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RESEARCH ARTICLE

# Scaling up restoration efforts by simulating the effects of fire to circumvent prescribed burns when preparing restoration sites in South African fynbos ecosystems

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## Abstract

The method of clearing alien species and the nature of the soil seedbank influence the quality of restoration outcomes, particularly in fire-prone ecosystems heavily invaded with fire-adapted alien species. One of the challenges encountered is reducing the likelihood of reinvasions when the invading species are equally responsive to restoration treatments. By simulating the fire effects that are required to regenerate native vegetation, the study tested whether the recovery of the native species could be initiated without conducting a prescribed ecological burn. In a case study of South African Cape Flats Sand Fynbos with a heavy invasion of *Acacia saligna*, the felled acacia were stacked into brush piles, with the litter raked off from the sowing areas and the collected seeds were pre-treated for germination. Despite the lack of a fire, the sowing of pre-treated seeds on raked plots led to good recovery of native vegetation over time. This was indicated by the recovery of higher density, cover and richness of native species in sown plots compared with unsown treatments. However, the recovery of native species had not approached the vegetation structure comparable to a reference site after 2 years; that is, only partial fynbos structure was recovered. The recruitment of acacia was less dense without fire, as hypothesised, and independent of treatment. However, over time, control plots had higher acacia cover than other treatments. Despite this sparse recruitment of acacia, the acacia seedbank decreased naturally to about 50% of the initial size over 2 years in control plots. Raking off litter during site preparation removed 50% of the acacia seedbank which decreased slightly thereafter. Consequently, the residual acacia seedbank was relatively similar across treatments after 2 and a half years. In conclusion, circumventing prescribed burns in heavily degraded fynbos ecosystems is a scalable restoration strategy, as recruitment of alien acacia was minimized, its seedbank declined significantly, and good native cover developed after clearing and sowing.

**KEYWORDS**
ecological restoration, fire avoidance, greater cape floristic region, invasion, large-scale, lowland sand fynbos, Mediterranean-type ecosystem

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## INTRODUCTION

Scale-related issues are at the core of most real-life global restoration challenges that require problem-solving and scalable research (Brancalion et al., 2014; Sigman, 2021). While reducing environmental degradation is necessary, scaling up ecological restoration efforts to keep abreast of the high rate of ongoing environmental degradation is critical. However, the implementation of large-scale restoration strategies, such as simulation of natural processes, collaborations, good governance, human involvement and financial provisioning, remains limited (Perring et al., 2015). Consequently, ecological restoration is lagging environmental degradation (Nsikani et al., 2022).

The success of large-scale ecological restoration depends not only on the type of interventions used but also on external factors which influence the interventions' effectiveness and efficiency, for example spatial and temporal scales, climate and seed availability (Caughlin et al., 2016). A long history of ecosystem degradation results in accumulation of legacy effects, which inherently influence the effectiveness of restoration treatments. For example, large volumes of biomass (wood, litter and seedbank), altered soil chemistry and depleted native seedbanks caused by acacia invasions (Le Maitre et al., 2011). These impacts can persist for up to 10 or more years (Nsikani et al., 2017) while influencing restoration efforts. Therefore, consideration of legacy effects and other factors of influence is required particularly when restoring invaded ecosystems. Herein, restoration efforts are further undermined when the invasive species undergoing control measures is equally responsive to restoration treatments used to regenerate native species. A good example is a fire-driven ecosystem such as fynbos—a South African Mediterranean-type ecosystem—long invaded by a fire-dependent alien species such as *Acacia saligna*. In this case, using fire to remove large volumes of biomass generated from felling acacia stands and to regenerate fynbos vegetation can aggravate the resurgence of acacia instead. Therefore, restoring fynbos ecosystems while controlling acacia invasions is highly challenging (Holmes et al., 2020).

The restoration potential of a fynbos ecosystem degraded by the invasive alien *Acacia saligna* is contained in the nature and size of the native residual soil seedbank. Acacia-dominated seedbanks following a long invasion history, (Le Maitre et al., 2011) retain high probability of reinvasions even after clearing acacia stands. A large acacia seedbank results in high density acacia recruitment if stimulated by fire (Strydom et al., 2017) while leaving behind a significant portion of the seedbank dormant. This high-density post-fire acacia resurgence together with the acacia's faster growth rate (Morris et al., 2011) and persistent seedbanks increases the likelihood of reinfestations, which ultimately outcompete recovering native species. To maintain persistence in a fire-prone ecosystem, a portion of the soil stored acacia seedbank remains unstimulated to germinate with or without a fire event (Tangney et al., 2020). According to Hall et al. (2021), 10% of the initial acacia seedbank (≈8500 acacia seeds/$m^2$) remains in the soil after high-density post-fire acacia recruitment (360.03 ± 432.75 acacia recruits/$m^2$), whereas 20% remained after 2 years when prescribed burning was unutilised. Apart from inevitably persistent seedbanks (Strydom et al., 2017), the likelihood of reinvasions is increased further by acacia's tendency to resprout whether not cleared correctly. Therefore, the ability to control acacia recruitment from the soil seedbank or resprouts from initial clearing is equally important to consider when restoring heavily degraded fynbos ecosystems (Hall et al., 2021; Holmes et al., 2020). The management of reinvasion risk is key to securing the resilience of recovering ecosystems.

Felling dense acacia stands generate large volumes of wood which might require removal, usually using fire, which is however not suitable in heavily degraded areas. Conversely, not using fire after clearing recruits less acacia (Richardson & Kluge, 2008) but deprives fynbos species of fire-related germination cues, retains large volumes of wood from alien clearing and retains thick layers of litter, and a bigger residual acacia seedbank (Hall et al., 2021). Consequently, without fire, some fynbos species may fail to germinate due to the lack of germination cues or failure to emerge through thick layer of acacia litter (du Toit, 2008; Facelli et al., 1999; Maclean et al., 2018; Marchante et al., 2011; Richardson & Kluge, 2008). Also, retaining acacia biomass is a fire hazard, which increases the risks of reinvasions and constrains seed-soil contact while reducing light penetration. These challenges expose cleared areas to aggravated degradation, especially if native species fail to establish successfully (Smit, 2004).

Given the poor post-fire recovery of native species in heavily degraded fynbos ecosystems (Hall et al., 2021; Krupek et al., 2016; Maclean et al., 2018), fire avoidance and the addition of fynbos seeds might possibly address some of the challenges described above. The sparse recruitment of acacia after avoiding fire creates an opportunity to scale up restoration efforts by allowing native species to establish in pockets between acacia germinants. Native regeneration could possibly be initiated by adding pre-treated fynbos seeds to boost the depleted native seedbank. However, the efficacy of regenerating a fire-driven ecosystem invaded with a fire-adapted species without conducting a prescribed burn has not been explored. Fire roles required to regenerate native vegetation can be simulated through seed pre-treatment techniques (Brown, 1993), while the removal of biomass and creation of a seed bed can be simulated using physical means. For example, stacking acacia slash into piles helps to remove biomass from sowing areas and raking off litter creates a seed bed. Seed pre-treatment and enhancement techniques have been used before as simulants for biological processes and ecological cues to mimic natural recruitment agents. Seed enhancement technologies are used to simulate fire effects, rainfall events and natural defence to overcome barriers impeding the recruitment and establishment of vegetation (Svejcar et al., 2021). For example, pre-treating fynbos seeds with fynbos-generated smoke (Brown, 1993), a heat pulse and scarification (Hall et al., 2017) were found capable of stimulating germination in most fynbos species in the absence of a fire (Mukundamago, 2016). Advanced seed enhancement technologies such as hydropriming, flash flaming, seed coating and seed conglomeration are promising techniques in improving the success of seed-based restoration interventions in drylands (Anderson et al., 2021; Berto et al., 2021; Hoose et al., 2022).

While seed addition is a highly recommended scaling-up strategy because it is cheaper than out planting (Barr et al., 2017), germination success and seedling survival in the field remain limited (Barr et al., 2017; Pedrini & Dixon, 2020). One of the factors contributing to poor regeneration of native species is poor seed quality and quantity (Maclean et al., 2018; Wijdeven & Kuzee, 2000). Seed handling practices during collection and storage can damage seeds (Berto et al., 2021; De Vitis et al., 2020), while provenance influences species adaptability (Bischoff et al., 2006). A lack of plants to collect seed from, limits sowing rates and diversity of seed mixes. To address the challenges of procuring large supplies of seeds and other resources needed for large-scale restoration operations, the applied nucleation technique has been found useful in improving restoration through economic and efficient resource use (Hulvey et al., 2017). This way, restoration efforts and resources are channelled towards sizeable

areas spread out over large areas. Through natural succession, the nascent foci are allowed to expand naturally and coalesce into a larger area over time (Corbin & Holl, 2012; Zahawi et al., 2013). Consequently, fewer resources are invested and are concentrated on priority microhabitats with a high likelihood of restoration success.

The study hypothesised that circumventing a fire in heavily degraded fynbos ecosystems would minimize the recruitment of acacia while addition of pre-treated fynbos seeds would initiate recovery of native vegetation. It built a case against fire use in low restoration potential areas based on the following: (1) lack of fire recruits less acacia (Hall et al., 2021; Richardson & Kluge, 2008), (2) not all fynbos species require fire-related germination cues (Hall et al., 2017; Mukundamago, 2016), (3) prescribed burns are beneficial if the restoration potential is high (Hall, 2018) or in areas dominated with native grasses, (4) offsite pre-treatment (smoke, heat pulse, scarification) of fynbos seeds can mimic fire-related germination cues (Brown, 1993; Hall et al., 2017, 2021), and (5) altered soil chemistry has no direct negative impact on the establishment of fynbos species, so volatilisation of nitrates using fire is not mandatory (Nsikani et al., 2018). Other factors used to inform the design of the study included large volumes of acacia biomass (wood, litter and seedbank), depleted native seedbank, natural recruitment agents, field conditions and availability of viable seeds.

The main objective of this study was to explore the efficacy of regenerating a fire-driven ecosystem without conducting a fire to control the recruitment of an invasive species equally responsive to fire. Instead, fire roles required to encourage recovery of native species were simulated while the invader seedbank was deprived of cues for breaking dormancy and stimulating germination. Therefore, we determined: (1) viable seed sowing rates and germination percentage of seeds in controlled and field conditions; (2) how the recruitment of native species responded to restoration treatments over time; (3) how the recruitment of acacia and non-woody alien species responded to restoration treatments over time; (4) how the size of acacia seedbank changed over time; and (5) how the vegetation recovery pathway compared with post-fire recruitment in a reference site over time.

## METHODS AND MATERIALS

### Field site description

A long-term, large-scale ecological restoration project has been underway on invaded parts of the 1500-ha Blaauwberg Nature Reserve (BBNR) since 2012 (Gibson, 2020). The reserve is a protected area located north of Cape Town in the Western Cape Province, South Africa (33.75″S, 18.48″E) (Figure 1), and contains the largest remaining conserved remnant of critically endangered Cape Flats Sand Fynbos vegetation. Restoration has been ongoing on this 400-ha fynbos remnant infested since the early 1950s with alien *Acacia saligna* as ascertained from aerial imagery. As restoration resources are limited and often focused on less severely degraded areas or catchment areas, this dense stand of acacia would not have been a priority for clearance had it been outside a protected area or in non-endangered vegetation (Hobbs, 2007; Reid et al., 2009). Therefore, successful restoration of this site will contribute towards global and national conservation targets (National Targets, 2020). Before colonization and acacia invasions, the study area may have been used periodically for extensive grazing by the Khoi-Khoi communities. It also has a well-known

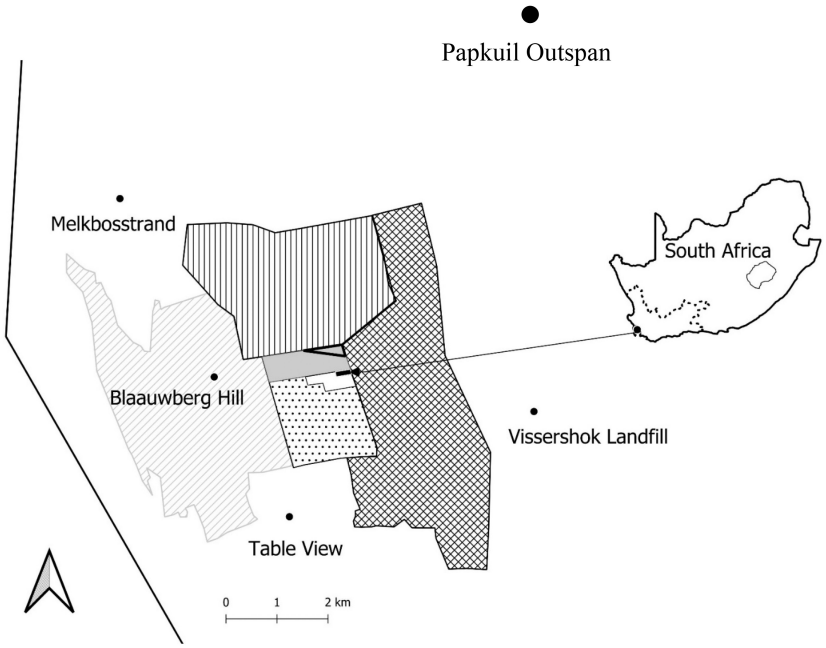



**FIGURE 1** Location of the study area and the surroundings at Blaauwberg Nature Reserve (grey striped) located in the City of Cape Town, Western Cape Province (dashed line), South Africa. The experimental area (black) forms part of the 400-ha acacia-invaded area (stippled) donated to the reserve. Restoration work is ongoing, including previous (grey) and current (white). Surrounding areas include private land: a farm (black strips) and an undeveloped fynbos area invaded with acacia (checked). Melkbosstrand and Table View are residential areas. The reference area (Papkuil Outspan) is located ≈21 km north-east of the restoration area.

colonial history as a battleground between the Dutch and the British in 1806. Following the European settlement, cattle were driven through the reserve area from the historic Blaauwberg Farm to Cape Town (P. Holmes, personal communication).

The first restoration trial was conducted on 96 ha of the 400-ha remnant in 2013 (Esler, 2019; Hall et al., 2021) followed by the present study on a 3-ha experimental area and a 24-ha management area. Papkuil Outspan (33°33′00″S 18°30′00″E) (Figure 1) was used as a reference site for this study as no other suitable and similar Cape Flats Sand Fynbos (CFSF) sites were found close to the reserve. Despite being categorized as Atlantis Sand Fynbos, the vegetation in Papkuil Outspan is similar in structure and dominant species to the CFSF found in BBNR (Rebelo et al., 2006). Also, this reference site experienced an accidential fire in November 2018 and therefore had a comparable vegetation age to the experimental plots cleared at BBNR in March 2019.

## Experimental design and data collection

The study consisted of a laboratory, nursery and field component. Laboratory experiments assessed seed quality to ascertain the physiological status—seed viability and fill—of the planted seeds and helped to calculate sowing rates used in the field trials. Nursery tests provided ambient conditions with additional moisture compared with field conditions. The main experiment was an observational field study measuring the response of vegetation recruitment to restoration treatments using vegetation metrics such as cover, density and richness.

## Seed preparations, viability tests and sowing rates

Selection of species and sowing rates used in the seed mix were guided mostly by seed availability. However, the species' significance in the ecosystem's structure and functioning was also considered as recommended by specialists or guided by literature (Frischie et al., 2020; Hall et al., 2017, 2021) (Appendix S1). So too were methods and areas of seed collection, cleaning and storage (Appendix S1). Seeds were collected locally from neighbouring fynbos remnants by supervised teams from the Expanded Public Works Programme (EPWP), reserve staff members, volunteers and a private company (Vula Environmental Services). Thirty-six native species consisting of annuals, ericoid shrub seeders, ericoid shrub resprouters, proteoid shrubs, forbs, graminoids and geophytes were selected from locally sourced seed lots (Appendix S1). There were very few remnants of overstorey species to collect seeds from, leading to very low sowing rates in proteoid shrubs. To pre-treat collected seeds, fire-related germination cues were simulated using smoke generated from fynbos biomass, heat pulse from oven and scarification using sandpaper (Brown, 1993; Hall et al., 2017; Holmes et al., 2022). Sowing rates of viable seeds were estimated from 'Clean Seed Equivalent' (CSE) per species (Frischie et al., 2020), whereas seed viability and seed fill were tested using tetrazolium and cut tests respectively (Frischie et al., 2020; Mukundamago, 2016; Waller et al., 2015). Small seeds (13 species) were difficult to cut and test for viability, so they were not tested.

## Nursery trial

A nursery experiment was set up to determine the germination percentage of seeds under controlled conditions and to help with the identification of seedlings in the field. A subsample of the seed mix was sowed in 15 trays (240 × 170 × 60 mm) filled with soil collected from the site, and three additional control trays were filled with soil only. After sowing seeds, the trays were watered manually three times a week until germination was initiated (Hall et al., 2017; Mukundamago, 2016; Nsikani et al., 2018; Waller et al., 2015). Thereafter, seed trays were transferred to a greenhouse and watered three times a week using a timed irrigation system. Recruitment was monitored on a weekly basis, and where possible, seedlings were identified and enumerated upon emergence. Alternatively, the seedlings were left to grow larger before they could be identified. Larger seedlings of rarer species were potted individually into plastic bags and donated to Westlake Conservation Centre for future use. Seedling density together with sowing rates was used to calculate the germination percentage of seeds sown per species.

## Field experiment

An experimental area of 3-ha deemed as low restoration potential and long-invaded (more than 70 years) with *Acacia saligna* was delineated on a portion of the reserve and subdivided into three 1-ha blocks. The area was pre-surveyed for density, cover and richness of both alien and native species to indicate its restoration potential and degree of invasion before and after felling acacia stands (Hall et al., 2021). In March 2019, the area was cleared of alien biomass by subcontractors from the City of Cape Town (CoCT)'s Biodiversity Management Branch's Invasive Species Unit. The alien clearing method comprised felling acacia stands, applying

herbicide on acacia stumps and stacking acacia biomass into brush piles (Figure 2a). This 'Fell & Stack' clearing treatment simulated fire roles required to remove biomass from restoration areas. While being left to rot over time, the acacia stacks provided habitats and nesting sites for snakes, rodents and birds (Perring et al., 2015) while it protected seeds and seedlings from strong winds. In addition to stacking acacia slash, the clearing treatment involved raking off litter from patches used as sowing and rake only treatment plots (Figure 2a,b). Raking off litter simulated removal of litter by fire to create a seedbed and to increase the contact between sown seeds and soil particles. Removing litter also exposed seeds (sown and residual seedbank) to diurnal fluctuating autumn temperatures required by some fynbos species to stimulate germination (Pierce & Moll, 1994). Also, restoration interventions were properly timed with appropriate seasons to simulate the regeneration of native vegetation in a natural environment to optimize seedling emergence and establishment (Albrecht & McCue, 2010; Anderson et al., 2021). For example, clearing operations were conducted in time with fynbos fire which normally burns in summer ahead of fluctuating diurnal autumn temperatures and winter rains (Kraaij & van Wilgen, 2014).

Fifteen sets of three 10×5 m plots were marked on the north-eastern, north-western, central, south-eastern and south-western parts of each 1-ha cleared block (Figure 2a,b). Each set comprised sowing (raked and sown), rake only (raked and unsown) and control (unraked and unsown) plots (Figure 2c). An area of 9×4 m was marked inside each 10×5 m plot, leaving a one-metre buffer zone between the sowing area and the edge of the plot. Treatment plots were also sampled for acacia basal area by measuring acacia diameters in 5×5 m subplots of each treatment plot (Figure 2c). In addition, six replicate soil cores (10 cm deep by 5 cm diameter) were

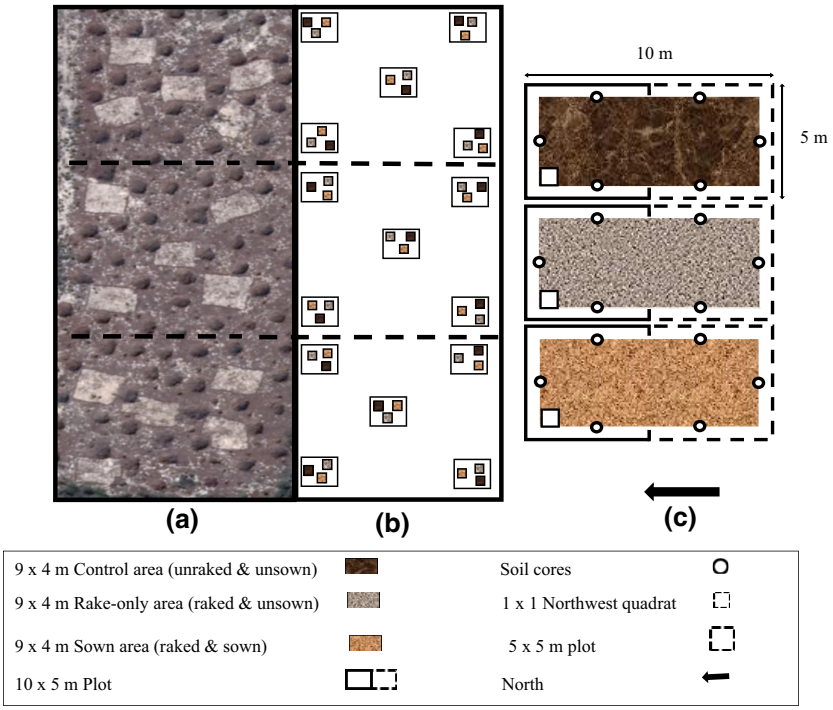



**FIGURE 2** Layout of three 1-ha blocks showing experimental design in the field. An aerial photograph of the area cleared in March 2019 shows patches of raked areas with stacks of cleared acacia slash in between. Each 1-ha block comprised five sets of three 10×5 m treatment plots (Figure 2b). In each 10×5 m plot, a sowing or sampling area of 9×4 m was marked, six soil cores were sampled, species density was enumerated from a 1×1 m quadrat placed on the north-west corner of the plot, and the density of acacia stands, and stem diameters were measured from the 5×5 m plot (Figure 2c).

collected per plot to enumerate the size of acacia seedbank at the time of initial clearing. The size of acacia seedbank was calculated from seed density per core for each plot (six cores representing 0.012 $m^2$ of surface area). Bare ground cover, litter cover and litter content were also scored. Litter content was quantified by weighing air-dried litter sifted from soil cores. A set of five reference plots was set up and sampled in a similar manner at Papkuil Outspan, a nearby reference area of Sand Fynbos.

Following site preparation, a pre-treated seed mix was broadcasted on sowing plots and gently raked in. Sowing was conducted in April 2019, a time closer to the rainy season and at the peak of diurnal temperature fluctuations (Brits, 1996). All plots were monitored for plant recruitment in response to restoration treatments at 6-month intervals for 2 years post-clearing (alternating spring and autumn of consecutive years). Fynbos seedlings normally emerge in response to winter rainfall provided that the seeds received cues for breaking dormancy and germination. Recruited species were identified to species level, their origin scored (alien or native) and assigned to a growth form (Appendix S2). Species that were initially unidentifiable were assigned a unique name until identification was possible. An alien species was regarded as any plant species that did not naturally occur in the reserve. For example, *Senecio pterophorus* was classified as alien since it originates from the Eastern Cape Province in South Africa (Manning & Goldblatt, 2012).

Projected percentage canopy cover per species was estimated visually per plot and per square metre. Total native cover was calculated by adding cover of each native species per plot and total species richness was calculated by counting the number of different species recorded per plot and per treatment. Similarly, growth form cover and richness were calculated using cover and richness of constituent species per plot and per treatment. Recruited species with negligible cover were assigned 0.001% cover. Density of recruited species was determined in a 1 × 1 m quadrat placed on the north-western corner of each plot except for colony-forming species like some grasses and restioids. Acacia germinants were cleared by hand-pulling and with loppers in October 2020 when their cover became considerably denser. The size of the acacia seedbank was sampled at the end of the experiment, that is 24 months, to determine how it changed over time in the absence of fire. To get an insight of how the acacia seedbank will change after 2 years (does it decline further or it remais constant), further sampling was conducted after 30 months. This was important to understand the extent of reinvasion risk posed by the residual seedbank in a subsequent fire event.

## Data analysis

All analyses were conducted in R version 4.1.0 (R Core Team, 2021). Descriptive statistics were used to summarize seed germination performance. One-way analysis of variance (ANOVA) was used to analyse data from pre-removal vegetation surveys to determine the preconditions of the restoration area. To assess the effects of restoration treatments on vegetation recruitment (native and alien) over time, general linear mixed effects models (GLMMs) were used. The same models were fitted on acacia seedbank data collected over time. GLMMs were calculated from the glmmTMB (generalized linear mixed models using Template Model Builder [Brooks et al., 2017]) packages in R, and data were subjected to various distribution errors. The nature of data and visual exploratory inspections were used to inform the selection of distribution errors per data set. For example, all count data (richness and densities) were, by default, initially

run on a glmmTMB with Poisson distribution errors on log link, whereas proportion data (cover, indices) were fitted with beta distribution errors on logit or probit links. However, default model fittings on some data (native richness, acacia plant and seed density) indicated significant over- or under-dispersion, heteroscedasticity and zero-inflation during model evaluation. Consequently, Gaussian (native richness) and negative binomial (acacia plant and seed density) distribution errors were fitted instead. Also, specifying the dispersion and zero-inflation components of the glmmTMB helped to solve model misspecifications and improved model fit. Individual models were evaluated for goodness of fit using residual diagnostics for hierarchical (multilevel/mixed) regression models found in DHARMa package (Harting, 2017).

The different model formulae specified the vegetation metrics as response variables to a function of explanatory variables, treatment, time, season and their interactions. Plot numbers were included as random variables to account for pseudo-replication (repeated measurements) in all models. The variance inflation factor was calculated before fitting models to check for multicollinearity between explanatory variables using the car package (Fox & Weisberg, 2018). No multicollinearity was detected. Where interactions were important, the $_{\text{INTERACTIONS}}$ (Fox & Weisberg, 2018) package was used to calculate and plot interaction effects.

To determine whether the recruitment of native species was on a recovery trajectory, we compared structural composition (growth form cover and growth form richness) between restored and reference plots over time. Structural composition was determined from total cover and richness of the constituent species per growth form in each plot over time. We also examined recruitment dissimilarity between restoration and reference plots by comparing the recruitment of species abundance in each plot in the restoration area to every reference plot. Dissimilarity between assemblages can be separated into turnover (or replacement) and richness difference (or nestedness-resultant component) (van Schalkwyk et al., 2020). We calculated beta diversity as the incidence-based dissimilarity measure either the replacement ($\beta_{SIM}$) or nestedness ($\beta_{SNE}$) components, using the $_{\text{BETAPART}}$ package (Baselga et al., 2013) from individual species abundance per $m^2$ in each plot over time. The GLMM models were fitted on multiple-site dissimilarity indices ($\beta_{SIM}$), ($\beta_{SNE}$) and ($\beta_{SOR}$) to investigate their relationship with treatment effects over time. Only seedlings were considered as recruited, and species resprouting after the fire (reference plot) or extant remnant (experiment plots) were excluded.

# RESULTS

## Restoration potential of experimental area

Prior to clearing acacia stands, there was approximately 71.4 ± 19.9% vegetation cover comprising of both alien and native species. The overstorey canopy cover was entirely acacia (≈67.6 ± 18.6%), with a few remnants of native species (≈3.7 ± 6.1%) in the understorey. The density of the acacia stand was 1.2 ± 0.6 plants/$m^2$ (12 000 ± 6000 plants/ha) with total basal cover of 32.2 ± 21.6 $cm^2/m^2$ (32.2 $m^2$/ha). Ground cover comprised 82.1 ± 16.2% litter and 14.1 ± 11.3% bare ground. A total of 10 native species surviving underneath the acacia canopy was recorded across the 15 plots (5 × 10 m) in the 3-ha cleared area. Of the 10 species recorded, seven were ericoid shrubs (mostly *Trichocephalus stipularis* and *Phylica cephalantha*), two were geophytes (*Brunsvigia orientalis; Bobartia indica*), and one was a restioid (*Restio* sp.) (Appendix S2). There were no native seedlings

recorded at the time; only alien *Raphanus* sp. Raking off the litter layer significantly reduced the number of acacia seeds found in raked plots, both sown and unsown ($F$ = 12.4, $p < 0.001$). The degree of invasion and restoration potential was assumed to be similar across the study site as no significant differences were found in the density of acacia plants ($F$ = 2.02, $p > 0.05$), in remnant species cover ($F$ = 0.524, $p > 0.05$) and remnant species richness ($F$ = 1.50, $p > 0.05$) amongst treatment plots.

## Viable seed sowing rates and germination percentage

Viable seed sowing rates were highly variable across species used in the seed mix whereby more than 1000/m$^2$ viable seeds of the annual *Oncosiphon grandiflorum* were sown opposed to 0.02/m$^2$ of the shrub *Protea repens* (Table 1). Germination percentage also varied widely amongst different species, in both the nursery and the field. Of the 34 species sown, 25 germinated in the nursery and only 20 in the field (Table 1, Appendix S2). Of those that germinated, germination success was much lower in the field compared with the nursery, except for *Thamnochortus punctatus* and *Adenogramma rigida* which germinated better in the field (Table 1).

## Field vegetation responses to restoration treatments

In total, we identified 89 indigenous plant species (Appendix S2) across 45 treatment plots at BBNR and 113 species across five plots at the reference site over the 2 years of monitoring. Thirty-four species were found in both experimental and reference plots. Fifteen alien annual species were found at BBNR treatment plots and two in the reference site plots (Appendix S2). No acacia plants or seeds were found in the reference plots (Appendix S2).

## Recruitment of native species over time

Native species cover increased gradually in all treatments over time (Table 2, Figure 3a). Initially, treatment alone had no effect on native species cover ($\chi^2 = 0.20$, df = 2, $p > 0.05$, Table 2, Figure 3a) but over time, sown plots yielded the highest native cover ($\chi^2$ = 15.61, df = 2, $p < 0.001$, Table 2, Figure 3a). Native cover became significantly higher in sown plots compared with other treatments after 12 months ($F$ = 4.74, $p < 0.05$, Figure 3a). Sowing treatment increased native species richness ($\chi^2$ = 21.31, df = 2, $p < 0.0001$, Table 2) after 6 months ($F$ = 9.98, $p < 0.001$, Figure 3b) without a significant increase thereafter ($\chi^2$ = 2.03, df = 2, $p > 0.05$, Table 2, Figure 3b). The density of recruited native seedlings was higher in sown treatment, 6 months after intervention ($F$ = 3.438, $p < 0.05$, Figure 3c).

## Recruitment of acacia and secondary alien invaders over time

The density of recruited acacia increased over time (Table 2, Figure 4a), independent of treatment ($\chi^2$ = 2.51, df = 2, $p > 0.05$, Table 2, Figure 4a). The same was true for the recruitment of acacia cover except that less acacia cover was recorded in sown plots over time (Table 2, Figure 4c). Consequently, acacia cover was highest in control plots and lowest in sown plots after 18 months ($F$ = 7.517, $p < 0.001$, Figure 4b). Despite starting with

**TABLE 1** Sowing rates per plot and percentage germination of seeds sown in the field. Sowing rates refer to an estimated number of 'clean seed equivalent' of viable seeds per square metre

| Growth form | Species | Sowing rates (No/m$^2$) | % Germination | |
|---|---|---|---|---|
| | | | Nursery | Field |
| Annuals seeders (Ann) | *Oncosiphon grandiflorum* | 1894.42[a] ± 1165.36 | 1.24 | 0.25 |
| | *Felicia tenella* | 6.51[a] ± 4.00 | 0 | 0 |
| | *Ursinia anthemoides* | 12.7[a] ± 7.81 | 42.14 | 3.15 |
| | *Heliophila coronopifolia* | 1[a] ± 0.60 | 0 | 0 |
| | *Osteospermum clandestinum* | 1.31 ± 0.80 | 0 | <1 |
| | *Senecio elegans* | 17.09[b] ± 10.51 | 0.2 | 0 |
| Ericoid shrub seeders (ERSe) | *Passerina corymbosa* | 1.3 ± 0.80 | 1.11 | 10.26 |
| | *Anthospermum aethiopicum* | 173.59 ± 106.78 | 37.96 | 5.53 |
| | *Erica plumosa* | 38.69[b] ± 23.80 | 0 | 0 |
| | *Erica ferrea* | 4.94[b] ± 3.04 | 7.44 | 2.7 |
| | *Cliffortia polygonifolia* | 13.31 ± 8.18 | 4.51 | 1 |
| | *Seriphium plumosum* | 2.23[b] ± 1.37 | 0 | 0 |
| Ericoid shrub resprouters (ERRe) | *Agathosma imbricata* | 8.06 ± 4.96 | 0 | 0 |
| | *Diosma oppositifolia* | 2.06 ± 1.27 | 6.07 | 0 |
| | *Erica mammosa* | 4.94[b] ± 3.04 | 40.6 | 28.34 |
| | *Phylica cephalantha* | 7.81 ± 4.81 | 10.13 | 0.85 |
| | *Trichocephalus stipularis* | 2.36 ± 1.45 | 9.85 | 2.82 |
| Proteoid shrub (Pr) | *Protea repens* | 0.02 ± 0.01 | 0 | 0 |
| | *Protea scolymocephala* | 30.48[b] ± 18.75 | 24.44 | 3.28 |
| | *Leucadendron salignum* | 5.75[b] ± 3.54 | 17.19 | 0 |
| Perennial forb or succulent (Seeders) | *Pelargonium capitatum* | 9.14 ± 5.62 | 93.24 | 3.65 |
| | *Adenogramma rigida* | 3.77 ± 2.32 | 0.031 | 15.93 |
| | *Lessertia frutescens* | 3.03 ± 1.86 | 46.12 | 4.4 |
| | *Lampranthus reptans* | 3.23 ± 1.99 | 68.24 | 8.24 |
| Graminoid shrub seeders (Gram) | *Thamnochortus punctatus* | 2.45 ± 1.50 | 0.3 | 51.78 |
| | *Pentameris pallida* | 2176.93[b] ± 1339.15 | 1.36 | 1.53 |
| | *Restio duthieae* | 0.26[b] ± 0.16 | 0 | 0 |
| Geophytes resprouters (Geo) | *Watsonia meriana* | 27.26 ± 16.77 | 22.2 | 1.96 |
| | *Gladiolus carinatus* | 0.87 ± 0.54 | 0 | 0 |
| | *Sparaxis bulbifera* | 64.41 ± 39.62 | 0.98 | 0 |
| | *Wachendorfia paniculata* | 22.42[b] ± 13.79 | 27.59 | 2.38 |
| | *Babiana villosula* | 2.65 ± 1.63 | 66.18 | 10.07 |
| | *Baeometra uniflora* | 81.45 ± 50.11 | 0 | 0 |
| | *Albuca cooperi* | 17.91[b] ± 11.02 | 17.73 | 1.49 |
| | *Chasmanthe floribunda* | 0.15 ± 0.09 | 0 | 0 |
| | *Morea fugax* | 5.67[b] ± 3.49 | 64.58 | 7.06 |

[a]Seed fill and viability were not accounted for either due to the small size of seeds or null/intermediate outcome from viability tests.

[b]Ordinary mean values of viable seeds per species sown in the 15 treatment plots.

a smaller acacia seedbank than control plots due to raking, raked plots lost a relatively smaller amount of acacia seeds thereafter. The acacia seedbank decreased most rapidly in control plots ($\chi^2$ = 53.42, df = 3, $p < 0.000$, Table 2, Figure 4c) until it was relatively similar in all treatments after 30 months ($F$ = 1.80, $p > 0.05$). There was no difference in the recruitment

**TABLE 2** Vegetation parameters (species cover, richness, densities and species composition) following a restoration intervention in 2019 and monitored in 6-month intervals until 2021 at Blaauwberg Nature Reserve, Western Cape, South Africa

| Variable | Estimate | SE | z-Value | *p*-Value |
|---|---|---|---|---|
| Native cover | | | | |
| Intercept | −4.69322 | 0.50383 | −10.523 | <0.001*** |
| Sown | 0.064325 | 0.396490 | 0.162 | 0.8711 |
| Rake | 0.176525 | 0.410657 | 0.430 | 0.6673 |
| Time | 0.46885 | 0.11253 | 4.166 | <0.001*** |
| Spring | 1.17502 | 0.48424 | 3.265 | 0.0152* |
| Time: Sown | 0.3994 | 0.12333 | 3.238 | 0.0012** |
| Time: Rake | 0.003304 | 0.021723 | 0.152 | 0.8791 |
| Time: Spring | 0.003283 | 0.021079 | 0.156 | 0.8762 |
| Native richness | | | | |
| Intercept | 2.28889 | 1.08487 | 2.110 | 0.03487 |
| Sown | 5.26666 | 1.11965 | 4.704 | <0.001*** |
| Rake | 1.86666 | 1.11965 | 1.667 | 0.09548 |
| Time | 0.17185 | 0.05901 | 2.912 | 0.003589** |
| Spring | 2.85555 | 1.02210 | 2.794 | 0.00521** |
| Time: Sown | −0.02667 | 0.06814 | −0.391 | 0.69554 |
| Time: Rake | −0.09444 | 0.06814 | −1.386 | 0.16574 |
| Time: Spring | 1.6222 | 0.3732 | 4.347 | <0.001*** |
| Acacia plant density | | | | |
| Intercept | −0.64775 | 0.40678 | −1.592 | 0.1113 |
| Sown | 0.74152 | 0.48428 | 1.531 | 0.1257 |
| Rake | 0.54361 | 0.51087 | 1.064 | 0.2873 |
| Time | 0.12744 | 0.02572 | 4.955 | <0.001*** |
| Time: Sown | −0.06022 | 0.03392 | −1.776 | 0.0758 |
| Time: Rake | −0.06135 | 0.03577 | −1.715 | 0.0863 |
| Acacia plant cover | | | | |
| Intercept | −6.26271 | 0.40832 | −15.338 | <0.001*** |
| Sown | 0.22563 | 0.49335 | 0.457 | 0.6474 |
| Rake | 0.23805 | 0.49197 | 0.484 | 0.6285 |
| Time | 0.29180 | 0.02410 | 12.110 | <0.001*** |
| Time: Sown | −0.07371 | 0.03337 | −2.209 | 0.0272* |
| Time: Rake | −0.04942 | 0.03282 | −1.506 | 0.1321 |
| Acacia seed density | | | | |
| Intercept | 8.226028 | 0.093334 | 88.14 | <0.001*** |
| Sown | −0.708441 | 0.144204 | −4.91 | <0.001*** |
| Rake | −0.876430 | 0.150598 | −5.82 | <0.001*** |
| Time | −0.033759 | 0.004620 | −7.31 | <0.001*** |
| Time: Sown | 0.011723 | 0.007434 | 1.58 | 0.11482 |
| Time: Rake | 0.020172 | 0.007518 | 2.68 | 0.00729** |
| Secondary alien cover | | | | |
| Intercept | −4.747568 | 0.355491 | −13.355 | <0.001*** |
| Sown | 0.041295 | 0.448507 | 0.092 | 0.9266 |
| Rake | 0.207777 | 0.466970 | 0.445 | 0.6564 |
| Time | −0.008812 | 0.019746 | −0.446 | 0.6554 |
| Spring | −1.621354 | 0.415370 | −3.903 | <0.001*** |
| Time: Sown | −0.042409 | 0.029730 | −1.426 | 0.1537 |

**TABLE 2** (Continued)

| Variable | Estimate | SE | *z*-Value | *p*-Value |
|---|---|---|---|---|
| Time: Rake | −0.053006 | 0.031927 | −1.660 | 0.0969 |
| Time: Spring | 0.152713 | 0.027532 | 5.547 | <0.001*** |
| Multisite dissimilarity indices | | | | |
| $\beta_{SIM}$ | | | | |
| Intercept | 0.6171762 | 0.0489325 | 12.613 | <0.001*** |
| Sown | 0.3312360 | 0.0434018 | 7.632 | <0.001*** |
| Rake | 0.0831582 | 0.0429242 | 1.937 | 0.0527 |
| Time | 0.0066517 | 0.0027207 | 2.445 | 0.0145* |
| Spring | 0.0667034 | 0.0463790 | 1.438 | 0.1504 |
| Time: Sown | −0.0121736 | 0.0028479 | −4.275 | <0.001*** |
| Time: Rake | −0.0008164 | 0.0028316 | −0.288 | 0.7731 |
| Time: Spring | 0.0280036 | 0.0027187 | 10.301 | <0.001*** |
| βsne | | | | |
| Intercept | −1.310750 | 0.094452 | −13.877 | <0.001*** |
| Sown | −1.196188 | 0.115577 | −10.350 | <0.001*** |
| Rake | −0.298074 | 0.103877 | −2.869 | 0.00411** |
| Time | −0.043735 | 0.005460 | −8.010 | <0.001*** |
| Spring | −1.127713 | 0.095538 | −11.804 | <0.001*** |
| Time: Sown | 0.055351 | 0.006835 | 8.098 | <0.001*** |
| Time: Rake | 0.011209 | 0.006573 | 1.705 | 0.08815 |
| Time: Spring | 0.016141 | 0.006106 | 2.644 | 0.00820** |
| $\beta_{SOR}$ | | | | |
| Intercept | 1.4877563 | 0.0399851 | 37.21 | <0.001*** |
| Sown | 0.0371918 | 0.0245866 | 1.51 | 0.130 |
| Rake | −0.0044388 | 0.0243412 | −0.18 | 0.855 |
| Time | −0.0104383 | 0.0021828 | −4.78 | <0.001*** |
| Spring | −0.4110276 | 0.0387059 | −10.62 | <0.001*** |
| Time: Sown | 0.0009401 | 0.0017636 | 0.53 | 0.594 |
| Time: Rake | 0.0025592 | 0.0017468 | 1.47 | 0.143 |
| Time: Spring | 0.0421064 | 0.0021167 | 19.89 | <0.001*** |

*Note*: Variables are presented with effects of restoration intervention (clearing, sowing, and raking) and their significant interactions on the recruitment of vegetation monitored over time during spring and autumn in 2019, 2020, and 2021. Effect sizes from GLMM models fitted using glmmTMB package specifying beta, gaussian, and negative binomial error are shown with parameter values (estimate), standard error (SE), *z*-, and *p*-value. '***', 0.001; '**', 0.01; '*', 0.05.

of alien annual species amongst treatments ($\chi^2$ = 0.48, df = 2, $p > 0.05$, Table 2, Figure 4d).

## Structural and species composition of recruited native species relative to reference area

The structural composition (growth form cover and growth form richness) was variable across treatments and sampling time (Figure 5a,b). Most of the typical growth forms found in fynbos ecosystems made up the total native cover of sown plots at the restoration site. However, it lacked representation of overstorey shrubs, some ericoid resprouters and sometimes geophytes. Reference plots had a more complete fynbos structure and had representation from each plant guild (Figure 5a,b). Unsown plots (rake

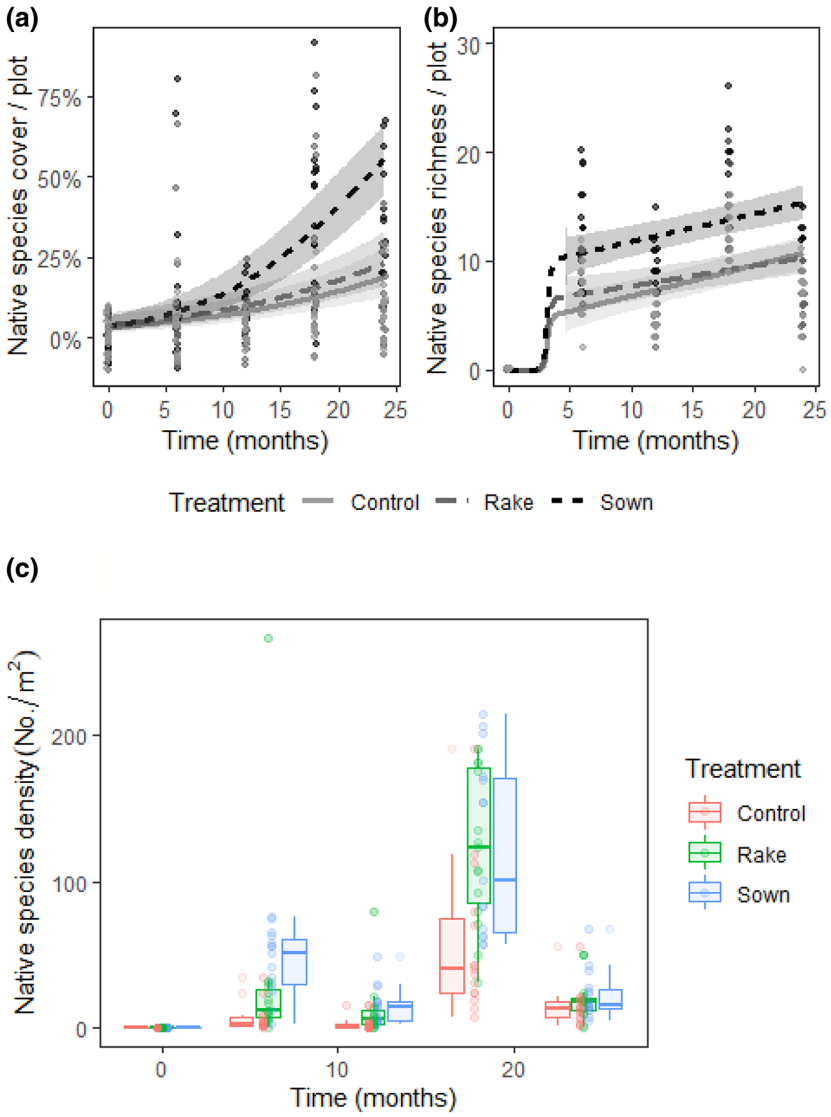



**FIGURE 3** GLMM effect plot of estimated (a) percentage cover of native species, (b) richness of native species and (c) number of native individuals/$m^2$ in response to restoration treatments over time. Native species cover excludes cover from remnant species and indicates the percentage cover per plot over time. Richness is the average number of species recorded per 4×9 m plot over time. Vegetation sampling was conducted in 6-month intervals. Shaded areas represent 95% confidence intervals while dots show data points. Treatments: Control = unraked and unsown, rake = rake only without sowing and sown = raked and sown.

only and control) only recruited graminoids, forbs and a few ericoid shrubs (Figure 5a,b) passively. The estimated dissimilarity index of species replacement ($\beta_{SIM}$) was initially higher in sown plots compared with other treatments ($\chi^2 = 52.03$, df = 2, $p < 0.0001$, Table 2, Figure 6a) but decreased over time ($\chi^2 = 21.42$, df = 2, $p < 0.0001$, Table 2, Figure 6a). None of the treatments had a significant effect on the overall beta diversity of recruited species over time (Table 2, Figure 6c).

## DISCUSSION

Barriers to germination success, seedling survival and succession inherently undermine restoration goals such as rapid plant establishment,

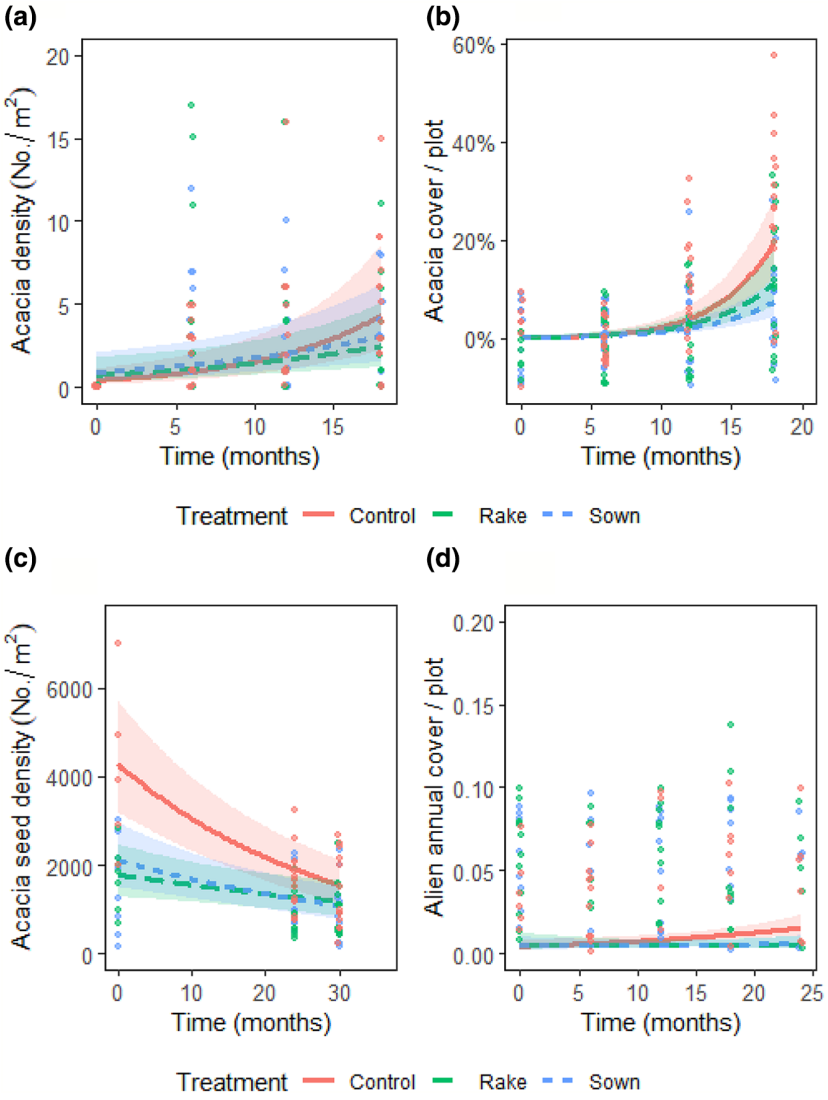



**FIGURE 4** GLMM effect plots of estimated (a) density of acacia plants/$m^2$, (b) percentage cover of acacia/plot, (c) density of acacia seeds/$m^2$, (d) percentage cover of other alien annual species (in two decimal places) per plot in response to restoration treatments over time. Shaded areas represent 95% confidence intervals while dots show data points. Treatments: Control = unraked and unsown, rake = rake only without sowing, and sown = raked and sown. Vegetation sampling was conducted in 6-month intervals. The reported cover and density of acacia plants were recorded before the first follow-up clearing conducted 20 months after the initial clearing.

long-term plant persistence and the functioning of restored ecosystems (Kettenring et al., 2014). Recovering native vegetation of a Mediterranean-type ecosystem (MTE) invaded by a woody invasive species that is equally responsive to restoration treatments is no different. Fire-prone plant species maintain persistence through fires via intact soil seed-banks (Tangney et al., 2020). However, when the invader species has built a large seedbank while the native seedbank depletes, restoration challenges are exacerbated, particularly if both the native ecosystem and species under control are fire-prone. Often, the fire required to encourage regeneration of the MTE instead recruits the invader species *en masse,* which rapidly outcompetes the sparsely recruited native species. The study investigated the efficacy of actively restoring Lowland Sand Fynbos of South Africa invaded with *Acacia saligna* without conducting a prescribed burn.

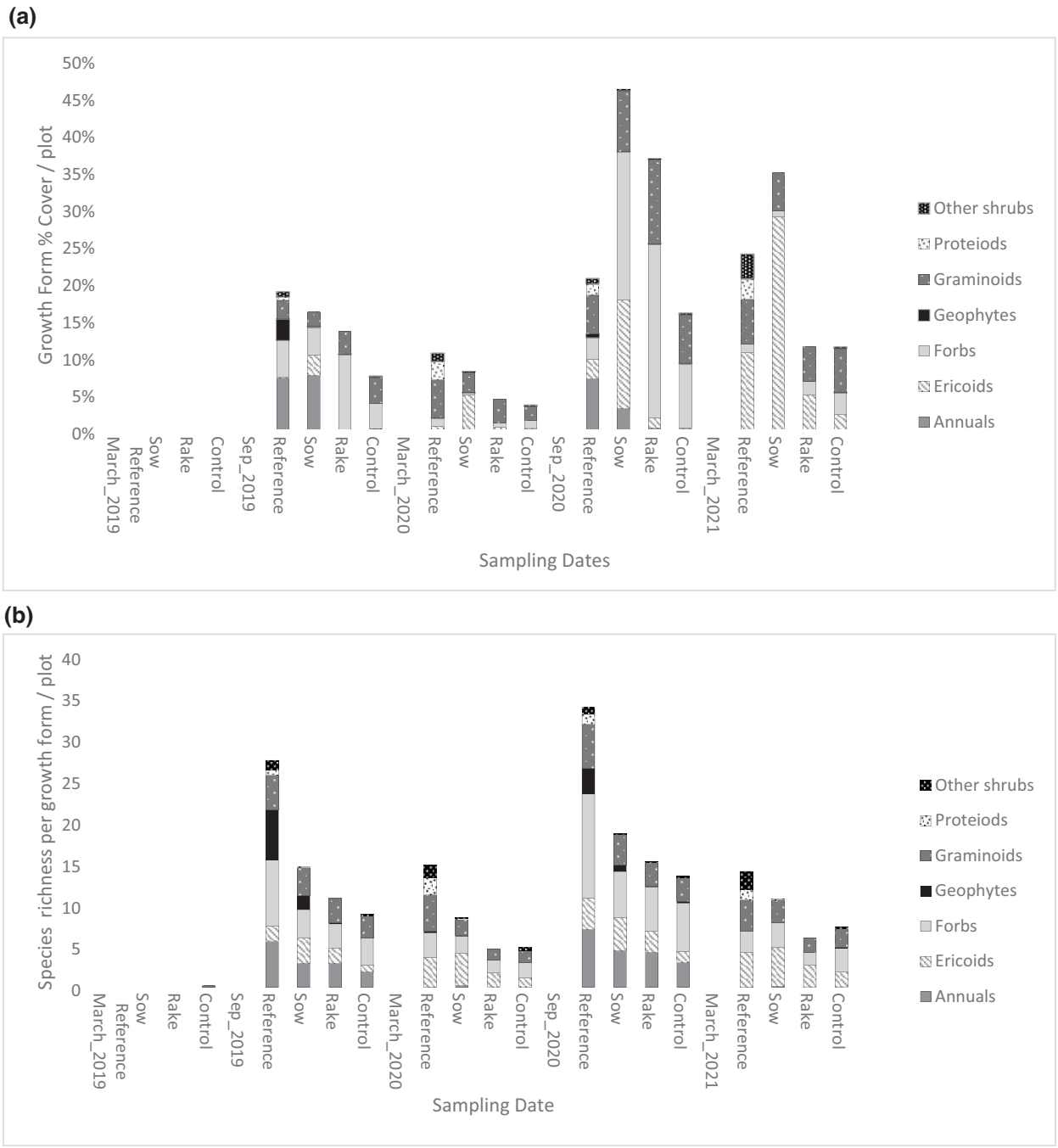



**FIGURE 5** Stack plots of (a) native cover and (b) species richness recorded in treatment and reference plots per growth form over time. The cover excludes resprouts after the fire in reference plots and extant remnants from invasion in experimental plots. Treatments: Control = unraked and unsown, rake = rake only without sowing, sown = raked and sown and reference = near pristine site.

We hypothesised that simulating fire effects through active means to avoid conducting a prescribed burn would minimize the recruitment of invasive acacia species while initiating the recovery of native species. Also, by sowing pre-treated fynbos seeds, we envisaged boosting the depleted native seedbank. Research outcomes supported the hypothesis that fire exclusion through simulations encourages regeneration of native vegetation in fynbos ecosystems heavily invaded by acacia. This was indicated by the observed gradual increase in native cover, partial recovery of fynbos structure, low acacia recruitment and the reduction in acacia seedbank during monitoring.

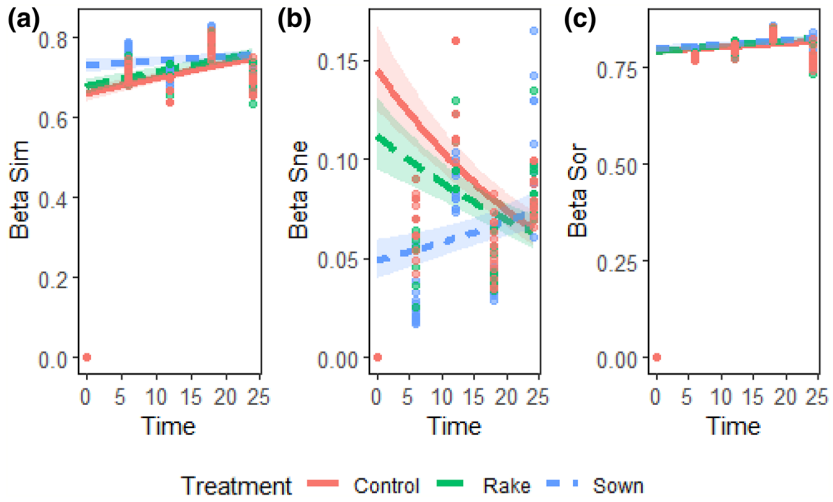



**FIGURE 6** GLMM effect plots of estimated dissimilarity of vegetation recruitment between reference and restoration plots in response to restoration treatment and over time. The dissimilarity is expressed using indices (a) species replacement ($\beta_{SIM}$), (b) richness difference ($\beta_{SNE}$) and (c) overall beta diversity ($\beta_{SOR}$). Treatments: Control = unraked and unsown, rake = rake only without sowing, sown = raked and sown. Shaded areas represent 95% confidence intervals while dots show data points.

Sowing pre-treated fynbos seeds into unburnt areas cleared of alien biomass initiated recovery of approximately 58% of total native cover and reintroduced approximately 15 fynbos species 2 years after the intervention. Species were recruited either actively from sowing or passively from residual seedbanks (mostly annuals and forbs) or both (a few ericoid shrubs). Despite showing a positive trajectory, recovery of partial fynbos structure in restoration plots had not approached a vegetation structure comparable to a reference site after 2 years. Restoration plots had poor species diversity but contained most of the typical growth forms found in fynbos reference ecosystems except for overstorey shrubs, some ericoid resprouters and most geophytes. The disproportionate semblance of fynbos structure and species diversity in restoration sites possibly resulted from factors other than a lack of fire, such as seed availability and the typically lower germination rate for resprouter species.

Considering the scarcity of local fynbos remnants to collect seeds from, collection of a diverse species seed mix of adequate quantities was a challenge. Firstly, in some species, only a few individuals were available, for example proteoids leading to short seed supplies and low sowing rates. Secondly, only a subset of fynbos species was present in extant remnants leading to a species-poor seed mix lacking representation of a complete fynbos ecosystem. Apart from limited seed supplies, another contributing factor to poor recovery of species diversity was the seed quality. Not all collected seeds were viable or had the potential to germinate given the physiology and ecology of native plant species. Seeds of many native plant species exhibit dormancy (Frischie et al., 2020), are exposed to infestation, mechanical damage, predation and sometimes abortion. Consequently, only a fraction of the collected lot was viable and germinable upon receipt of cues to break dormancy and germination. Hence, a need to ascertain seed quality (viability, vigour, provenance, germinability and physiology) and procure adequate species-rich seed supplies (Barr et al., 2017; De Vitis et al., 2020) is required to avoid costly restoration failures (Lippitt et al., 1994).

The ecophysiology of some species might have prevented their recovery through active sowing. Most ericoid resprouters (constituting an important

growth form in fynbos ecosystems) typically recruit poorly from seeds. This plant guild is not entirely dependent on seeds for maintaining populations and thus invests less in seedling recruitment (Marais et al., 2014). This possibly explains why *Agathosma imbricata* and *Diosma oppositifolia* (both ericoid resprouter shrubs) seeds failed to germinate both in the nursery and the field. Contrary, some species failed to survive despite successfully germinating in the field, for example *Protea scolymocephala*.

In general, low seedling survival rates and chronically low establishment of seeded native species are typical of dryland ecosystems such as fynbos (Hoose et al., 2022; Pérez et al., 2019; Svejcar et al., 2021). Most mortality occurs between germination and emergence (Hoose et al., 2022) owing to hostile field conditions such as aridity, poor nutrient content and diseases. Legacy effects from acacia invasions might have further aggravated low rates of seedling survival as invaded sites were drier, lacking diverse microhabitats and with altered soil chemistry (Le Maitre et al., 2011). In this study, soil chemistry of the restoration site and its effects on the recruitment of fynbos species was assumed the same as previous findings—Hall et al. (2021)—considering the same study area and invasion history. Also, previous studies had shown that altered soil chemistry has no direct negative impact on the germination and establishment of most fynbos species (Nsikani et al., 2018). According to Maclean et al. (2018), the major cause of limited restoration success is seed limitation as opposed to legacy effects of invasions.

Given that not all fire functions required to regenerate fynbos vegetation were accounted for in this study, fire simulations might not have met recruitment needs for some species to establish successfully. Consequently, proteoid species which require wetter areas or easy access to the water table failed to establish in the field, unlike restioids which can survive with a much lower water table (Rebelo et al., 2006) and germinated better in the field, for example *Thamnochortus punctatus*. Loss of seeds and seedlings to faunal activities (fossorial, granivorous and grazing) might have contributed to low seedling emergence and survival in some species.

Despite this partial recovery of fynbos structure, excluding fire after clearing dense stands of acacia satisfactorily encouraged native regeneration. Considering that only less than five acacia germinants/$m^2$ were recruited after avoiding fire compared with 360.03 ± 432.75 acacia recruits/$m^2$ (Krupek et al., 2016) when acacia slash was burnt, the 'no fire' treatment had better control of acacia resurgence. Consequently, follow-up clearing was conducted 18 months later after the initial clearing compared with the post-fire follow-up clearing which was conducted within 6 months (Hall et al., 2021). At that time, the acacia canopy from recruits had almost closed on ground cover. The sparse recruitment of acacia allowed recruited native species to establish with minimal competition from recruited acacia and minimal disturbance from follow-up clearing. Meanwhile, the acacias sheltered recovering natives from wind erosion and desiccation by creating microsites of windbreaking and hydro lifting. Working on the same site, Hall et al. (2021) indicated that high density acacia recruitment within 6 months post fire, resulted in very poor recovery of native vegetation. Consequently, follow-up clearing was required after 6 months together with follow-up sowing (Hall, 2018). This was a costly and time-consuming exercise while damaging the natives due to trampling and extensive use of herbicides (Krupek et al., 2016). The post-fire follow-up clearing costed R33 257/ha ≈ US$ 2299.93/ha (Hall et al., 2021) compared with R4 626.62/ha ≈ US$319.96/ha when fire was avoided.

The choice to avoid fire use should consider the resilience of recovering areas when subjected to field disturbances such as faunal activities, subsequent fire and possibly future reinvasions (acacia and secondary invaders). For example, the 'Fell and Stack' clearing method is a fire hazard

as it retains large volumes of acacia biomass thus increasing the risk of reinvasion in the event of a fire when the residual seedbank is relatively large. Stack arrangement could help to improve the resilience of recovering areas and minimize the risks of unplanned fires (Lehman, 2022). Firstly, stacks could be arranged in a pattern which reduces the portion of acacia seedbank exposed to fire stimulation. For example, placing the stacks on boundaries of the restoration area opposed to scattering them across the entire area. Bordering the restoration area with stacks could also help to keep large mammals away from restoration area, while acting as seed traps and windbreaks. Alternatively, stacks could be used to reduce the amount of area lying open after clearing especially if there are not enough seeds to sow the entire restoration site. Thus, reducing the windows of opportunity for secondary invaders. Using stacks, cleared areas could be partitioned into sizeable patches that are easier to rake, sow and require less seeds given limited sowing tools (Broadhurst et al., 2016) and low seed quantities (Vacchiano et al., 2018). Once established, restoration patches could possibly build the resilience and sustenance of recovering areas and provide co-benefits such as attracting seed dispersers and pollinators (Mangachena & Geerts, 2017, 2019) while replenishing the native seedbank and out-competing invaders. Applied nucleation is considered a potential large-scale restoration strategy (Corbin & Holl, 2012; Lehman, 2022; Zahawi et al., 2013), which allows native regeneration to naturally expand from restoration patches.

The acacia seedbank ceased to reduce significantly after 2 years in all treatments, but this decrease plateaued thereafter and retained ≈ ± 2000 acacia seeds/$m^2$. This indicates how vulnerable the recovering areas are to reinvasions. Physical removal of acacia seeds through raking litter contributed the highest acacia seed losses in raked plots compared with natural seed losses incurred over time. Acacia seed losses in control plots occurred naturally and over time through decay, germination, granivory or dispersal by ants (Holmes, 1990; Richardson & Kluge, 2008). The plateaued seed losses recorded in all treatments after 30 months possibly marked the depletion of the transient portion of the acacia seedbank, leaving behind the persistent portion. A significant amount of acacia seed which is found in the litter layer is highly transient and is quickly lost via natural means (Strydom et al., 2017). Acacia seeds buried deeper (>10 cm) possibly via soil turnover caused by fossorial mammal burrowing activities or washing down burrows are highly persistent (up to 50 years) (Strydom et al., 2017). This portion is inaccessible and can remain protected for a very long time.

Acacia seeds buried deeper in the soil are responsible for the species' persistence through hostile environments such as high fire temperatures, predation and decay (Tangney et al., 2020). Sixty-four per cent of the deeply buried acacia seeds germinating from >10 cm depths emerge successfully (Tangney et al., 2020). It is this worrisome portion of the residual seedbank which requires management to secure the resilience of areas undergoing restoration The inevitably persistent portion of residual acacia seedbank poses high threats of acacia reinvasions and places an emphasis on planning and budgeting for long-term follow-up clearing. The transient portion can be managed actively through raking (though impractical over large spatial areas), high fire temperatures or passively by allowing it to decline naturally over time, provided seed addition is prevented.

Lastly, raking litter without sowing was envisaged to create bare ground which is a window for the recruitment of secondary invaders (Geerts et al., 2022; Nsikani et al., 2020). Given the lack of fire to kill shallow invasive grass seedbanks (Hall, 2018) and this creation of bare ground, the recruitment of secondary invaders was anticipated. However, the recruitment of secondary invasive species was minimal, and no considerable cover

was recorded. Perhaps, these invaders had not yet established a good seedbank in the area. Nsikani et al. (2018) also found that secondary invader recruitment was lower in unburnt areas as opposed to areas burnt by high and low fire intensities.

## RECOMMENDATIONS AND CONCLUSION

Many ecological management problems involve making ecologically sound decisions when budgets are constrained in an ever-changing environment. Often decisions are taken based on the trade-off between economic costs as well as short- and long-term probabilities of success. Therefore, land managers require guidance through best practices which support their efforts. Restoration managers in invaded fynbos ecosystems seek to maximize the establishment of native vegetation while avoiding wastage of limited resources such as scarce seeds and money. If the method is appropriate, the best restoration intervention should initiate native regeneration while minimizing acacia recruitment and reducing risks of reinvasion.

It is possible to initiate good recovery of native species while controlling acacia recruitment by circumventing a fire, making the strategy cheaper and less damaging. This ability to bypass the invaders responsiveness to fire is a scalable strategy to restore fire-driven systems. However, it requires further development to address its shortfalls, for example fire hazard and susceptibility to reinvasion. Coupling the strategy with seed enhancement technologies (Anderson et al., 2021; Hoose et al., 2022) to regenerate a species-diverse ecosystem is required to build strong resilience against future reinvasions. Although they are part of the ecosystem, disturbances from faunal activities and fire should be held back until recovering areas are resilient. Future studies can explore how long it takes for recovering areas to regain resilience and know when to incorporate faunal activities and conduct management fires. An intact vs depleted native seedbank might be a good indication of resilience and time to conduct a management fires.

Restoration is a lifetime process and as discussed earlier, it is currently impractical to restore fynbos ecosystems and control acacia invasions from a single intervention. The complexity of the challenges explained previously, for example persistent acacia seedbank and limited seed supply, requires a plan and budget for long-term continuous improvement and acacia control. Managers can use the restorative continuum to guide their restoration efforts towards achieving an alternative state to recover ecosystem function and diversity. The initial attempts can focus on partial native regeneration using foundation species whose seeds are easier to collect, germinate in the field and are highly resilient to acacia invasions (remnant species). However, sowing rates of such species must be kept minimal to avoid species dominance. Species not requiring a fire to germinate and whose seeds are dispersed by wind could also be considered for the initial restoration phase to establish nodes of recovery. Thereafter, rare and difficult species may be reintroduced from out-plantings at a later stage when foundation species have created microhabitats. Meanwhile, recovering areas should constantly be monitored and managed against acacia resurgence through long-term follow-up clearing.

Other innovative methods to improve the strategy's effectiveness could include spatial patterning using different stack arrangements and remnant species to locate restoration points. Stacking away from restoration patches or burning stacks closer to restoration patches before sowing may help shelter seed and seedlings from faunal activities. Lastly, litter may be

removed using leaf blowers and suction harvesters as opposed to raking, which is labour-intensive (Nsikani et al., 2017).

## AUTHOR CONTRIBUTIONS

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

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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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