6

Note: The bold values indicates the significance which is included in p columns.

Table S2). Fire with deer exclusion and no canopy gap led to the second lowest Hill Shannon diversity of all treatments (9.1 species; 95% CI [7.9–10.3]; Figure 3). In contrast, burned areas with a canopy gap and deer presence had the highest Hill Shannon diversity (18.1 species; 95% CI [16.4–19.7]; Figure 3). Unburned plots with deer presence or no gap overhead had roughly the same Hill Shannon diversity as the most disturbed plots (17.9 species; 95% CI [15.3–20.4]; Figure 3), although there were no major differences in Hill Shannon diversity between any of the unburned treatments.

3.3 | Seed community composition

Despite having similar Hill Shannon diversities, burned plots with a canopy gap overhead and deer presence had very different seed species compositions in comparison to unburned plots with deer presence and no canopy gap ($F=3.4$, $p=0.004$; Figure 4; Table S3). Further, burning led to seed communities that were significantly different from nearly all unburned plot seed communities ($F=2.5$, $p<0.001$; Figure 4). Burned plots with no gap overhead and deer presence had the most similar seed bank communities to most of the unburned treatments.

Within burned treatments, plots with a canopy gap and deer presence had significantly different communities than all other burned treatments (Figure 4; Table S3). Burned plots with no canopy gap and deer presence had different seed communities than burned plots with deer exclusion and a canopy gap overhead ($F=4.8$, $p=0.006$). In contrast, burned plots with deer exclusion and no canopy gap overhead had the most variable seed community, which overlapped with two other treatment's seed communities (burned plots with deer exclusion and a canopy gap; burned plots with deer presence and no canopy gap (Figure 4). The presence or absence of canopy gaps and deer exclusion in unburned plots had no effect on seed bank communities and there were no differences in seed community amongst any of the unburned plots ($F=0.99$, $p=0.5$; Figure 4).

In addition, burned areas with canopy gaps and deer exclusion had several indicator species, including *Rubus* (shrub; $p=0.003$),

Phytolacca americana (forb; $p=0.02$), *Sambucus* (shrub; $p=0.02$) and *Aralia spinosa* (shrub; $p=0.05$). In contrast, burned areas with canopy gaps and deer presence had *Ageratina altissima* (forb; $p=0.001$), *Carex* spp. (graminoid; $p=0.005$), *Verbena urticifolia* (forb; $p=0.03$), *Viola pubescens* (forb; $p=0.02$) and *Solanum carolinense* (forb; $p=0.1$) as primary indicator species. *Viola rotundifolia* (forb; $p=0.06$) was the primary indicator for plots that were burned with deer excluded and no gaps. There were no indicator species for burned plots with no canopy gap and deer presence, whereas the indicator for unburned plots with a gap overhead and deer presence was *Sassafras albidum* (tree; $p=0.07$).

When comparing 2013 seed communities to extant plant communities sampled in disturbance treatments over time (2000 [pre-treatment], 2001, 2002, 2006 and 2013), burned plots with a canopy gap overhead and deer presence had extant plant and seed bank communities that differed at every measured time point ($F=19$, $p<0.001$; Figure 5; Table S4). By 2013, burned plots with a canopy gap and deer presence maintained a unique seed bank in comparison to the extant understory, with 75% of the seed species not being found in the extant understory.

4 | DISCUSSION

Using a 13-year experiment that factorially manipulated several historically important disturbances, we show how disturbance interactions cause lasting imprints on the seed bank community. Specifically, interactions among low-intensity fire, canopy gap creation and continuous deer browsing left distinct disturbance legacies in the seed bank community (Figure 6). Despite the importance of these disturbances in forests broadly, this study is the first, to our knowledge, to test how interactions between fire, canopy gaps and deer presence can change the seed bank. This work on seed bank legacies provides new applied and theoretical insight towards how biodiversity and forest communities are maintained and develop following multiple disturbances. Further, these altered seed banks represent a critical reservoir of biodiversity that will influence

TABLE 2 Forb, graminoid, shrub, tree and vine seed abundance response to individual and combined disturbance treatments. Each variable corresponds to a single model.

Treatments	Forb seed abundance			Graminoid seed abundance			Shrub seed abundance			Tree seed abundance			Vine seed abundance							
	χ^2	df	p	AICc	χ^2	df	p	AICc	χ^2	df	p	AICc	χ^2	df	p	AICc				
Fire		1		472	3.3	1	0.07	323	1	1	0.02	485	5.3	1	0.02	403	1	1	247	
Deer		1		497		1		325	1	1		491		1		408	1	1	264	
Gap		1		494		1		326	1	1		498		1		408	1	1	263	
Fire × Deer		1		473	3.2	1	0.07	323	3.5	1	0.06	474		1		406	1	1	250	
Fire × Gap	7.7	1	0.01	463		1		327		1		485		1		408	8.1	1	0.004	243
Deer × Gap		1		499		1		327		1		492		1		412		1	267	
Fire × Deer × Gap		1		470		1		330		1		477		1		414		1	250	

Note: The bold values indicates the significance which is included in *p* columns.

community structure and reorganization following subsequent disturbances (Gioria & Pyšek, 2016; Seidl & Turner, 2022).

4.1 | Individual disturbances

In partial agreement with our first hypothesis, only burning increased average seed bank species density, likely driven by a post-fire increase in the proportion of forb species. These increases in species density in the seed bank after a single fire were relatively small and similar to the changes in aboveground forb species density following prescribed fire found by Hutchinson et al. (2005) and Keyser et al. (2012). These results contrast with Shi et al.'s (2022) global meta-analysis of relationships between fire and seed banks, which found either null or negative influences of fire on forest seed species richness and abundance. These differences in results are likely due to our sites not having been burned in at least 100 years (Adams et al., 2012), meaning that our single, low-intensity experimental burn may have favoured fire-dependent species without reducing habitat for fire-intolerant species.

4.2 | Canopy gaps and deer

In contrast to our second hypothesis, combined canopy gaps and deer exclusion in unburned areas had little effect on the seed bank. This differs with the strong interaction these disturbances had on seed bank species occurrence probability found by Shinoda and Akasaka (2020) in a temperate forest in Japan. That canopy gaps and deer exclusion, or lack thereof, had no influence on seed banks except in the presence of fire indicates the importance of burning in shaping fire-dependent plant communities. However, if deer densities were higher in our study site, it is possible that there would have been an interaction between deer exclusion and canopy gaps in unburned plots, as several studies in Japan, the United States and Poland have found that canopy gaps lead to increased browsing that can alter plant communities (Kuijper et al., 2009; Takatsuki, 2009; VanderMolen et al., 2021; Walters et al., 2020).

4.3 | Fire and canopy gaps

In agreement with our third hypothesis, we found that the combination of a prescribed fire and canopy gap strongly increased seed abundance in comparison to plots that were only burned or only had a canopy gap overhead. In this scenario, fires cleared existing biomass, created microsite heterogeneity and stimulated seed germination through heat and smoke, which allowed for a pulse of plant growth from the seed bank. The abundant resources and associated heterogeneity within burned plots with a canopy gap then allowed for plants to invest in seed production within the growing season, thereby replenishing the seed bank (Beck et al., 2023; Carbone et al., 2024).

Burning and canopy gaps also led to an increase in forb seed abundance and species density, similar to Hyatt (1999) who found

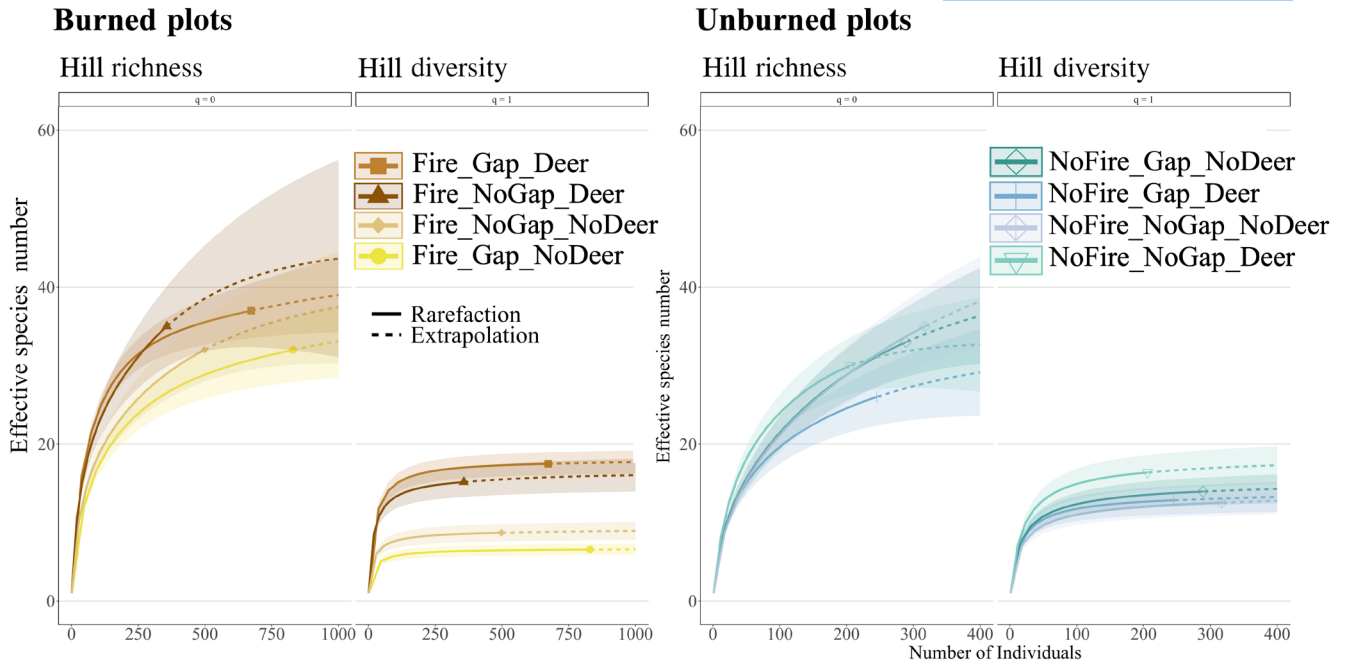


FIGURE 3 Seed bank Hill richness and Hill Shannon diversity by treatment. Shaded regions represent 95% confidence intervals. Rarefaction and extrapolation were calculated in the iNEXT package (Chao et al., 2014).

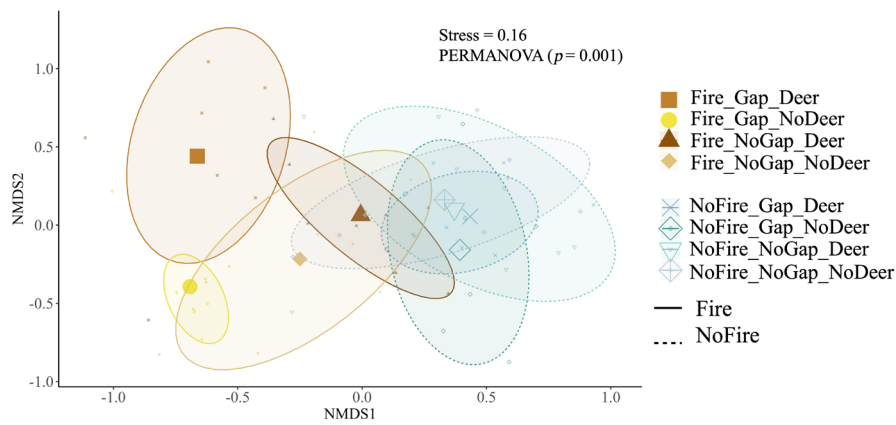


FIGURE 4 NMDS showing seed community differences amongst burned and unburned disturbance treatments.

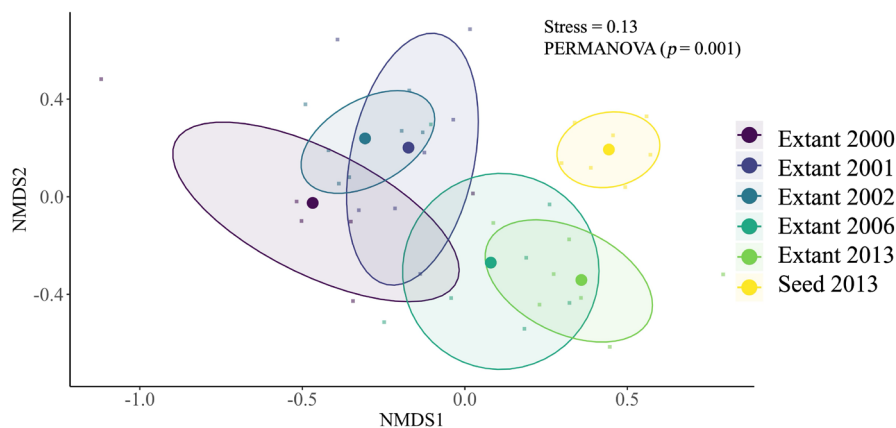


FIGURE 5 NMDS showing differences within burned plots with a canopy gap and deer presence amongst seed communities in 2013 (yellow) and extant plant communities sampled in 2000 (pre-treatment), 2001, 2002, 2006 and 2013.

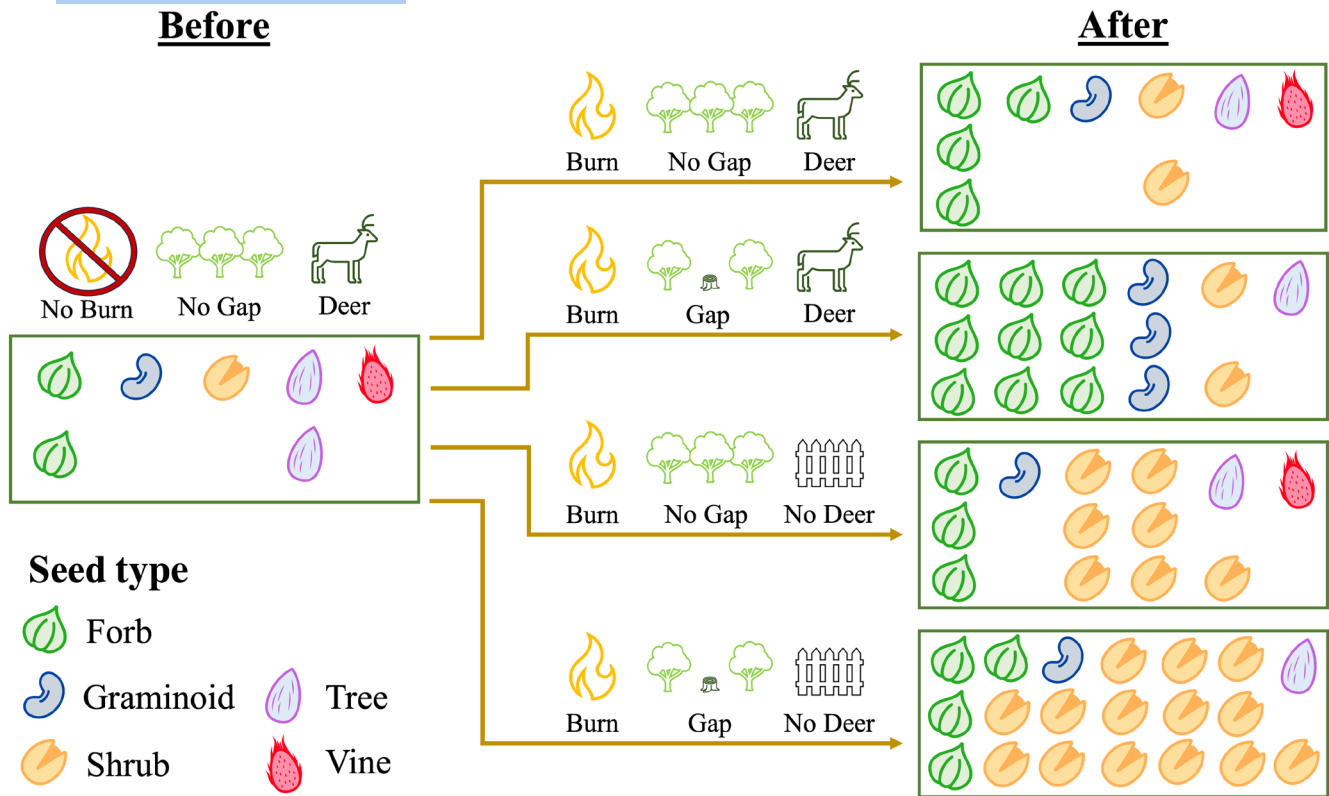


FIGURE 6 Schematic representing disturbance pathways to different seed bank communities found in our results. Burning with a closed canopy and deer presence led to a slight increase in forb seed abundance, burning with deer presence and a canopy gap led to a substantial increase in forb and graminoid abundance. In contrast, burning and deer exclusion led to a substantial increase in shrub seed abundance, particularly with a canopy gap overhead.

that forbs increased substantially with open canopies. Increased forb seed abundance parallels the increase in forb cover with fire and canopy gaps found by Royo et al. (2010) in this same experiment, which suggests that the forbs that initially germinated following these disturbances reached sexual maturity and established a long-term presence in the seed bank. It is also possible that combined fire and canopy gaps may be a way to increase forb growth and seed bank persistence, which is often desired within fire-dependent systems (Lettow et al., 2014; Yantes et al., 2023).

4.4 | Fire and deer exclusion

In contrast to our fourth hypothesis, we found that fire and deer exclusion decreased the seed bank's classic Shannon diversity and Hill Shannon diversity due to a parallel increase in shrub seed abundance. Ruderal shrubs, such as *Rubus*, were likely able to grow prolifically from the seed bank after a single low-intensity fire due to an increase in light and other resources (Borden et al., 2021; Reich et al., 1990). These shrubs, which produce highly palatable fruits, could then invest in reproduction in a high-resource environment without fruit being removed by deer browsing (Carbone et al., 2024; Gill & Beardall, 2001; Myers et al., 2004). As a result, long-lived shrub seeds accumulated in the seed bank and made the relative

proportions of seed life forms highly uneven, thereby decreasing classic Shannon diversity and Hill Shannon diversity. These results provide nuance to the finding that high densities of ungulate herbivores can reduce seed abundance (Beauchamp et al., 2013; DiTommaso et al., 2014; Levine et al., 2012; Tamura, 2019), as low and moderate deer browsing in burned areas seemingly maintains higher seed biodiversity by creating a more heterogeneous environment that allows for more even relative abundances of seed banking species.

4.5 | Fire, canopy gaps and deer exclusion

The combination of fire, canopy gaps and deer presence led to the most unique seed communities and the highest Hill Shannon diversity, similar to results for aboveground plants found by Royo et al. (2010) within this same experiment. In contrast, fire, canopy gaps and deer exclusion had a compounding effect on the seed bank and led to the lowest Hill Shannon diversity, likely due to these treatment's synergistic influence on *Rubus* (shrub) seed abundance. *Rubus* seed abundance in areas that were burned and had both deer exclusion and a canopy gap was substantially higher than in areas that were just burned and had deer exclusions. Nevertheless, the same deer-driven mechanism likely applies, wherein *Rubus* grew into a high

resource environment due to fire and canopy gaps and its highly palatable fruits dropped into the seed bank, thereby saturating the soil with *Rubus* seeds (Donoso & Nyland, 2006; Mladenoff, 1990; Widen et al., 2018). *Rubus* seeds can survive belowground for decades and readily germinate with disturbance (Donoso & Nyland, 2006), making it very likely that this seed legacy will become apparent in the understory following the next fire or canopy gap-creating event.

Shrubs are known to heavily compete with herbaceous species such as forbs and graminoids (Van Auken, 2009). The increase in *Rubus* seeds with deer exclusion may explain why we see a concurrent decrease in graminoid and forb seed abundance, as dense and fast-growing *Rubus* would shade-out the shade intolerant herbaceous species before they could reproduce and drop seed. That we might expect entirely different seed legacies depending on the presence or absence of herbivores in a burned environment with a canopy gap provides critical insight for land managers battling woody encroachment in formerly fire-prone ecosystems. The influence of herbivory on encroaching shrubs in the presence of burning and tree harvesting has been demonstrated globally in open-canopy forests and savanna ecosystems (Ding & Eldridge, 2024; Knapp et al., 1999; Stevens et al., 2017), but few have tested how these combined disturbances influence the subsequent seed bank. Our results suggest that the reintroduction of herbivores in open and burned ecosystems would reduce shrubs both aboveground and belowground.

4.6 | Fire-driven plant communities

Fire combined with canopy gaps and deer exclusion treatments led to unique seed bank communities in comparison to unburned areas with deer exclusion or a canopy gap treatment. These results support Grubb (1988) who found that fire and seed communities are coupled and that different disturbance events lead to different long-term seed banks. Fire was the strongest driver of community change in our study, with added community differentiation when deer and canopy gap treatments were applied (Figure 6).

Several studies theorize that aboveground and belowground plant communities should homogenize and converge with increasing disturbance due to there being greater ruderal species survival (Ma et al., 2021; Plue et al., 2021). In our study, seed communities in burned plots with a canopy gap and deer presence were substantially different from all extant communities at each time point. This result does not support our fifth hypothesis and suggests that the seed bank consistently maintains a unique species assemblage and likely changes over time due to many seeds having relatively short longevity in situ (Hille Ris Lambers et al., 2005; Probert et al., 2009). Nevertheless, even in the plots with the most reintroduced disturbances, 75% of all species in the seed bank in burned plots with a canopy gap and deer presence were not found in the extant understory in 2013, highlighting how the seed bank maintains an important reservoir of biodiversity over time. Additionally, extant plant communities were compositionally variable in comparison

to the seed bank, indicating that there is likely greater diversity to be found within seed banks than our sampling intensity indicates (Plue et al., 2021; Plue & Hermy, 2012). Thus, we believe the forest seed bank represents an important reservoir of native plant biodiversity, especially considering that 16% of taxa were non-native to North America and these taxa represented only 1% of total germinants.

5 | RUDERAL SPECIES, ECOLOGICAL MEMORY AND FUTURE CONSIDERATIONS

The novelty of this seed bank study highlights our limited understanding of how multiple disturbances influence forest succession, reorganization and future legacies. In our experiment, reintroducing disturbances favoured many ruderal species in the seed bank, several of which have shared genera and functional groups with those noted in Bossuyt and Honnay's (2008) review of European seed bank restoration potential. Although many of these seed banking species would be considered 'weeds' by land managers and of low restoration potential, ruderal species can play an important role in ecosystem restoration and succession (Kirkman et al., 2007; Palacio et al., 2016; Richmond et al., 2005). For instance, *Rubus*, the most important indicator species in our germination experiment, has been shown to reduce forest floor temperatures, hide tree seedlings from browsers and fix nutrients as biomass, which prevents nitrogen from leaching post-disturbance (Donoso & Nyland, 2006; Widen et al., 2018). These ruderal species are eventually shaded-out by growing trees, so their survival strategy is to create dense seed banks that buffer them from year-to-year variability and can germinate after the next vegetation-clearing disturbance (DeMalach et al., 2021; Ristau & Royo, 2020).

There could also be generalizable patterns in how the seed bank responds to certain combinations of disturbance. Based on our results, we expect fire, canopy gaps and ungulate exclusion to create a long-lasting shrub seed legacy, especially considering that shrub seeds are often more persistent than extant understory plants (Plue et al., 2017). A shrub seed bank would then continually recur following infrequent low-intensity fire and canopy gap creation in the absence of herbivores, thereby cementing an ecological memory of a shrub-dominated system in the seed bank (Johnstone et al., 2016). This ecological memory likely cannot be broken except through burning more frequently or manipulating the intensity of ungulate browsing (Jögiste et al., 2017; Nowacki & Abrams, 2008). These disturbance legacies and ecological memories make sampling the forest seed bank a valuable exercise to determine which combination of disturbances to apply in a restoration or management setting, particularly as the climate changes and many seed banking species are favoured by warmer conditions (Abella, 2022; Auffret et al., 2023).

The high numbers of disturbance-dependent species in the seed bank may also shed light on why many studies find a

'seed bank bias', wherein forest seed bank communities have low compositional similarity to those of aboveground plants (Hopfensperger, 2007; Larson & Suding, 2022). Our study appears to represent what Larson and Suding (2022) define as a 'parallel tracking' seed bank bias, wherein diversity increases in both the extant understory and seed bank across a gradient of increasing disturbance frequency despite there being compositional dissimilarity between both communities. The seed communities in our study are likely different from the extant understory because seeds of formerly living plants have slowly accumulated in the soil over 13 years and the ecosystem has not been burned or harvested recently. Compounding this seed bank bias, many studies under-sample the seed bank (Plue et al., 2021). These factors may then contribute to the assumption that seed banks are not an important source of biodiversity or component of forest development (Hopfensperger, 2007; Larson & Suding, 2022); however, our study provides evidence to the contrary.

Future studies that evaluate the influence of multiple disturbances on forest seed banks should make several considerations. First and foremost, our study highlights why researchers should think beyond how trees respond to multiple disturbances. Often, many layers of a forest are forgotten in relation to multiple disturbances, such as the understory or the seed bank (Gilliam, 2007; Gilliam & Roberts, 2003; Spicer et al., 2020). The fast-growing seed bank species in our study can heavily influence forest succession and it can take decades for the effects of multiple reintroduced disturbances to become fully apparent amongst tree communities, making the understory and seed bank an excellent study system in a multi-disturbance scenario. Further, seed bank studies should measure several functional traits rather than just species richness or diversity. This is one of the primary gaps in our understanding of seed communities, as species traits may be important in determining seed bank legacies following multiple disturbances (Larson & Suding, 2022; Saatkamp et al., 2019). Future work should also evaluate how seed banks vary with combinations of disturbance intensities, frequencies and severities in forest biomes and regions outside of North America, considering that the majority of multi-disturbance studies occur in the United States and Canada (Antwi et al., 2022; Foster et al., 2016; Kleinman et al., 2019). It is critical that we consider and test disturbances in tandem, especially since increased prescribed burning and canopy structural heterogeneity could help support forest carbon sequestration and biodiversity (Ehbrecht et al., 2021; Hiers et al., 2020; Ryan et al., 2013), while large ungulates are often far above historic densities and are now a dominant contemporary disturbance with many interactive effects (Bernes et al., 2018; Carpio et al., 2021; Reed et al., 2023; Rooney & Waller, 2003). With greater and more nuanced multi-disturbance inquiry, we may be able to better detect nonlinear disturbance responses in forests around the world and improve research integration into meta-analyses (Buma, 2021; Mori et al., 2017; Sasaki et al., 2015). To this end, through our experimental and long-term approach to measuring how multiple disturbances influence the seed bank, we advance our

limited understanding of how multiple drivers of change influence the forest seed bank, succession and biodiversity.

AUTHOR CONTRIBUTIONS

Alejandro A. Royo and Walter P. Carson contributed to experimental design, data collection and curation; Samuel P. Reed developed hypotheses, analysed data, created figures and wrote each manuscript draft; Alejandro A. Royo, Walter P. Carson, Castilleja F. Olmsted, Lee E. Frelich and Peter B. Reich contributed to conceptualization, writing and editing manuscript.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

Data and code available at Dryad Digital Repository at <https://doi.org/10.5061/dryad.Ogb5mkm8v> (Reed et al., 2024).

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SUPPORTING INFORMATION

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

Table S1: Total species-specific abundance, proportional abundance, and native status to West Virginia.

Table S2: Seed bank Hill richness and diversity in response to each treatment combination.

Table S3: Seed bank community differences by treatment tested using pairwise PERMANOVA.

Table S4: Seed and extant herb pairwise comparison within burned plots with a canopy gap and deer presence.

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