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RESEARCH ARTICLE

Delaying a prescribed burn to scale up the restoration of alien-invaded Lowland Sand Fynbos in South Africa

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Abstract

Fire-adapted species invading fire-prone ecosystems in Mediterranean climate regions are difficult to control because they are equally responsive to restoration treatments. We assessed the efficacy of delaying a prescribed burn to promote the recruitment of native species in a Lowland Sand Fynbos ecosystem invaded by alien *Acacia saligna*. Acacia stands were felled and fallowed for 2 years before burning the slash and sowing pre-treated fynbos seeds. We hypothesized that sowing pre-treated fynbos seeds after fallowing cleared areas before burning would improve the regeneration of native species. Fallowing cleared areas would reduce the density of acacia seeds and post-fire acacia recruitment while allowing felled acacia biomass to dry and decay over time leading to improved prescribed burn properties. Sowing pre-treated fynbos seeds improved the recovery of native cover but had little effect on the recovery of native species diversity after 2 years. Although the rapid recruitment of annual native species did not affect acacia density, it might have contributed to reduced post-fire acacia cover and allowed the native perennial species to establish. After 2 years of fallowing cleared areas, the density of acacia seeds and post-fire acacia recruitment was reduced by ≈50% and 80% respectively. Although too dense to be outcompeted by recruited native species alone, this reduced acacia recruitment helped to decrease and delay the need for follow-up acacia clearing as it was where burning occurred soon after felling acacia stands. The recruited native species managed to establish before the acacia emergents were removed unlike where burning occurs soon after felling and where native species were outcompeted resulting in the need for follow-up sowing. In conclusion, building resilience against acacia resurgence by increasing the pool of sown species to recover a good cover of native species in combination with the timely removal of acacia recruits can help to scale up restoration.

KEYWORDS
Acacia saligna, Fabaceae, Greater Cape Floristic Region, invasive species, prescribed burn, recruitment, regeneration, wildfires

INTRODUCTION

Many plant species in fire-prone ecosystems persist via soil seed banks (Auld & Denham, 2006; Tangney et al., 2020). When restoring fire-driven ecosystems that are invaded by fire-dependent alien species, the likelihood of restoration success depends on factors such as the ratio of

native to alien species in the soil seed bank, as well as the intensity and severity of fire (Holmes, Esler, Gaertner, et al., 2020; Holmes, Esler, van Wilgen, & Richardson, 2020). The degree and duration of alien invasions determine the nature of the seed bank, the accumulation of biomass, and other impacts (Holmes, Esler, Gaertner, et al., 2020; Holmes, Esler, van Wilgen, & Richardson, 2020). Often, these invasions cause a reduction in the native seed bank density and richness (Holmes, 2002). In many cases, invasive plant removal alone does not translate to the recovery of native vegetation, owing to the absence of native propagules and altered ecosystem functioning (Hall, Bastos, et al., 2021; Hall, Holmes, et al., 2021). Most large-scale alien control interventions in fire-driven ecosystems focus on alien clearance alone, hoping that the cleared areas will be restored passively after the next wildfire (Nsikani et al., 2017). However, autogenic recovery is improbable in areas with a long history of invasion where the biotic thresholds have been crossed, e.g. depleted native seed bank and feedback loops created (Aronson et al., 1993; Gaertner et al., 2012; Geerts et al., 2022; Holmes, 2002; Holmes, Esler, Gaertner, et al., 2020; Holmes, Esler, van Wilgen, & Richardson, 2020). In such cases, active interventions, e.g. the addition of seeds, are required to facilitate and direct the recovery of native vegetation on a restoration trajectory towards a structurally representative condition. This can be challenging, particularly if the invasive species being controlled is equally adapted to the biophysical environment or equally responsive to the restoration treatments applied to encourage native regeneration. A prime example is using fire treatments to restore a Mediterranean-type ecosystem that is heavily invaded by a species originating from another Mediterranean climatic region.

The use of prescribed burns in fire-prone South African Cape Flats Sand Fynbos, heavily invaded by fire-dependent wattle species originating from Australia, e.g. *Acacia saligna*, epitomizes the problem. Previously, it was thought that these invasions could be controlled by using fire treatments to stimulate mass germination of acacia to deplete the soil-stored acacia seed banks. However, this was deemed unviable and uneconomic over large areas because it resulted in repeated and intensive follow-up clearing of emergent seedlings post-fire (Pieterse & Cairns, 1986). The mass germination of acacia after fire treatments poses challenges to restoration, particularly where the regeneration of native species is the primary goal. Consequently, nowadays there is some reluctance in conducting prescribed ecological burns shortly after felling acacia stands when the acacia seed bank is very large (Krupek et al., 2016). Though necessary to remove acacia slash and to stimulate germination of the residual seed bank, such a treatment can be counter-productive in areas with acacia-dominated seed banks. The heat pulse stimulates high-density post-fire acacia emergence while native species are sparsely recruited from the depleted native seed bank (Hall, Bastos, et al., 2021; Hall, Holmes, et al., 2021). This is problematic for restoration, as native species are outcompeted by the *en masse* recruitment of acacia which germinates and grows faster than the native species (Morris et al., 2011). The control of this high-density acacia recruitment is difficult to implement over large spatial scales and can be damaging to the recruited native species due to extensive foliar herbicide application and trampling (Krupek et al., 2016). Consequently, we initially proposed evading this problem by avoiding fires in areas with relatively large acacia seed banks (Ngwenya et al., 2023). However, fires should not be avoided indefinitely due to their ecological importance but also cannot be avoided, particularly if people are living within a fire-prone ecosystem. Human populations increase the risk of ignition to an already highly flammable vegetation type such as fynbos (van Wilgen et al., 2010).

Seed bank size and seed longevity in the soil are important factors to consider when designing control measures for hard-seeded invader species such as acacia (Strydom et al., 2017, 2019). The acacia seed bank and its legacy effects may persist for over 50 years, while countering the re-establishment of native vegetation (Strydom et al., 2017). Although ≈90% of the original acacia seed bank is lost to high-density post-fire acacia recruitment and fire mortality, the residual portion remains viable and persistent for decades making it difficult to control reinvasions (Auld & Denham, 2006; Hall, Bastos, et al., 2021; Hall, Holmes, et al., 2021; Holmes, 1990; Strydom et al., 2017). Without fire treatments, acacia mass germination can be avoided while the acacia seed bank is reduced significantly (50%–80%) within 2 years post-clearance (Hall, Bastos, et al., 2021; Hall, Holmes, et al., 2021; Holmes & Moll, 1990; Ngwenya et al., 2023). Most acacia seed bank decline happens naturally in the first year or two post-clearance due to predation, decay, or seed movement deeper into the soil (Holmes & Moll, 1990). When the seeds are buried deeper in the soil, they become inaccessible to predators and decay is slower, causing the residual acacia seed bank to remain largely stable until a fire results in mass acacia germination (Hall, Bastos, et al., 2021; Hall, Holmes, et al., 2021; Holmes, 1989b; Ngwenya et al., 2023). However, the acacia seed bank is not exhausted by a single fire event as a portion remains persistent for decades (Strydom et al., 2017). This shows that choosing to burn or not after felling acacia makes little difference to the residual acacia seed bank after 2 years (Hall, Bastos, et al., 2021; Hall, Holmes, et al., 2021; Ngwenya et al., 2023). Our study proposes waiting for the post-clearance acacia seed bank to decline by >50% before fire treatments are conducted. This reduction in the acacia seed bank is anticipated to reduce the high-density post-fire acacia recruitment and minimize the persistent portion of the residual seed bank. This could strengthen the long-term resilience of native regeneration against future acacia resurgence. Two years of fallowing is assumed optimal since the most significant declines in acacia seedbanks occur within this post-clearance time frame (Hall, Bastos, et al., 2021; Hall, Holmes, et al., 2021; Ngwenya et al., 2023). Therefore, extended fallow intervals might be of little value in reducing the acacia seed bank further, although it might help reduce the above-ground acacia slash (Holmes, 1989a; Ruwanza et al., 2013).

The dynamics of most fire-adapted seed banks are explained by the existence of a trade-off between seed burial depth, dormancy, recruitment, and seed survival through high temperatures from fire (Auld & Denham, 2006; Tangney et al., 2020). The shallower the seed burial, the higher the risk of mortality from high temperatures during a fire, whereas seeds buried too deep in the soil are protected from the heat pulse or they may germinate but may fail to emerge from such depths (Auld & Denham, 2006; Tangney et al., 2020). Once buried deeper in the soil and below the zone of soil heating, seeds can remain for decades, since the heat shock required to break the dormancy of acacia seeds declines with soil depth (Auld & Denham, 2006). *Acacia saligna* can germinate from depths up to 10 cm but not deeper than that as such seeds are unlikely to receive any heat pulse from a fire, except perhaps from a severe fire such as a burning brush pile (Holmes & Moll, 1990). In the absence of fire, the transient portion of the seed bank is lost when recently dispersed acacia seeds germinate (the soft portion that has not yet developed a water-impermeable seed coat), decay (fresh seeds), are predated or dispersed deeper in the soil over time (Holmes, 1990). Forty-five percent of buried, fresh acacia seeds decayed in the first year, but thereafter, this decay rate was much lower (Holmes, 1989a; Holmes & Moll, 1990). However, the recent (fresh) seed input only represents a small proportion of the

total soil seeed bank, and therefore it does not account for the whole seed bank but only the latest seed input if buried (Holmes & Moll, 1990). The proportion of seeds that remain dormant may be affected by prevailing humidity and temperature although these remaining seeds are hard and remain dormant despite wet-dry cycles (Holmes & Moll, 1990; Tozer & Ooi, 2014).

Recruitment in fire-driven ecosystems is sensitive to fire regimes and fire properties. Typical fynbos fires are characterized by a variable fire return interval and season (van Wilgen et al., 2010). Fire frequency may vary from 4 to 40 years, but for many fynbos ecosystems a fire cycle between 10 and 30 years is optimal (Geerts, 2021; Kraaij et al., 2011; van Wilgen et al., 2010). Historical fynbos wildfires covered large areas, were typically high intensity (spread fast), and burned during the hot, dry season (van Wilgen, 2013). Invasive species change vegetation conditions by altering the amount and composition of biomass, which affects fire properties. For example, acacia biomass is woodier, and wetter compared to the shrubby and flammable fynbos biomass (van Wilgen & Richardson, 1985). Therefore, the conditions in these invaded areas result in fires whose properties differ from natural fynbos fires due to the increased fuel load and water content in the biomass. Often these fires are more severe and slow-moving compared to fynbos fires. When the invaded area burns under severe weather conditions, residual heat release is higher than in normal fynbos. Severe and slow-moving fires transfer more heat to the ground and may kill native surface seed banks and rootstocks of resprouter species, resulting in barren soils (Holmes, 2001; Holmes et al., 2000).

Prescribed burns should be planned to mimic fire regimes and properties of reference ecosystem wildfires to optimize native recruitment response. However, the properties of a wildfire are difficult to emulate if the vegetation is highly degraded with altered species composition, structure, and dynamics. By delaying prescribed burns after initial alien clearing, we envisaged that fallowing cleared areas could allow the acacia slash to dry and decay, thus reducing the water content and fuel load to improve the properties of the ecological burn (Ruwanza et al., 2013). The reduced acacia biomass and moisture content would result in a quick and less severe prescribed burn, thus reducing damage to native seeds and rootstocks (Ruwanza et al., 2013). Reducing acacia slash to improve fire properties and to reduce post-fire acacia mass germination (from a reduced acacia seed bank) are anticipated to encourage the regeneration of species-diverse native vegetation.

In this study, the response of vegetation recruitment to a 'Fell, Fallow & Burn' restoration treatment followed by sowing pre-treated seeds was assessed over time. We investigated whether simulating the veld conditions of an undisturbed fynbos ecosystem would reduce the density of post-fire acacia recruitment and encourage the recruitment of species-diverse native vegetation. We envisaged that fallowing felled areas would allow the acacia seed bank to decline before a fire, thus reducing the density of post-fire acacia emergence. Also, a delayed prescribed burn would reduce acacia slash and help to improve the properties of the ecological burn. Second, we investigated improving the establishment of native vegetation by post-fire sowing of pre-treated seeds in plots compared to paired unsown plots. Specifically, we investigated the following parameters after felling, fallowing, and burning acacia slash before sowing pre-treated fynbos seeds: (1) The effects of sowing on the recruitment of native vegetation over time, (2) the effects of sowing on the recruitment of acacia and other herbaceous alien vegetation over time, and (3) the effects of fallowing cleared areas on the recruitment of acacia and its seed bank over time.

METHODS

Field site description

The study was conducted at Sandown Conservation Area in Cape Town, Western Cape Province, South Africa. This is a biodiversity offset area of Critically Endangered Cape Flats Sand Fynbos resulting from nearby residential development. The offset is part of a fynbos corridor linking the Table Bay and Blaauwberg Nature Reserves (Ngwenya et al., 2023; Figure 1). The 34.3 ha area was initially cleared of *A. saligna* (Port Jackson willow) and some *Leptospermum laevigatum* (Australian myrtle) in August 2017. The experimental plots were set on Management Unit 5 (MU5; 7.55 ha) (Figure 1). No pre-surveys were conducted before alien clearing in 2017. However, the density and basal cover of acacia stumps from the 2017 initial clearing were found to be the same as those found at BBNR in 2019. Based on these findings, it was assumed that the degree of invasion in the Sandown area was like that at Blaauwberg Nature Reserve (BBNR) since they had similar invasion histories as per aerial images (Ngwenya et al., 2023). Similarly, it was presumed that the acacia seed bank at Sandown in 2017 was representative of the acacia seed bank at BBNR in 2019 as the invaded area was continuous between the two sites which are within 8 km of each other (P. M. Holmes, personal observation). During fallowing, both woody and non-woody invader species were cleared from the site by the contractor in November 2018 and August 2019.

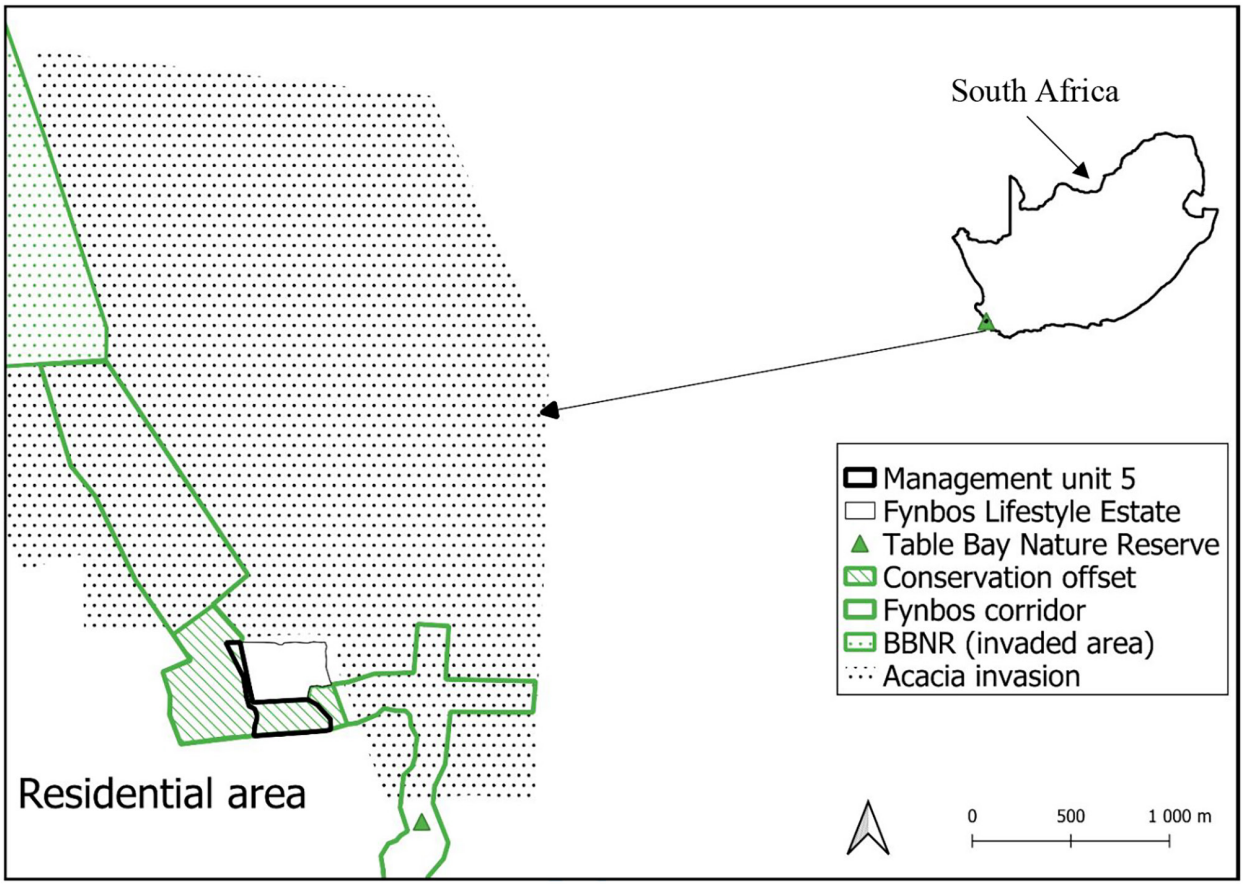

FIGURE 1 Map of the Sandown area showing the conservation offset for residential development and Management Unit 5 (MU5) and the Fynbos corridor linking Blaauwberg Nature Reserve (BBNR) and Table Bay Nature Reserve. The acacia invasion spanned the entire Sandown area to BBNR, barring a few fynbos remnants. The study was conducted on management unit 5, which was a part of the conservation offset. The residential development is expanding into most of the areas that are invaded by *Acacia saligna*.

Experimental design and data collection

The study consisted of a laboratory, nursery, and field component whereby the laboratory and nursery experiments assessed the viability and percentage germination of the collected seeds under controlled environments. The field experiment investigated the regeneration of native vegetation over time in response to the restoration treatments, i.e. the delayed prescribed burn.

Seed preparation, testing, and sowing rates

The seeds used in this experiment were collected from local fynbos remnants by various parties including the Expanded Public Works Programme (EPWP), reserve staff members, volunteers, and a seed-collecting private company (Vula Environmental Services). A total of 34 fynbos species was collected to represent annual, ericoid shrub (reseeders & resprouters), proteoid shrub, forb, graminoid, and geophyte growth forms (Appendix S1). Species selection for the seed mix was guided by availability, species significance, and contribution to the ecosystem's structure and functioning. The methods of seed collection, storage, and pre-treating were guided by previous literature and expert advice as shown in Appendix S1. All seeds were treated with smoke generated from burnt fynbos biomass while additional treatments required by some species, e.g. heat pulse and scarification, were implemented using an oven and sandpaper respectively. Seed viability was tested using tetrazolium and was used to estimate the sowing rates of viable seeds from the clean seed equivalent (CSE) per species (Frischie et al., 2020).

Seed germination in controlled environments

To understand the germination potential of collected seeds, an experiment was set up in the nursery whereby a subsample of 100 pre-treated seeds from each species was sown in a tray measuring 240 × 170 × 60 mm. Each tray was filled with soil collected from the site and the seeds were sprinkled on top and covered thinly in soil. Three additional control trays were filled with soil only. After sowing, the trays were watered manually three times a week until germination was initiated (Hall et al., 2017; Ngwenya et al., 2023; Waller et al., 2015). The number of germinated seeds was assessed and expressed as germination percentage per species.

Field set-up

To investigate the response of vegetation recruitment following a delayed prescribed burn, 15 pairs of experimental plots (5 × 10 m) were marked on the 7.55-ha restoration site before burning in February 2020 (Figure 2a,c). The treatment plots were broadcasted with pre-treated fynbos seeds and gently raked (Figure 2b) following the burning of acacia slash after two and a half years of initial clearing, while the control plots were left unsown. Delaying the prescribed burn allowed the acacia biomass to decay and dry up over time. Through reduced biomass and water content, the veld conditions would more closely mimic those of a fynbos ecosystem, i.e. sclerophyllous and flammable, and help to simulate the properties of a fynbos fire when it burns, i.e. fast-moving and not severe. Also, the burning and sowing times were synchronized with the

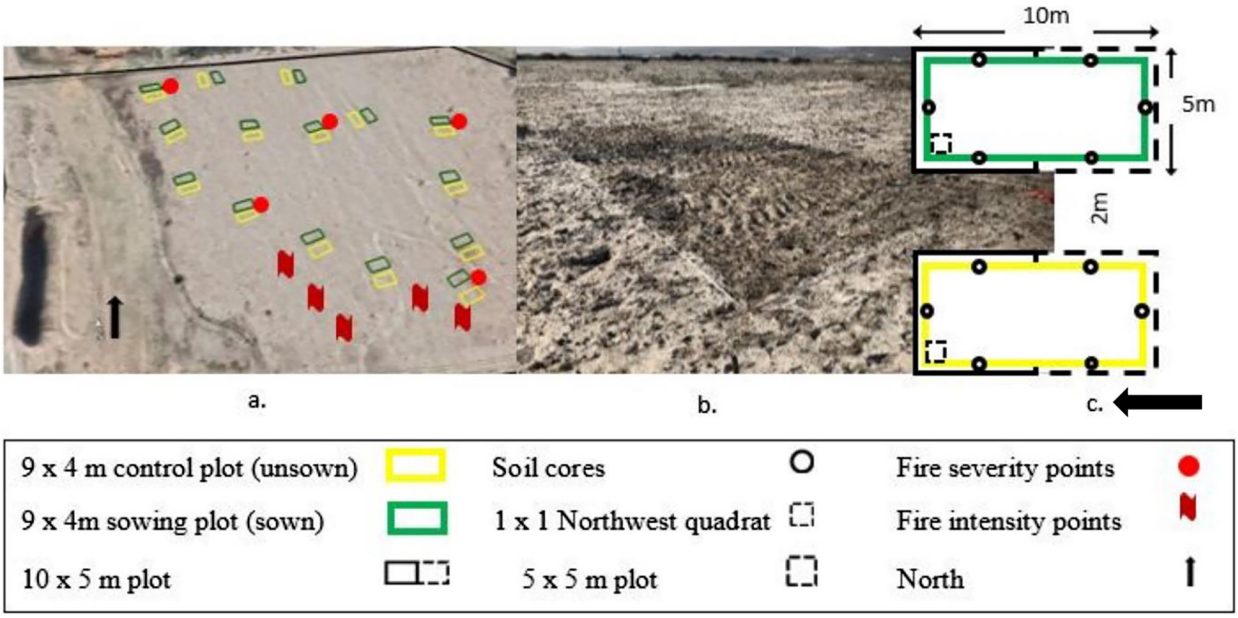

FIGURE 2 Fifteen (5×10 m) pairs of sowing (green) and control (yellow) plots were marked on Management Unit 5 as displayed in (a), showing on aerial imagery taken 5 months post-prescribed burn. A buffer of 1 m was marked on the plots to separate sowing areas from the surrounding unsown areas and to account for seed movement. Fire severity (heat) and fire intensity (spread rate) measurements were monitored from the points marked in red. (b) Photograph taken after sowing one of the plots with a pre-treated Fynbos seed mix. (c) Shows the spatial arrangement of sampling plots in the field that were pre-surveyed and monitored over 2 years.

local fire and growing seasons, e.g. exposing the seeds to autumn fluctuating diurnal temperatures and winter rainfall. However, owing to the Covid pandemic lockdown restrictions, sowing was delayed by a month to 18 May 2020.

Data collection

Before conducting a prescribed burn, the experimental area was surveyed for the degree of acacia invasion, restoration potential, and acacia seed bank like Ngwenya et al. (2023) (Figure 2c). Remnant indigenous cover and diversity of the restoration site were used as an indicator of the restoration potential whereby indigenous cover of <10% was deemed as low restoration potential (Hall, Bastos, et al., 2021; Hall, Holmes, et al., 2021). The acacia seed densities were estimated as the size of the acacia seed bank per one square metre whereby six replicate soil cores were collected from each plot to represent the surface area of 0.012m^2 (Hall, Bastos, et al., 2021; Hall, Holmes, et al., 2021). Each soil core measured 10 cm deep by 5 cm diameter and was sifted to remove sand, placed in a plastic bag, and taken to the laboratory to count the number of acacia seeds (Figure 2c) (Hall, Bastos, et al., 2021; Hall, Holmes, et al., 2021; Tozer, 1998). The acacia seed bank was sampled before and after burning acacia biomass over the two-year monitoring period. The formula: (Final – Initial amount)/Initial*100 was used to calculate the percentage change in acacia seed bank between periods, e.g. during falllowing. The recruitment of vegetation was monitored in all plots during spring and autumn for 2 years and the recruited species were identified (Appendix S2). The vegetation metrics used to monitor the recruitment response were species cover, richness, and density. Species cover was estimated visually as a percentage projected canopy cover per plot and per 1 square metre while species richness represented the number of different native

species recorded per plot. Species density was determined by counting the number of individuals per species in a 1 × 1 m quadrat placed on the north-western corner of each plot (Figure 2c). When deemed necessary, acacia seedlings were removed from the plots by hand-pulling or cutting below the root crown using loppers (herein referred to as follow-up acacia clearing), to facilitate the establishment of native species. Two follow-up clearing operations were conducted, one in November 2020 and another one in November 2021.

Measurements of fire properties

On the 18th of February 2020, a prescribed burn was conducted on MU5 from 10:35 a.m. until 12:00 p.m. The northern end of the experimental area (Plots 9, 10, and 12) was burnt using a back burn and the remainder using a head fire (Figure 2a). Weather conditions such as wind speed, wind direction, temperature, and humidity were recorded during the burn using a mobile phone weather app (Daily Weather). Having the Global Positioning System (GPS) switched on from the mobile phone allowed the app to retrieve onsite weather conditions. Fire-related properties such as soil temperature, heat release, flame height, and fire spread rate were measured (van Wilgen & Holmes, 1986). Soil temperature changes were measured using a set of nine-level temperature-sensitive labels (RSPro, United Kingdom). The sensitive labels were buried at different soil depths (0, 1, and 4 cm) of the soil's upper layer where most of the seeds are found. Temperature strips used were sensitive to the following temperature ranges; 204–260, 116–154, and 71–110°C. Temperatures falling below 71°C or exceeding 260°C temperature ceilings were assumed to be too cool and hot, respectively, for heat pulse seed dormancy breaking. Because these temperatures could not be detected on the thermo-strips, they were assumed to be 50°C if falling below 71 and 300°C if above 260°C. One day after the fire, thermo-strips were dug and retrieved to record temperature readings. Missing strips were assumed to have been consumed by heat and scored as 300°C. The height of the flame was measured relative to the height of flagpoles placed in the experimental area. The intensity of the fire was measured as the rate of fire spread calculated from the time it took the fire front to move between flagpoles of a known distance apart.

Fire severity was measured as the amount of heat released during burning. It was estimated indirectly from the amount of water evaporated by the fire and the maximum temperature recorded at the soil surface. Five cans (330 mL) filled with water to the top were randomly placed on sown plots and five on control plots (Figure 2a) before the fire was started. The amount of water in the cans before and after the fire was measured. The heat released by the fire was calculated from the energy required to boil and evaporate the water using the formula $Q = m.\Delta H_v$ (Q = heat energy in joules [J], m = mass of water lost in grams [g], ΔH_v = heat of vaporization). This heat energy was required to increase the temperature of water from ambient temperature to 100°C and to convert water to steam (Trollope, 1984). The study used 1 millilitre (mL) of water ≈1 g water, specific heat capacity ≈1 calorie (cal)/g °C, 1 cal = 4.184 J, the heat of vaporization of water ≈540 cal/g °C in the calculations.

Data analysis

All analyses were done in R version 4.1.0 (R Core Team, 2021). Descriptive statistics were used to analyse the restoration potential,

degree of acacia invasion, and properties of the prescribed burn in the experimental area. A Kruskal–Wallis test was used to analyse data on acacia seed density before and after fallowing as well as on the recruitment of acacia before and after follow-up clearing. General linear mixed-effects models (GLMMs) were used to analyse the effects of restoration treatments on the recruitment of vegetation and the size of the acacia seed bank post-fire. GLMMs were calculated from the generalized linear mixed models using Template Model Builder (glmmTMB) packages in R (Brooks et al., 2017). The model formulae specified the vegetation metrics as response variables (native species cover and richness, alien species cover and acacia seed densities) to a function of predictor variables (treatment, time, season, and interactions). Plot numbers were included as random variables in all models to account for pseudo-replication. Individual models were evaluated for goodness of fit using residual diagnostics for multilevel regression models in the DHARMA package (Harting, 2017). Where model misspecifications were detected, the model formula was adjusted by incorporating the overdispersion and zero-inflation components or by changing the distribution errors to improve the model fit. We used Cohens' *d* and Hedges's *d* at 95% confidence level as a measure of the effect sizes between treatments at different sampling time intervals (Lakens, 2013). The effect sizes are categorized based on the values of Cohen's *d* and Hedge's *d* whereby the effect size is considered negligible if Cohen's *d* is <0.15 and huge if Cohen's *d* is >1.45 as an example (Laken's, 2013). For the GLMM models, Cohens's *d* was calculated from the Estimated Marginal Means using the emmeans package in R (https://cran.r-project.org/web/packages/glmmTMB/vignettes/model_evaluation.pdf).

RESULTS

Pre-conditions of the experimental area

Before clearing, the acacia stand density was 0.99 ± 0.91 plants/m^2 (9900 ± 9100 plants/ha) with a total basal cover of 10.9 ± 17.9 m^2/ha. Two years after clearing, vegetation canopy cover comprised 20.8 ± 18.4% including alien and native species before burning acacia slash. Slash constituted 70.5 ± 27.3% of ground cover. A total of 24 native species and 14 alien species were recorded across the experimental area during pre-fire surveys. Of the 24 native species recorded, there were 14 ericoid shrubs, 1 geophyte, 8 graminoids (grasses and sedges), and 1 restioid (Appendix S2). The most prevalent non-woody alien species recorded were *Tithonia* sp., *Raphanus* sp., and *Erigeron* sp. (Appendix S2).

Fire intensity and severity

On the day of the burn, the maximum temperature was 24°C, air pressure was 1015 hPa, humidity at 52%, wind speed of 13 km/h, and wind direction varied between southerly (West Southwest) and Southeast to Northwest. The fire had an average flame height of 2.00 ± 1.39 m, and it travelled at 0.03 ± 0.01 m/s while releasing 502 ± 88.3 kJ of heat energy causing the soil surface temperatures to reach at least 250°C (Figure 3). The average maximum soil temperature decreased significantly with soil depth ($p < 0.001$, $R = 0.64$, Figure 3). The highest recorded soil temperatures were 237 ± 67.7°C at the soil surface, 136 ± 37.9°C at 1 cm, and 56 ± 19°C at 4 cm deep (Figure 3).

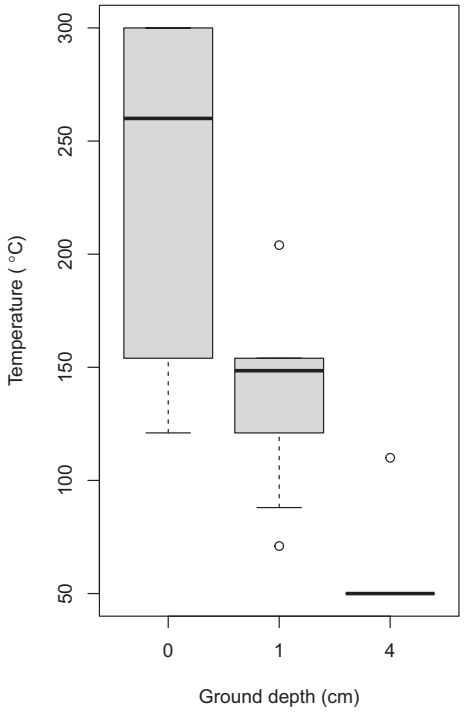

FIGURE 3 Maximum and minimum soil temperatures reached at different soil depths during the prescribed burn. The temperatures were recorded from thermo-strips that were buried at 0, 1, and 4 cm depths into the ground.

Sowing rates and germination percentage

Sowing rates for viable seeds were highly variable across the 23 tested native species ranging from zero for most proteoid species to 5138 seeds/m^2 for *Trichogyne repens*. Most of the proteoid seeds were either rotten or hollow and none of the full seeds were viable (Table 1) resulting in very low sowing rates. The low sowing rates for most ericoid resprouters resulted from limited seed supplies. More species germinated in the nursery compared to the field whereby 30 out of the 34 species sown both in the nursery and field were able to germinate in the nursery whereas only 17 germinated in the field (Table 1). Some species might have germinated but failed to establish successfully in the field, e.g. most *Sparaxis* seedlings were dug out and their bulbs were eaten after germination. Very few fynbos species germinated from unsown control trays in the nursery which were dominated by weedy species including *Tithonia* sp., *Erigeron* sp., and *Raphanus raphanistrum*.

Post-fire vegetation recruitment in the field

In total, we identified 130 indigenous plant species (Appendix S2) across 30 treatment plots at Sandown Conservation Area over the 2 years of monitoring. This is a large increase in native species richness compared to the 24 species recorded pre-burn. There were 21 alien species other than acacia (Appendix S2).

Recruitment of native species

Both native species cover and richness (Table 3, Figure 4a,b) increased significantly in all treatments over 2 years. However, there was more native

TABLE 1 Sowing rates per plot and percentage germination of seeds sown in the nursery and field.

Growth form	Species	Viable seed sowing rates (No. viable seeds/m^2)	Germination percentage	
			Nursery (%)	Field (%)
Annuals	*Oncosiphon grandiflorum*	na	100	100
	Osteospermum clandestinum	na	21	0
	Senecio elegans	na	35	0
	Ursinia anthemoides	na	74	1.55
Ericoid shrub reseeders (ERSe)	*Anthospermum aethiopicum*	129	25	7.14
	Cliffortia polygonifolia	120	5	13.90
	Erica axillaris	18	0	0
	Erica plumosa	na	0	0
	Helichrysum teretifolium	na	5	0
	Metalasia densa	na	1	5.88
	Passerina corymbosa	111	15	0.02
	Trichogyne repens	5140	7	52.30
Ericoid shrub resprouter (ERRe)	*Agathosma imbricata*	1.20	2	0
	Diosma oppositifolia	0.61	7	0
	Erica mammosa	15.1	14	0
	Phylica cephalantha	26.8	15	2.04
	Trichocephalus stipularis	0.82	7	0

(Continues)

TABLE 1 (Continued)

Growth form	Species	Viable seed sowing rates (No. viable seeds/m^2)	Germination percentage	
			Nursery (%)	Field (%)
Proteoid shrub (Pr)	*Protea repens*	0	5	0
	Protea scolymocephala	0	1	0
	Leucadendron salignum	0	15	7.14
Perennial forb (Reseeders)	*Pelargonium capitatum*	14	11	0
	Leysera gnaphalodes	760	13	1.05
Perennial graminoid reseeders (Gram)	*Thamnochortus punctatus*	214	3	0.07
	Pentameris pallida	3330	30	100
	Restio duthieae	na	0	0
	Willdenowia incurvata	na	0	0
Geophytes resprouters (Geo)	*Albuca cooperi*	198	22	0
	Baeometra uniflora	38.4	70	0
	Chasmanthe aethiopica	0	11	0
	Gladiolus carinatus	3.65	63	0
	Othonna sp.	24.7	17	0
	Sparaxis bulbifera	67.3	82	12.50
	Wachendorfia paniculata	14.8	45	11.30
	Watsonia meriana	76.6	44	3.27

Note: Sowing rates refer to an estimated number of "clean seed equivalent" viable seeds per square metre. Viability tests were not conducted on small seeds and 'na' was used to indicate such species.

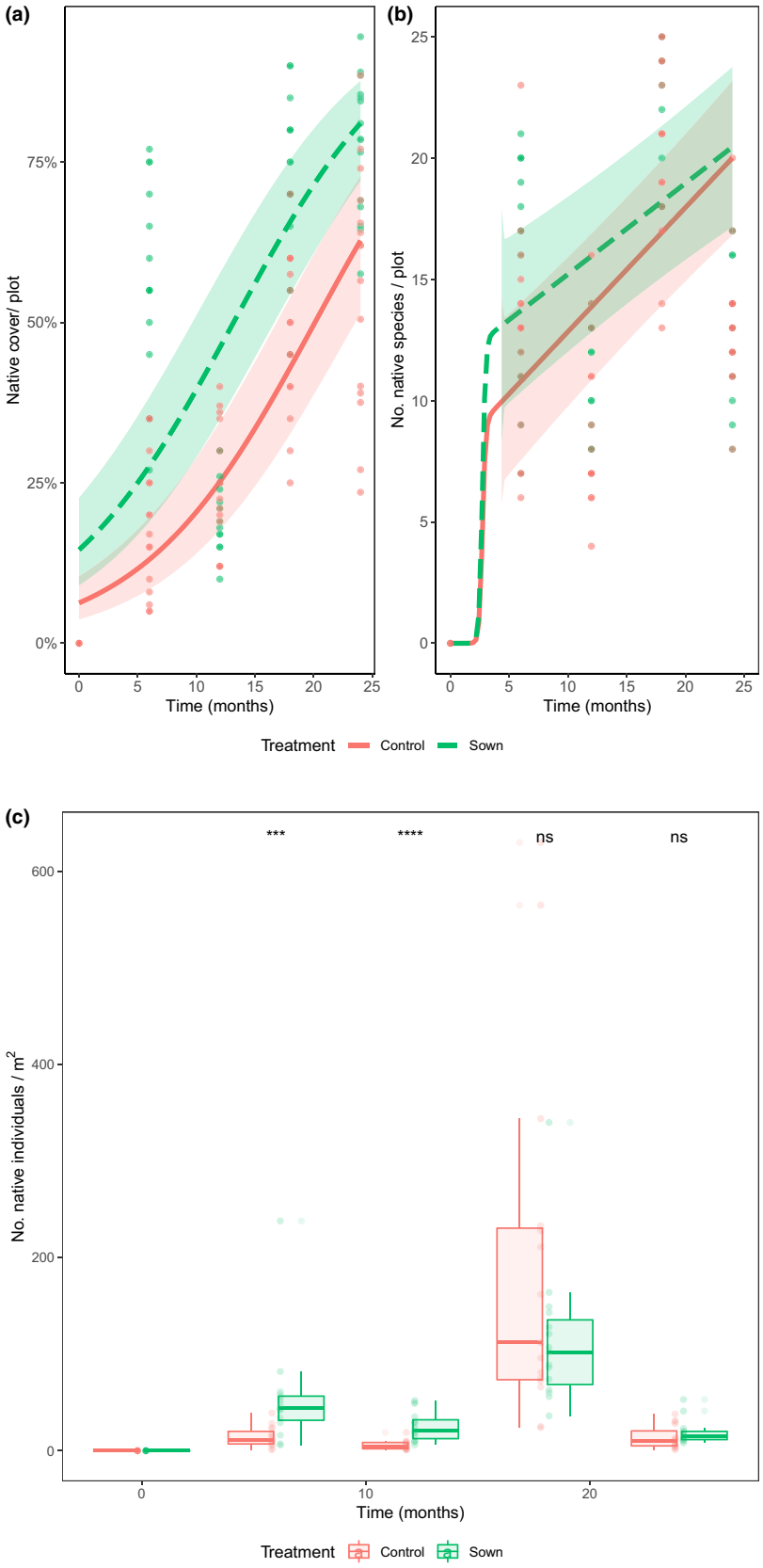

FIGURE 4 The GLMM interaction effects between treatment and time on the recruitment of native species (a) percentage native cover/plot, (b) native species richness/plot, and native species density/m^2 (c) in response to a delayed prescribed burn over time. The 95% confidence interval is indicated by the shaded area and data points by dots. The following significance levels were used: ***$p < 0.001$, **$p < 0.01$, *$p < 0.05$ and *ns* > 0.05 (R Core Team, 2021).

TABLE 2 Comparison of acacia recruitment (cover and density) between treatments per sampling period before and after follow-up clearing operations at 8- and 20-months post-fire.

		Kruskal–Wallis-sum test		
Variable	**Time (months)**	**Chi square**	**df**	***p***
Acacia cover (% cover/plot)	0	1.77	1	0.184
	6	3.35	1	0.0673
	12	7.95	1	0.0048**
	18	10.9	1	0.00094***
	24	7.58	1	0.00592**
Acacia density (No./m^2)	0	0.0521	1	0.819
	6	1.35	1	0.245
	12	7.11	1	0.00769**
	18	1.14	1	0.285
	24	8.83	1	0.00297**

Note: The following significance levels were used: 0 '***' and 0.001 '**' (R Core Team, 2021).

cover in sown plots than in control plots (Cohen's $d = 0.57$, Figure 4a). Most of the native cover recorded within the first year was from annual species as opposed to perennial species, but this was the opposite in the second year. Sowing pre-treated fynbos seeds increased the native species richness in sown plots after 6 months, but it had little effect thereafter, such that both sown and control treatments had similar species richness after 2 years (Cohen's $d = 0.25$, Table 3, Figure 4b). However, the abundance of native plants recruited in the sown plots was higher than in unsown plots, particularly after 6 and 12 months (Hedges's $d_{(6\ \text{months})} = 0.80$, Hedges's $d_{(12\ \text{months})} = 1.69$, Figure 4c).

Recruitment of alien species

Acacia cover was higher in control plots than in sown plots over time (Cohen's $d = 0.62$, Table 2, Figure 5a) despite recruiting relatively similar acacia densities over 2 years (Cohen's $d = 0.25$, Table 2, Figure 5b). The recovery of native species cover might have helped to reduce the growth and cover of recruited acacias. Follow-up clearing helped to decrease acacia cover and density in both sown and control plots (Figure 5b). However, there were slightly more acacia plants in control plots than in sown plots after 12 and 24 months (Cohen's $d = 0.25$, Table 2, Figure 5b). Recruitment of alien species other than acacia was similarly low in both treatment plots over 2 years (Cohen's $d = 0.05$, Table 3, Figure 5c).

Change in acacia seed bank

Leaving cleared areas fallow for 2 years reduced the acacia seed bank from 3860 ± 1550 to 1240 ± 633 seeds/m^2, an approximate 75% decrease over 2 years ($p < 0.001$, $F = 36.6$). Post-fire acacia recruitment reduced the acacia seed bank further leaving behind a relatively small $\approx 411.11 \pm 653.58$ seeds/m^2 but persistent portion which decreased gradually over 2 years to 313.22 ± 451.88 seeds/m^2 (Table 3, Figure 6). Losses of acacia seeds were relatively similar between treatments (Cohen's $d = 0.05$, Figure 6).

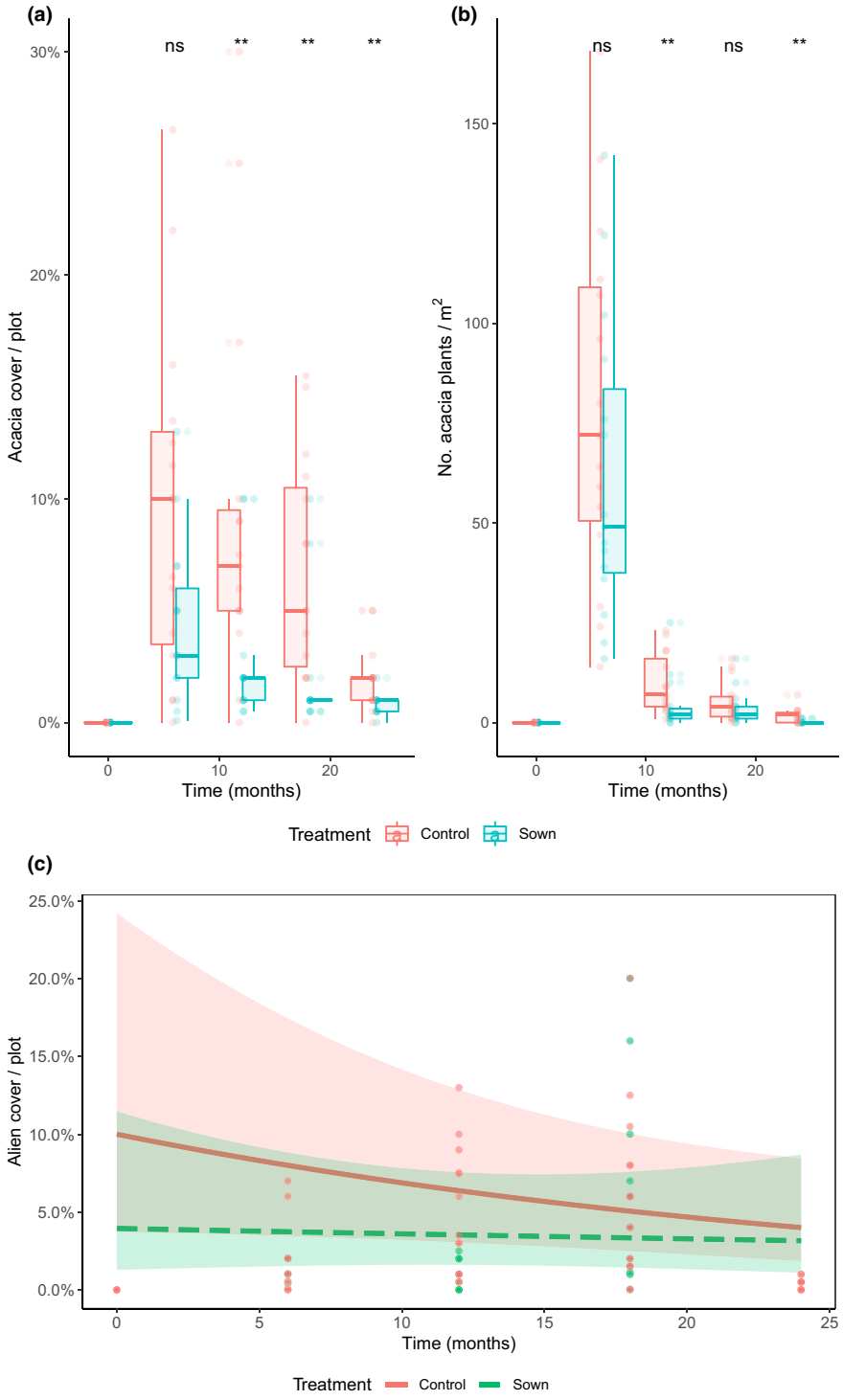

FIGURE 5 Changes in (a) acacia cover/plot and (b) acacia densities/m^2 as well as the GLMM effects on the recruitment of (c) other alien cover/plot over time. Follow-up alien clearing was conducted eight and 20 months after conducting a delayed prescribed burn. The box and whiskers show the mean values, spread, and skewness of the data, and the dots as data points. The 95% confidence interval is indicated by the shaded area. The following significance levels were used: 0 '***', 0.001 '**', 0.01 '*', 0.05 '.' and *ns* > 0.05 (R Core Team, 2021).

DISCUSSION

Here we show that sowing pre-treated fynbos seeds following a delayed prescribed burn facilitated the recruitment of native species and resulted in

TABLE 3 Differences in the recruitment of native and alien vegetation and the reduction of acacia seed bank over time.

Variable	Estimate	SE	z	p
Native species cover/plot				
Intercept	−3.73	0.314	−11.9	<2e-16***
Time	0.166	0.0145	11.4	<2e-16***
Treatment: Sown	0.932	0.153	6.10	1.04e-09***
Season spring	2.15	0.333	6.47	1.01e-10***
Time: Season spring	−0.08	0.0192	−4.18	2.91e-05***
Native species richness/plot				
Intercept	4.00	1.55	2.58	0.00999**
Time	0.368	0.0832	4.43	9.56e-06***
Treatment: Sown	3.73	1.53	2.45	0.0144*
Season spring	4.35	1.63	2.66	0.00777**
Time: Treatment sown	−0.137	0.089	−1.54	0.124
Time: Season spring	0.358	0.0995	3.60	0.000314***
No. Acacia seeds/m^2				
Intercept	7.36	0.115	64.15	<2e-16***
Treatment: Sown	−0.318	0.174	−1.83	0.0675
Time	−0.0727	0.0105	−6.90	5.08e-12***
Time: Treatment	0.0165	0.0148	1.12	0.264
Alien species cover/plot				
Intercept	−2.03	0.481	−4.23	2.39e-05***
Treatment: Sown	−0.866	0.542	−1.60	0.110
Time	−0.0982	0.0295	−3.33	0.000882***
Season spring	−2.53	0.553	−4.59	4.50e-06***
Time*Sown	0.0292	0.0354	0.828	0.406
Time*Season	0.187	0.0367	5.10	3.36e-07***

Note: The results were generated from a GLMM specifying beta distribution for native and alien cover, Gaussian error for native species richness and negative binomial error for acacia seed bank size. The following significance levels were used: 0 '***', 0.001 '**' 0.01 '*', 0.05 '.' and *ns* > 0.05 (R Core Team, 2021).

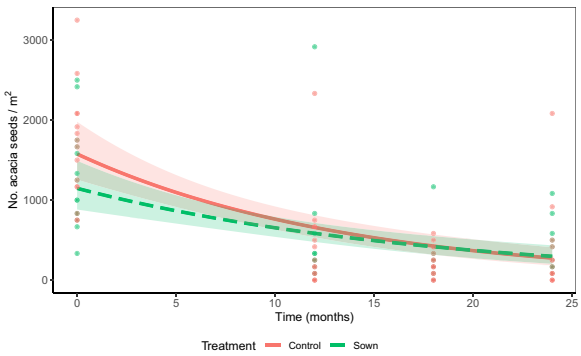

FIGURE 6 The GLMM interaction effects on the change in acacia seed bank post-fallowing and post-fire. In 2017, the acacia seed bank was assumed as 3860 ± 1550 seeds/m^2 based on sampling plots nearby the study site but decreased to an estimated 1240 ± 633 seeds/m^2 in 2019. The shaded area shows 95% confidence interval, and the dots are data points.

the rapid establishment of native cover within a year of sowing. However, this sowing effect had little influence on the density of post-fire acacia recruitment. The cover from native annual species contributed to the

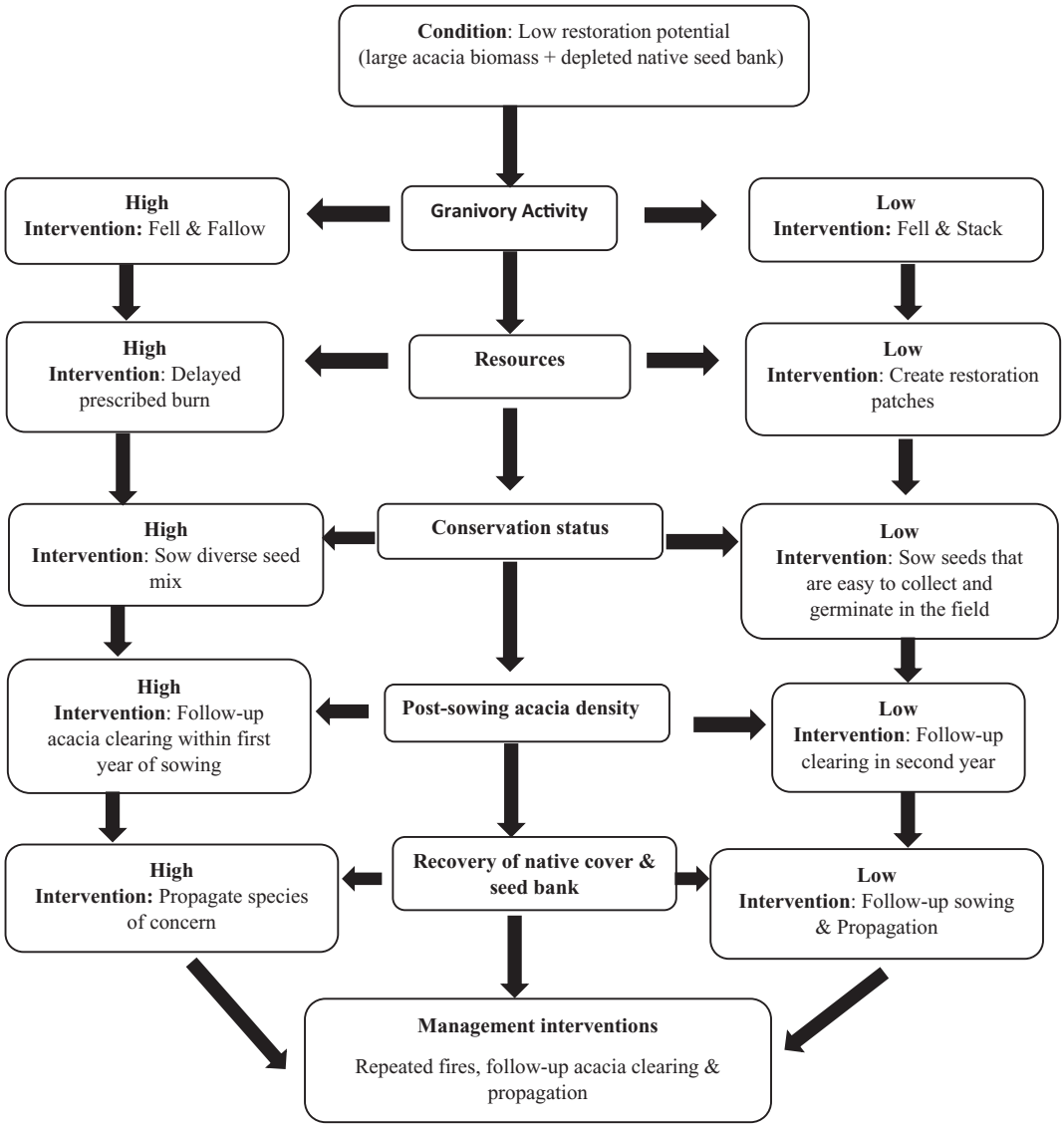

FIGURE 7 A simple protocol for long-term restoration practice over multiple fire cycles to guide managers with best practices and choice of restoration treatment in low restoration potential. The decision tree shows how the condition of the restoration sites can possibly influence the choice of a restoration treatment. Practitioners can factor in some of the aspects such as priorities, objectives, and availability of budgets to further inform the selection of the restoration treatment and decision making.

suppressed growth of the recruited acacias which allowed the recruited perennial native species to establish themselves before annual species dieback (personal observation, Appendix S3, figure 8.1). Thereafter, the young acacia plants had to be removed to prevent the native perennial species from being outcompeted by the faster-growing acacias (Le Maitre et al., 2011). The young acacia plants were removed by hand pulling or cutting below the root crown using loppers. Consequently, improved native recovery was evident in sown plots as 75 percent of native cover and ≈20 fynbos species per plot were recorded over 2 years of monitoring. The extent of native recovery and the ability of the native cover to reduce acacia cover indicates how building ecosystem resilience through sowing native species and follow-up clearing of acacia can minimize acacia resurgence. This emphasizes the importance of restoring a good cover, abundance, and diversity of native species in combination with regular follow-up clearing of acacia to suppress the resurgence of invasive species cover (Csákvári et al., 2023; Gaertner et al., 2012).

Despite this success in regenerating native vegetation, there was a lack of establishment of some native species sown in the field. Some species failed to germinate or, after germinating, failed to establish in the field, e.g. *Sparaxis bulbifera* owing to various factors such as field conditions, ecophysiology, and seed limitations (Barr et al., 2017; Berto et al., 2021; de Vitis et al., 2020; Holmes et al., 2022; Hoose et al., 2022; Maclean et al., 2018). As a consensus, dryland ecosystems such as fynbos are difficult to restore because they experience low establishment from seeds and low seedling survival rates (Hoose et al., 2022; Pérez et al., 2019; Svejcar et al., 2021). The harsh field conditions that might have contributed to this poor establishment include post-sowing granivory, grazing, and weather (personal observation). Granivory might have been problematic for species with larger seeds such as *Diosma oppositifolia*, *Trichocephalus stipularis*, and *Protea repens* considering that small seeded species such as *Oncosiphon grandiflorum* and *Trichogyne repens* established successfully. Gerbils can dig out acacia seeds (similar size as most ericoid shrub seeds) to 10 cm depth (Holmes & Moll, 1990). Also, most fynbos ericoid resprouters such as *Agathosma imbricata*, *Diosma oppositifolia*, and *Trichocephalus stipularis* and less reliant on seeds to re-establish as they regenerate from post-fire resprouting (Marais et al., 2014).

Apart from the pre- and post- fire field conditions, the depleted native seed bank and a lack of viable seeds contributed to the poor establishment of some species (Hall et al., 2017; Hall, Bastos, et al., 2021; Hall, Holmes, et al., 2021). Limitations posed by the quality and quantity of seeds sown in the field remain the greatest hindrance to the restoration of species-diverse fynbos ecosystems (Ngwenya et al., 2023). The sowing rates used in the experiments were well short of the seeding rates recommended by Merritt and Dixon (2011). For example, the viable seed sowing rates for the ericoid resprouter and proteoid species were very low, i.e. below 3 seeds/m^2. Likewise, 34 species made up the seed mix, out of the ≈559 plant species found within the local Sand Fynbos ecosystem, of which 45 are Red List plant species (Raimondo, 2009). Apart from the short supply of native seeds, poor seed handling practices during seed collection and storage might have contributed to this low or zero germination percentage in some species. For example, the proteoid species most likely lost viability during storage, as sowing usually yields their recruitment (Hall et al., 2017; Hall, Bastos, et al., 2021; Hall, Holmes, et al., 2021). Seeds are scarce in nearby local fynbos remnants (where permission is provided for seed collection), and habitat fragmentation impacts mutualisms and therefore seed quality (Hall, Bastos, et al., 2021; Hall, Holmes, et al., 2021; Pauw, 2007). Nevertheless, if available, increasing the sowing rates and species diversity in the mix could improve overall germination percentages and species richness (Hall, Bastos, et al., 2021; Hall, Holmes, et al., 2021; Ngwenya et al., 2023). While it is not required to reintroduce all species to recover ecosystem function, it is advisable to recover species-diverse ecosystems since the long-term resilience of ecosystems increases with an increase in species richness and diversity (Csákvári et al., 2023; Holmes & Richardson, 1999).

The notable differences in the effects of sowing pre-treated fynbos seeds after a delayed prescribed burn treatment compared to sowing pre-treated seeds after excluding fire (Ngwenya et al., 2023), was the rapid recovery of higher native cover, higher species richness, and increased abundance of the recruited native species. For example, 130 native species were recorded across the 30 plots at the delayed burn restoration sites compared to 89 indigenous species recorded across 45 plots at the fire exclusion restoration site. Also, 75% versus 58% native cover/plot and 20 versus 15 native species/plot recruited over 2 years in delayed burn

and fire avoidance restoration treatments, respectively. Therefore, emulating fynbos fire properties from a delayed prescribed burn might have encouraged the regeneration of native vegetation. The resultant fire which measured ≈250°C on the ground surface while travelling at 0.03 ± 0.01 m/s and releasing 502 ± 88.3 kJ of heat energy may have, to an extent, mimicked the fynbos fire temperature regimes. This way, the delayed fire stimulated the germination of the residual native seed bank (if any) as opposed to killing it, thus resulting in improved regeneration of native vegetation compared to when acacia slash was burnt in a more intense fire soon after felling. In the latter, follow-up sowing had to be conducted as native species failed to regenerate successfully due to competition from very high-density post-fire acacia recruitment (Hall, Bastos, et al., 2021; Hall, Holmes, et al., 2021). The unsuccessful establishment of natives might have resulted from poor fire properties of the prescribed burn (severe & slow-moving) given the high fuel load and water content in the acacia biomass (Holmes et al., 2000; van Wilgen et al., 2011). Nonetheless, the depleted native seed bank, more so than the fire effect, is most likely the greatest barrier to restoring a species-diverse fynbos ecosystem considering that long-lived obligate seeders have low persistence in Lowland Sand Fynbos (Cheney et al., 2019; Hall, Bastos, et al., 2021; Hall, Holmes, et al., 2021; Holmes, 2002; Ngwenya et al., 2023).

The fallowing of cleared areas before conducting a prescribed burn allowed the acacia seed bank to decline naturally. Since 80% of the acacia seed bank is located in the upper 6 cm of the soil, seeds are vulnerable to predation, mechanical damage, and decay, or else they are dispersed deeper in the soil (Auld & Denham, 2006; Holmes, 1989; Holmes, Esler, Gaertner, et al., 2020; Holmes, Esler, van Wilgen, & Richardson, 2020; Tozer, 1998). This reduction in the acacia seed bank resulted in reduced densities of post-fire acacia recruitment (70 ± 27.3 acacia saplings/m^2), an almost five-fold reduction compared to if burning had occurred shortly after initial clearing (360 ± 27.3 acacia saplings/m^2) (Krupek et al., 2016). Although significantly reduced, the density of 70 acacia saplings/m^2 was still too high relative to fire exclusion treatment (Ngwenya et al., 2023) and, in the absence of follow-up clearing, would still outcompete recruited native species (personal observation). Therefore, follow-up acacia clearing was necessary although to a lesser extent burning occurred shortly after felling acacia stands (where native species were outcompeted outright by mass acacia germination). Manual clearing of 70 ± 27.3 acacia saplings/m^2 for the lowest impact on natives was deemed uneconomic, laborious, and unviable over larger spatial areas (Hall, Bastos, et al., 2021; Hall, Holmes, et al., 2021; Krupek et al., 2016).

The delayed fire treatment helped to reduce the 'fallowed' acacia seed bank through fire mortality and recruitment, but a small portion was retained in the soil. Five percent of this remaining seed bank was stimulated to germinate by the delayed prescribed burn while the rest was most likely killed by the high fire temperatures or germinated but failed to emerge and establish (Hall, Bastos, et al., 2021; Hall, Holmes, et al., 2021; Holmes, 1990). Compared to previous findings where fire treatments were conducted soon after initial clearing, the acacia seed bank was reduced by 90% yet only four percent of this portion (90%) was stimulated to germinate successfully while the rest disappeared. This very small percentage of the acacia seed bank stimulated to germinate is still too dense and outcompetes the sparsely recruited native species. This high risk of acacia reinvasions posed by the residual acacia seed bank might undermine restoration efforts in the event of future fires. This requires managers to plan for long-term control of acacia reinvasions.

CONCLUSION AND RECOMMENDATIONS

In conclusion, fynbos seed banks are depleted after dense acacia invasion and are insufficient to regenerate a species-rich fynbos ecosystem. Sowing a diverse and adequate mix of pre-treated fynbos seeds is necessary to supplement the depleted native seed bank. Fallowing after initial clearing is a good option for returning a good native cover but still requires follow-up clearing of acacia. The control of acacia invasions through alien clearing alone is neither adequate nor sustainable to prevent future acacia reinvasion. Fire treatments shortly after clearing are undesirable in restoration areas having very large acacia seed banks and should only be conducted when the post-clearance acacia seed bank is reduced when there is adequate pre-treated fynbos seeds to sow, and an adequate budget for repeated and timely follow-up acacia clearing to build resilience against acacia resurgence (Gaertner et al., 2012; Holmes, 2002). Where resources are limited and the acacia seed banks are large, fire treatments should be avoided until the cleared areas have built some degree of resilience against acacia resurgence.

Ideally, fire treatments should be conducted when the acacia seed bank has declined to very low seed densities to make high-density post-fire acacia emergence impossible. However, this is nearly impractical because the persistent portion shows little decay after a single fire cycle and it may take decades or several fire cycles to achieve such a reduction (Holmes, 1990; Strydom et al., 2019; Tozer, 1998). While burning after fallowing is by far better in lessening acacia recruitment than burning immediately, managers should weigh up the risks of delaying a prescribed burn and tackling the consequences of an untimely, unplanned fire when it happens. A simple protocol for long-term restoration practice over multiple fire cycles has been included to guide managers on options and best practice for managing restoration sites with low restoration potential (Figure 7). Finally, harsh environmental conditions such as granivory and drought were hypothesized to be the major barriers to the seed-based restoration of larger-seeded species in the field. Future restoration research should explore seed enhancement techniques to protect seeds and seedlings from granivores and dessication in the field.

AUTHOR CONTRIBUTIONS

Duduzile K. Ngwenya: Conceptualization (lead); data curation (lead); formal analysis (lead); funding acquisition (supporting); investigation (lead); methodology (equal); project administration (lead); resources (supporting); software (lead); supervision (equal); validation (equal); visualization (lead); writing – original draft (lead); writing – review and editing (lead). **Patricia M. Holmes:** Conceptualization (lead); data curation (equal); formal analysis (supporting); funding acquisition (lead); investigation (equal); methodology (equal); project administration (lead); resources (lead); software (supporting); supervision (lead); validation (lead); visualization (supporting); writing – original draft (supporting); writing – review and editing (lead). **Sjirk Geerts:** Conceptualization (supporting); data curation (supporting); formal analysis (supporting); funding acquisition (supporting); investigation (supporting); methodology (equal); project administration (supporting); resources (equal); software (supporting); supervision (equal); validation (equal); visualization (supporting); writing – original draft (supporting); writing – review and editing (supporting). **Karen J. Esler:** Conceptualization (lead); data curation (supporting); formal analysis (supporting); funding acquisition (lead); investigation (supporting); methodology (supporting); project administration (lead); resources (lead); software (supporting); supervision (lead);

validation (lead); visualization (supporting); writing – original draft (supporting); writing – review and editing (equal).

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CONFLICT OF INTEREST STATEMENT

None.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available on request from the corresponding author. The data are not publicly available due to privacy or ethical restrictions.

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SUPPORTING INFORMATION

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

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