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RESEARCH ARTICLE

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Soil seed bank resilience in passively restored endangered Sand Fynbos following a century of pine plantations

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Societal Impact Statement

Ecosystems are rapidly being transformed, pushing us towards irreversible losses and even extinctions. The Kunming-Montreal Global Biodiversity Framework aims to curb biodiversity decline. An intriguing solution lies in seed banks—where plants store seeds in the soil. Restoration efforts can revive lost ecosystems by leveraging these seed banks. In the fynbos of South Africa, this study found that it is possible to bring back ecosystems that were lost as long ago as 100 years if conditions are right. Managers can achieve best results by applying a dry season prescribed burn following removal of the driver of degradation (e.g. pine plantations or invasions).

Summary

- Soil-stored seed banks are a critical evolutionary strategy for plants as they can stabilize population dynamics in response to environmental fluctuations such as droughts and natural disturbances such as fires, thus improving ecosystem resilience. This study aimed to assess resilience during the first restoration cycle of endangered Sand Fynbos following pine harvesting and a prescribed burn in South Africa.
- We compared above ground populations and soil-stored seed bank composition and focused on six perennial fynbos focal species in five 1 m^2 plots. All six species are obligate reseeders with soil-stored seed banks but represent a variety of important fynbos growth forms and seed types.
- We found that native soil-seed bank density following over a century of plantation forestry and 10 years after the first fynbos restoration burn was comparable to, or exceeded, densities measured in other fynbos studies, especially seed banks of alien-invaded fynbos ecosystems. The early years following pine harvesting and a restoration burn likely provide a pest- and predator-free window of opportunity in which plants may re-establish and flourish.
- Our results show that even for old forestry plantation areas, ecological restoration to the historic vegetation community is feasible, where there is retained seed bank resilience, through a combination of passive and active restoration methods. Ecological restoration in cases where soil seed banks persist is therefore a viable and

critically important method to attain 30% conservation of terrestrial land in ecosystems with less than 30% remaining, as part of the Kunming-Montreal Global Biodiversity Framework.

KEYWORDS
fire, germination, growth forms, invasive alien trees, recruitment, soil seed banks

1 | INTRODUCTION

Governments around the world have adopted the Kunming-Montreal Global Biodiversity Framework, committing to halt and reverse biodiversity loss by 2030 (Stephens, 2023). Among the goals are the effective conservation and management of at least 30% of the world's land, and restoration of 30% of degraded terrestrial ecosystems (Hughes & Grumbine, 2023). In many global biodiversity hotspots, this conservation target is unattainable without achieving successful ecological restoration of degraded ecosystems (Myers et al., 2000). This is true in the Cape Floristic Region biodiversity hotspot located in South Africa, which is also the world's smallest floral Kingdom (Goldblatt, 1978). Ecosystems in the core Cape Floristic Region continue to decline owing to intensive pressures from agricultural and urban expansion as well as through alien plant invasions (van Wilgen et al., 2012). Degradation is particularly acute in lowland areas that encompass the highly threatened Sand Fynbos ecosystems (Holmes et al., 2012; Skowno et al., 2019). Here, ecological restoration is a priority towards meeting local and international conservation targets (Skowno et al., 2019). For invaded fynbos ecosystems, passive restoration is often possible and cost-effective owing to long-lived soil-stored seed banks (Holmes, Esler, van Wilgen, & Richardson, 2020). We define passive restoration as management to remove the stressor(s) that caused degradation, such as invasive alien trees and fire suppression (Holmes, Esler, van Wilgen, & Richardson, 2020). Active restoration refers to additional actions to re-introduce missing components of the ecosystem (Holmes, Esler, van Wilgen, & Richardson, 2020). Passive restoration of fynbos from viable soil-stored seed banks does exclude important guilds such as serotinous species that store seeds in canopy seed banks and resprouting species with very small seed banks, especially where above ground fynbos has not been present for some time (Holmes, Esler, van Wilgen, & Richardson, 2020).

Soil-stored seed banks are a critical evolutionary strategy as they can stabilize population dynamics in response to environmental fluctuations such as droughts and natural disturbances such as fires, thus improving ecosystem resilience (del Cacho & Lloret, 2012). In addition, persistent soil-stored seed banks support passive restoration in degraded grassland ecosystems (Kiss et al., 2018), subalpine meadows (Ma et al., 2019) and in fynbos ecosystems (Galloway et al., 2017; Holmes & Cowling, 1997a). In such cases, assessment of the soil seed bank provides managers with information on the restoration potential of degraded sites (Rayburn et al., 2016). In other ecosystems such as savannas, soil seed banks confer resilience to the grass layer, but not the tree canopy layer (Scott et al., 2010). A similar situation was noted for neotropical forest, whereby the woody species were not represented in the soil seed bank, but were present in the litter and juvenile banks, which are defined as seedlings and saplings that have their growth arrested while awaiting a light gap (Lipoma et al., 2020). Similarly in fynbos riparian ecosystems the soil seed bank was dominated by herbaceous species with evidence of seed bank persistence following invasion by alien trees (Tererai et al., 2014; Vosse et al., 2008).

The dominant vegetation of the Cape Floristic Region comprises fynbos, which is a shrubland ecosystem vulnerable to invasion by alien trees including pines, acacias, gums and hakeas (Goldblatt, 1978; Holmes, Esler, Gaertner, et al., 2020). Introduced to the Cape largely for plantation forestry, these tree taxa are pre-adapted to the local conditions (including climate, soils and summer fires), grow faster and taller than native fynbos species, and spead into uninvaded natural vegetation (van Wilgen et al., 2020). They form dense, monospecific stands over several fire cycles of recruitment in the absence of interventions (Holmes, Esler, van Wilgen, & Richardson, 2020). These invasions have a negative impact on biodiversity (Galloway et al., 2017; Hall et al., 2021; Mostert et al., 2017) and also reduce water yields from catchments which negatively affects the economy (Le Maitre et al., 2016; Rebelo et al., 2022). Invasive alien trees further influence ecosystem properties such as biomass, fire regime (mainly increasing fire severity) and soil characteristics (e.g. enhanced soil nitrogen following acacia invasion; Nsikani et al., 2017). Despite a large investment in alien vegetation control in South Africa, invasive tree species continue to spread (van Wilgen et al., 2012; van Wilgen et al., 2022) and ecological restoration remains a conservation and water security priority. Ecological restoration is key to reducing re-invasions, i.e. clearing and ensuring native biodiversity returns, whether passively or actively. Recently, pine plantations in the western Cape Floristic Region were exited (harvested and withdrawn) from commercial forestry (Van Wilgen, 2015), and this provides an opportunity to investigate spontaneous succession potential and the resilience of the passively recovering ecosystems after timber harvesting.

Once dense stands of alien trees are formed, flowering and seed set in fynbos species fails, preventing seed bank replenishment. Although many fynbos species have persistent soil seed banks (Holmes, 2002; Holmes & Cowling, 1997b), every fire that sweeps through an invaded stand further depletes this residual seed bank through germination or seed and seedling mortality and as a result fynbos restoration potential declines with each fire cycle of dense alien tree invasion (Holmes, Esler, van Wilgen, & Richardson, 2020). Those species with aerial seed banks (e.g. both reseeding and resprouting serotinous *Protea*, *Leucadendron*, *Widdringtonia*, *Brunia* species) are the first to be locally extirpated (Holmes & Cowling, 1997a). Our study focusses on Cape Flats Sand (CFS) Fynbos recovery following over a century of forestry plantations (mostly pines, *Pinus pinaster* until the 1950s, thereafter *Pinus radiata*) in the Tokai Park section of Table Mountain National Park, Cape Town. Cape Flats Sand Fynbos is rich in endemic (16) and threatened (>100) plant species and has four globally extinct or extinct in the wild species (Red List of South African Plants, n.d.; Rebelo et al., 2011). Although CFS Fynbos once extended 545 km^2 across the Cape Town municipal area, 85% of its former habitat has been lost, and over half of the remaining habitat is highly degraded by soil disturbance and invasive alien vegetation, primarily the Australian Port Jackson Wattle, *Acacia saligna* (Hall et al., 2021; Rebelo et al., 2006). Only 5% is formally conserved, mostly as small remnants, with 60% of conserved land also in a degraded state (van der Merwe, 2024). As a result, CFS Fynbos is classified as a critically endangered ecosystem (Keith et al., 2013; Skowno et al., 2019). Ecological restoration of surviving remnants is therefore a top conservation priority and aligns with the United Nations Decade on Ecosystem Restoration (2021–2030) initiative to prevent, halt and reverse habitat degradation (UN, 2020).

How long-lived the persistent portion of the fynbos soil seed bank is in the absence of fire is unknown, but was estimated to be between 30 and 50 years in one study (Galloway et al., 2017). Yet at Tokai Park the exited plantation compartments that burnt in a prescribed fire following more than a century of forestry anecdotally showed moderate, though variable, passive recovery from the soil seed banks (personal observations 1998–2023). The resilience of this passively restored vegetation will depend on whether degradation thresholds have been crossed (Gaertner et al., 2012). Key to the resilience of restoring ecosystems will be the restoration of the residual soil seed bank during the first restoration cycle (del Cacho & Lloret, 2012). The aim of this study was to assess fynbos vegetation resilience during the first restoration cycle following pine harvesting and a prescribed burn at Tokai Park. A restoration (or recruitment) cycle in fynbos vegetation is defined as the period following a restoration burn event, during which the recruitment and establishment of fynbos takes place (Bond & Van Wilgen, 1996). The second restoration cycle, for example, is the period after the second fire event following restoration of the site. A restoration cycle is usually synonomous with fire-cycle in fynbos, as the majority of species require fire-related cues to germinate and establish. The aim of the study was achieved by comparing above and below ground vegetation composition and focusing on patches of six perennial fynbos species. All six species are obligate reseeders with soil-stored seed banks but represent a variety of important fynbos growth forms (shrub, shrublet, graminoid perennial) and seed types (0.2–20 mg; passive, ballistic, wind and ant dispersed). The key research questions addressed are:

- Are fynbos soil seed banks replenished during the first restoration cycle following plantation removal?
- Are there differences in seed bank resilience among the focal species' growth forms?
- How does soil seed bank resilience differ in the second restoration cycle following plantation removal?

2 | METHODS

2.1 | Study site

The study site is within Tokai Park, a section of Table Mountain National Park (TMNP), a nature reserve and World Heritage Site that includes Cape Flats Sand (CFS) Fynbos on the low-lying sand plain (Figure 1). These areas were used for plantation forestry (*P. pinaster*, *P. radiata* and *Eucalyptus* species) from 1887 to 2010, with compartments supporting two or three rotations of harvested timber (C. Botes, personal communication, 2006). Owing to poor financial viability, new plantations were halted from 2005 and the harvested areas passively restored to fynbos, usually following a prescribed dry season burn (personal observation). During the forestry era, it was observed that small wild fires stimulated the germination of CFS Fynbos propagules in the soil, providing evidence that some seed banks persist (Petersen et al., 2007). Furthermore, open areas among the trees were noted to support a range of native species, including the Red Listed *Diastella proteoides*, *Serruria glomerata* and *Lachenalia reflexa* (Morris, 1996) suggesting that the area retained some restoration potential.

In 2010, all the study compartments were clear-felled of plantations in the summer and given a prescribed restorative burn in autumn of 2011 to remove slash (Table 1). Subsequently, the fynbos was allowed to passively recover. All blocks have been weeded of emergent alien species (i.e. 'alien clearing'; passive restoration) by volunteers since 2005, such that no woody alien plant species have subsequently set seed. Block A16b manifested dense *A. saligna* stands following restoration, which required a specialist team to remove plants by cutting below ground. Herbicides have generally not been used for these efforts. Fires after 2010 are prescribed ecological burns that generally burnt the entire compartment.

Cape Flats Sand Fynbos vegetation comprises about 100 ha of Tokai Park, grading into Peninsula Granite Fynbos on the low-mid slopes and Peninsula Sandstone Fynbos on the upper slopes of TMNP (Rebelo et al., 2006). The contiguity of these vegetation types further enhances the conservation value of any restored Tokai CFS Fynbos remnants within the national park, as ecological processes such as pollination, seed dispersal and fire operate at larger scales, and are more likely to be resilient here than in the smaller, isolated remnants on the Cape Flats within urban Cape Town.

Each forestry compartment has a slightly different history relating to the alien tree species planted, number of rotations and fire incidence. This information was extracted from the forestry records for Tokai Park, accessed at https://tokaipark.com/tokai-park/adopt-a-plot/on 7 April 2024 (Table 1).

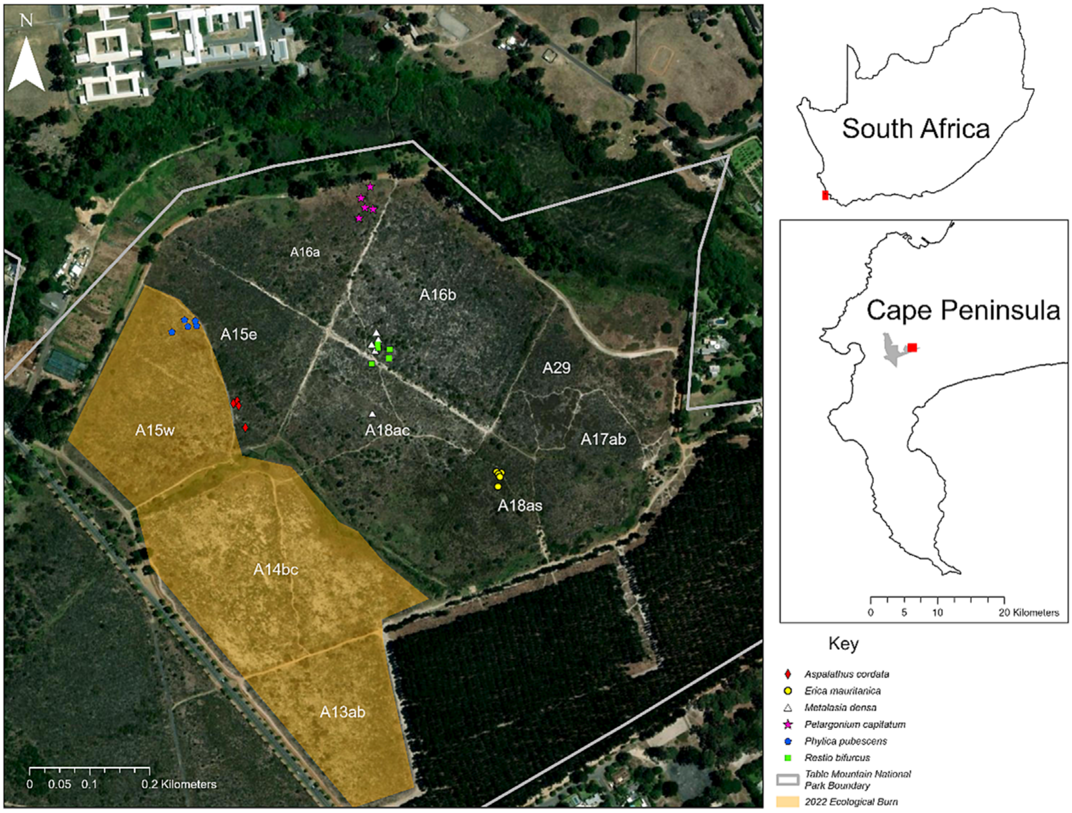

FIGURE 1 Location of Cape Flats Sand Fynbos within Tokai Park, Table Mountain National Park, South Africa, showing the extent of the 2022 ecological burn and the six focal species' patches (plots shown) within their labelled forestry compartments. Dark green trees to the south are the remaining non-harvested pine plantations.

TABLE 1 Management history for each forestry compartment number (#) included in the study at Tokai Park, South Africa. Spatial data on the extent of historical fires are not available. In 2010, all these compartments were clear-felled in summer, given a prescribed restorative burn in autumn 2011 to remove slash, and the fynbos was allowed to passively recover. Fires after 2010 are prescribed ecological burns that generally burnt the entire compartment. A prescribed burn of blocks A16 and A18 for autumn 2023 was postponed (still unburned in 2024).

#	Management history
A15w	*Eucalyptus* (1887); *Pinus pinaster* (1928); fires (1941, 1949, 1958); *P. radiata* (1976); ecological burn (2011, 2022)
A15e	*Eucalyptus* (1887); *P. pinaster* (1928); fires (1941, 1949, 1958); *P. radiata* (1976); ecological burn (2011, 2022: western half of the compartment)
A16a	*Eucalyptus* (1887); *P. pinaster* (1928); *P. radiata* (1968); ecological burn (2011)
A16b	*P. pinaster* (1889); *P. radiata* (1941); *P. radiata* (1981); ecological burn (2011)
A18ac	*P. pinaster* (1898); *P. radiata* (1940); *P. radiata* (1973); ecological burn (2011)
A18as	*P. pinaster* (1898); *P. radiata* (1942); *P. radiata* (1987); ecological burn (2011)

2.2 | Study species

Six fynbos perennial species were selected as focal species for the seed bank study, comprising four shrubs, an herbaceous perennial/subshrub and a restioid (shrubby graminoid in the Restionaceae) tufted perennial (Table 2, Figure S1). The study species were selected as they all have soil-stored seed banks but their diaspores differ morphologically according to dispersal and burial modes (e-Flora of South Africa, 2022; Seed Information Database, n.d.; Manning & Goldblatt, 2012). Additionally, the selected growth forms represent important structural components of the fynbos plant community, namely ericoid-leaved shrubs, larger-leaved shrubs, restioids and non-woody perennials. *Erica mauritanica* occurs in just one small patch at Tokai Park and was included as a locally rare species to assess whether it could be detected in the soil seed bank during the first restoration cycle as an indication of small population resilience (Figure S1).

Proteaceae are another important component of CFS Fynbos; however, those with soil-stored seeds (e.g. *Leucospermum* and *Serruria*

TABLE 2 Growth form, seed characteristics and localities selected for the six focal fynbos species at Tokai Park, TMNP. Information from Manning and Goldblatt (2012)), e-Flora of South Africa (https://www.worldfloraonline.org/taxon/wfo-0000037543) and Seed Information Database (https://ser-sid.org/species/a4440de0-4e51-4cc2-b54a-3c4d2a60d4e3).

Focal species	Growth form	Diaspore (seed) description	Dispersal mode	Compartment
Phylica pubescens Aiton	Medium-lived ericoid shrub	Large (20.6 mg), hard coat	Ballistic, ant	A15e
Aspalathus cordata (L.) R. Dahlgren	Medium-lived shrub	Medium (6.6 mg), hard coat	Ballistic	A15e&w
Metalasia densa (Lam.) P.O. Karis	Long-lived ericoid shrub	Small (0.32 mg)	Wind	A18ac and A16b
Erica mauritanica L.	Long-lived ericoid shrub (locally rare)	Small (0.02 mg)	Passive, wind	A18as
Pelargonium capitatum (L.) L'Her.	Forb/shrublet	Medium (3.9 mg), hard coat	Wind, hygroscopic	A16a
Restio bifurcus Nees ex Mast.	Restioid, tufted perennial	Small (1.4 mg)	Passive	A18ac and A16b

species) were too scattered across the site to include. The serotinous species (*Protea* and *Leucadendron* species) retain canopy-stored seeds and are absent from the soil seed bank, therefore outside the scope of this study. However, they have been successfully reintroduced at Tokai Park, from seeds collected in the adjacent Sandstone Fynbos at Silvermine. An historical flora list exists for the nearby Bergvliet farm (Rourke et al., 1981), immediately adjacent to Tokai Park, indicating appropriate potential species for re-introduction, both for canopy and soil-stored guilds (Rourke et al., 1981).

2.3 | Seed bank comparison in first restoration cycle

2.3.1 | Vegetation surveys

A locality, hereafter 'focal species patch', or 'patch', was selected for each of the six focal species based on their relative abundance in the plant community (Figure 1, Table 2) and five 1 m^2 vegetation plots randomly established within each focal species' range, located at least 5 m apart. Typically for fynbos vegetation community studies a plot size of 50–100 m^2 is used. However, our primary aim was to examine focal species' seed bank resilience not study above ground community composition, and this plot size is sufficient for that purpose. The above ground plant community was assessed in summer, in January 2021 in 10-year-old vegetation, by recording the presence of all species in the plot, both alien and native species. Projected canopy cover (as a percentage) was also estimated for each plant species and overall. Note that winter ephemerals, including geophytes, are dormant at this time and generally were not visible or recorded.

At each corner of the 1 m^2 plot, a soil core (5 cm diameter × 15 cm depth) was extracted and the four cores per plot combined into a composite sample in a double paper bag and labelled with the plot number and focal species' name. The 30 samples were stored dry in the laboratory until required for the seed bank assessment commencing in autumn of the same year (April 2021). Due to being collected during the dry summer season (January), the soil samples were dry, but were allowed to air dry further in the laboratory until required for the seed bank assessment.

2.3.2 | Seed bank study

The germinable soil seed bank was assessed using the seedling emergence approach (Holmes & Cowling, 1997b). The soil samples were placed in flat seedling trays over a layer of washed river sand; five trays per focal species patch. Germination cues for fynbos are fire-related; therefore, trays were watered with smoke water to stimulate germination (using Kirstenbosch instant smoke plus seed primer discs; https://seedsandall.co.za/product/kirstenbosch-instant-smoke-plus-seed-primer). In May 2021, the trays were placed in the Stellenbosch University Forestry and Wood Science Department greenhouse, which is open-ended and tracks the ambient temperature fluctuations, including the winter minimum temperatures required to trigger germination in fynbos species (Brown & Botha, 2004). A heat pulse was not applied, and instead, the soil core samples were first sieved to count and record any larger, hard-coated seeds that require this cue (e.g. *Aspalathus*, *Phylica*, *Pelargonium*) before returning them to the trays. Five control trays were set up with washed river sand to detect any seed contamination in the nursery, leading to a total of 35 trays. Trays were kept moist with automatic mist irrigation and monitored for seedling emergence six times between July and October (the winter wet germination season), after which no further seedling emergence occurred. Emerging seedlings were removed once identified, and nursery conditions minimized post emergent mortality. Seedlings were identified to species level where possible, otherwise to genus or family level. Alien species were also recorded and marked as such. Three different taxa of weeds (unidentifiable) were recorded as being introduced via the control, and these 24 individuals were removed from the dataset prior to analysis, being assumed to be nursery or river sand contaminants.

2.4 | Post-fire seedling emergence in second restoration cycle

One of the study compartments (A15e) was burnt again in a March 2022 prescribed burn (Figure 1). This provided an opportunity to assess vegetation recovery and *Phylica pubescens* recruitment in a second restoration cycle after plantation removal. In June 2023, 15 months post-fire in the wet winter season, the five 1 m^2 plots for this focal species were revisited using the GPS localities for the plots. Vegetation surveys were conducted, and canopy cover was estimated as described above. In addition, the number of seedlings of *P. pubescens* inside the plot and extending to a 3 m radius was recorded to allow for dispersal. *Phylica pubescens* is myrmecochorous and seeds are moved short distances to ant nests (generally <1–3 m, Bond & Slingsby, 1983). Some 13 species of ants have established in the area, including several seed dispersers (iNaturalist, 2024).

2.5 | Data analyses

Plant community composition was compared among the plots of the six focal species' patches using SIMPER and ANISOM analyses with the Vegan Package (Dixon, 2003; Oksanen et al., 2022) in R Studio for both above ground and below ground (seed bank) datasets for the first restoration cycle study (RStudio, 2020; R Core Team, 2024). In addition, species richness and the Shannon diversity, Simpsons diversity and Pielou evenness indices were computed for each focal species' community for both above and below ground plant community composition for both the first, and for *P. pubescens*, also the second restoration cycle. Plant community composition data were categorized into growth forms to compare above and below ground community structure. Seed bank densities were calculated per m^2 by multiplying the emergence data by 25.5 for each focal species. This value was obtained by multiplying 19.63 cm^2 by 5 plots and by 4 samples (392.6 cm^2) and taking the quotient of 10,000 cm^2. This 19.63 cm^2 was obtained due to the diameter of each core being 5 cm. Principal component analysis (PCA) was conducted on vegetation community composition data for both above and below ground data using the stats and ggplot2 packages in R Studio (R Core Team, 2024; Wickham, 2016).

3 | RESULTS

3.1 | Vegetation patterns during the first restoration cycle

3.1.1 | Seedling emergence

Total native soil seed bank densities in the 10-year-old plant communities of each of the six focal species ranged from 3150±330 to 8940 ±1290 seeds per m^2 (mean±SE). Much of the seed bank comprised short-lived species and ephemerals (63–84%) (Figure 2). Identified alien species had a soil seed bank density between 25±25 and 381 ±180 seeds per m^2 (mean±SE). There was an overall average of five to 10 native species detected in the seed bank of focal species samples.

Five of the six focal species emerged as seedlings from their soil seed bank samples in the nursery: *Metalasia densa* (45 individuals), *Erica mauritanica* (24 individuals), *Restio bifurcus* (6 individuals), *Pelargonium capitatum* (5 individuals) and *Phylica pubescens* (4 individuals). It should be noted that the emerged *Erica* seedlings could not be identified to species level, but were assumed to be *E. mauritanica* as they only emerged in this patch. Ten other *Erica* species have been recorded at Tokai Park, four of which were reintroduced after pine harvesting. However the only species near to the *E. mauritanica* population was one observation of *Erica multumbilifera*. Three species (*M. densa*, *P. capitatum*, *R. bifurcus*) also emerged in soil samples from other focal species' plots but only *Restio* was more abundant in another patch (*Erica*) than its own (Table S1, Figure 3). Sieving for the larger hard-coated seeds that may require a heat pulse germination cue yielded nine *Aspalathus cordata* in its own patch and two additional *P. capitatum* seeds. No seedlings of *Aspalathus cordata* subsequently emerged from the soil seed bank samples. Detected seed bank densities of the focal species ranged from 102 seeds/m^2 (*Phylica pubescens*) to 1148 seeds/m^2 (*Metalasia densa*) (Table S1).

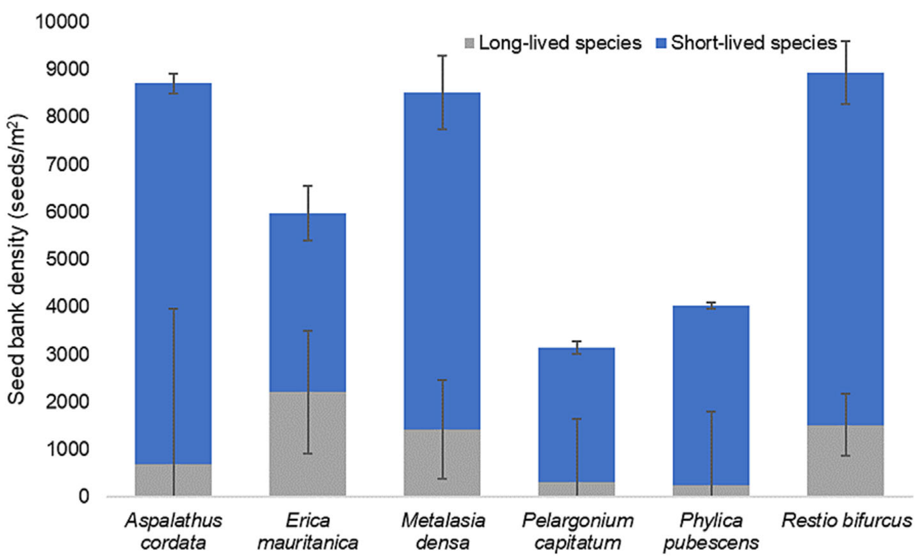

FIGURE 2 Total native soil seed bank densities (seeds/m^2 + SE; $n = 5$) in the six focal species patches, divided into long-lived perennial species (those typically surviving more than 4 years in the above ground vegetation) and short-lived or ephemeral species, at Tokai Park, South Africa.

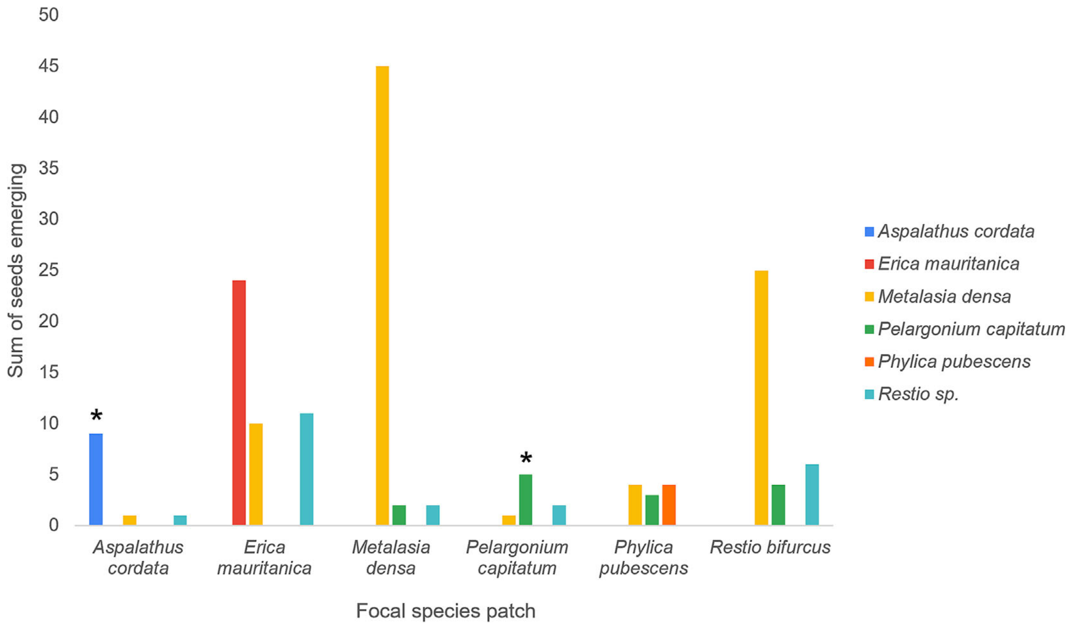

FIGURE 3 Number of seedlings of focal species to emerge from each of the six focal species patches (total number over five trays), including the larger hard-coated seeds that were counted following sieving that did not germinate (indicated by *), in the study at Tokai Park, South Africa. For values, see Table S1.

3.2 | Comparison of above and below ground vegetation communities

There is a significant difference in above ground community composition among the six plant patches (R 0.9528; $p = 1\text{e}{-04}$), with the key differences in composition being driven almost entirely by the focal species of each patch (Dataset S1, Dataset S2). In general, for above ground communities, *Metalasia densa* and *Restio bifurcus* patches are the least species-rich, diverse and even (Figure 4). Conversely, for below ground communities, results of the ANOSIM suggest a significantly even distribution of high and low ranks within and between groups (R 0.4123; $p = 1\text{e}{-04}$), suggesting high similarity in community composition (Dataset S3, Dataset S4).

There is no observable assosciation between above ground plant and below ground seed communities, based on the above ground vegetation survey and the seedling emergence study. Some patches have similar diversity indices above and below ground (e.g. *Erica mauritanica* and *Phylica pubescens* for all indices except evenness) and others have quite different indices (e.g. *Restio bifurcus* for all indices except evenness), while still others vary (e.g. *P. capitatum*) (Figure 4). The only index that is consistently higher in above ground communities relative to below ground is evenness.

Above ground focal species patches were relatively distinctive in plant species composition compared to the below ground seed communities (Figure 5). Below ground only two dinstinctive communities emerged: one which was similar for *Restio bifurcus* and *Metalasia densa* patches, and one for the other four focal species patches. Above ground there was good separation for all patches except for *Erica mauritanica* and *Restio bifurcus* which were quite similar in vegetation composition. For both above and below ground vegetation communities, principal components 1 and 2 account for very little of the variance (i.e. only about 22–25%). Both above and below ground communities were sufficiently sampled, as the species accumulation curves demonstrate equilibrium is reached (Figure S2, Figure S3).

In general, in terms of status, there is a lower proportion of alien relative to native species above compared to below ground at Tokai Park (Figure 6). These were predominantly alien annuals; only three acacia seedlings emerged in the seedling emergence trial as plants were cleared after the 2011 fires and never flowered or seeded. In terms of growth forms, below ground seed banks are dominated by graminoids while above ground communities at 10 years post-fire are dominated by shrubs or restioids (Figure 7). Grasses do dominate these fynbos communities early in the post-fire succession (2–5 years) but are then over-shadowed by shrubs.

3.2.1 | Vegetation patterns post-fire in the second restoration cycle

Phylica pubescens recruited inside only one of the original five plots in which it dominated, but had recruited successfully close to four of the five plots although densities varied considerably (Figure 8). The below ground community was dominated by graminoids and geophytes were present (Figure 9). However following the prescribed burn, forbs (herbaceous dicotyledons) dominated above ground in one-year old vegetation. Diversity and evenness were lower for seed banks compared to above ground vegetation (Figure 10). Diversity indices were similar or higher post-fire for the above ground *P. pubescens* 1-year-old plots (Figure 10).

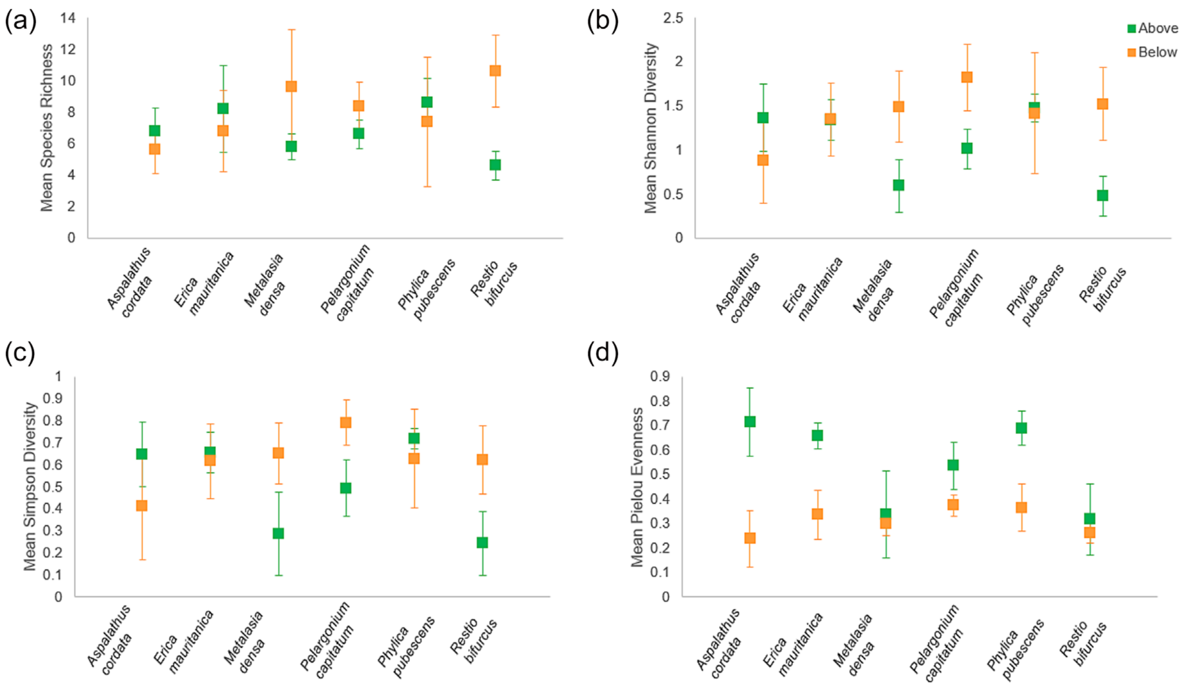

FIGURE 4 Diversity indices (mean ± standard deviation): (a) species richness, (b) Shannon-Weiner species diversity index, (c) Simpson diversity and (d) Pielou's measure of species evenness for above (green) and below (orange) ground plant communities in the six focal species patches 10 years post-fire at Tokai Park, South Africa. For values, see Table S2.

4 | DISCUSSION

4.1 | Vegetation patterns during the first restoration cycle

Total native soil-seed bank density at Tokai Park (ranging from 3150–8940 seeds m^{-2}), following over a century of plantation forestry and 10 years after the first fynbos restoration burn was comparable to, or exceeded, densities measured in other fynbos studies (1950–2250 seeds m^{-2}, Holmes, 2002), especially seed banks of alien-invaded fynbos ecosystems (18 seeds m^{-2}, Hall et al., 2021). As unlikely as this result seems, the reasons may be threefold: firstly, plantation rotations were sufficiently short (<50 years) to prevent total mortality of fynbos seed banks; secondly, pine rotations potentially allowed for about 7 years of fynbos regeneration and survival prior to pine canopy closure, thus some replenishment of the soil seed banks likely occurred by species not requiring a strong fire-related germination cue; thirdly, pine shading and horizontal rooting structures eliminate habitat for rodents thus reducing seed losses through granivory (Rebelo et al., 2019). This contrasts with the situation following dense alien acacia invasion whereby canopy closure is rapid and the acacias provide seed resources to maintain granivores, provided nesting sites remain available (Holmes, 1990). Native seed bank richness was slightly lower or similar to pristine fynbos, and similar to recently alien-invaded fynbos stands measured previously (Galloway et al., 2017; Holmes & Cowling, 1997b). The low alien soil seed bank densities were largely due to the fact that woody alien plants were removed (weeding by volunteers) and not allowed to replenish their seed banks, such that figures are persistent seeds carried over through the restorative burn. This demonstrates the power of follow-up alien tree clearing in fynbos, especially when clearing takes place before the invasive alien trees are able to set seed.

The early years following pine harvesting and a restoration burn likely provide a pest- and predator-free environment in which plants may re-establish and flourish. For example, at Tokai Park, it is possible that following the restoration burn the plants were well below carrying capacity, at low density with little competition, and thus, plants may have been able to produce an above average number of seeds. In addition, if the fynbos-adapted seed predators and parasites had not recovered following a century of pine plantations, the effective input into the seed banks might be much higher than in established fynbos. This granivore- and pathogen-free period presents a critical window of opportunity in fynbos restoration. This once-off benefit in the restoration trajectory may also extend to flowering, seed set and seed bank replenishment. This concept of 'windows of opportunity' is recognized in the ecological restoration literature, specifically as a short period in which environmental conditions are favourable for establishment (Van Belzen et al., 2022). There has also been research into how these windows may be created, lengthened or mimicked to enhance vegetation recolonisation, for example in salt marshes (Fivash et al., 2021). In particular, carrying capacity has shown to be an important factor in creating windows of opportunity for successful reintroduction of species (Tielke & Vos, 2024). It is therefore recommended that restoration researchers and managers of fynbos systems understand and capitalize on these critical windows of opportunity to improve restoration outcomes.

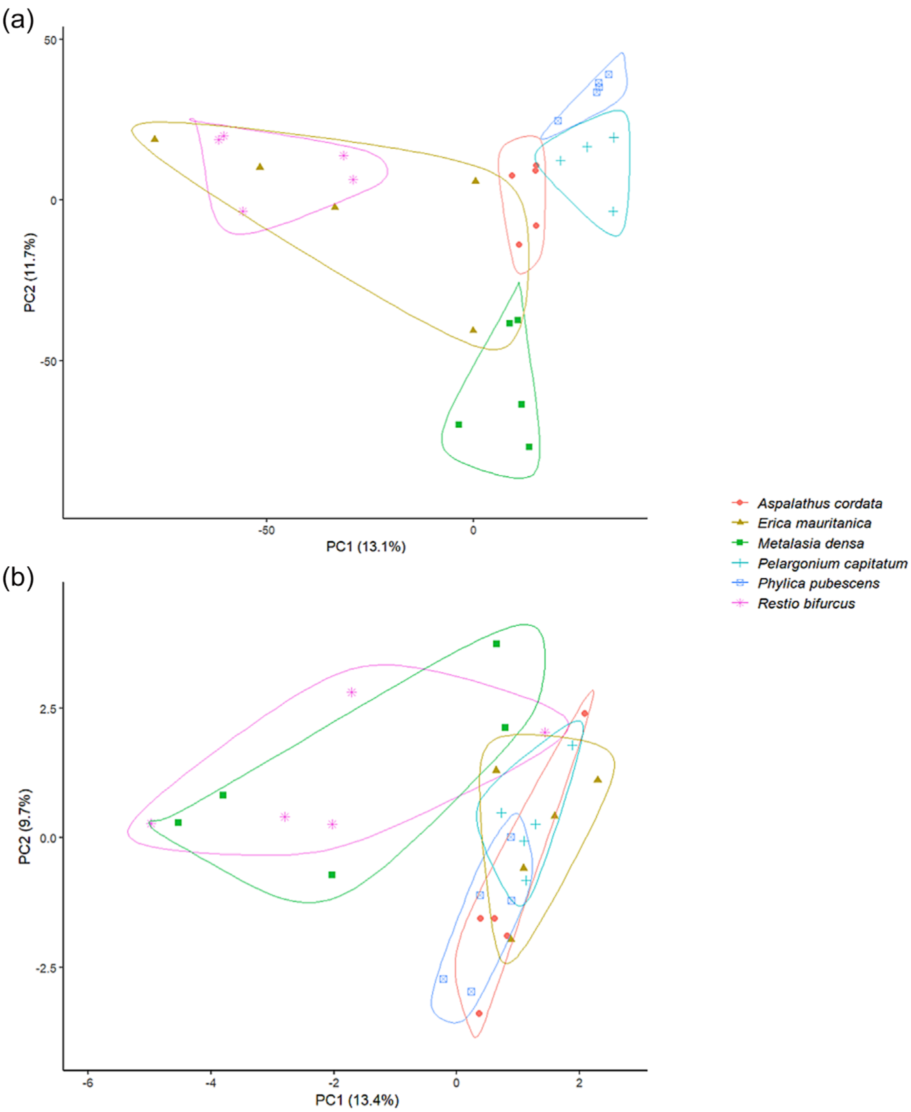

FIGURE 5 Principal components analysis (PCA) for (a) above ground and (b) below ground vegetation communities in the six focal species patches 10 years post-fireat Tokai Park, South Africa.

4.2 | Differences in seed bank resilience among growth forms including reflections about the second restoration cycle

Seed bank representation differed among growth forms: whereas shrubs dominated the above ground vegetation (except for the *Restio* focal species patch in which restioids dominated) the below ground community was dominated by graminoids (grasses and sedges). Forbs and geophytes were relatively more prominent below ground than above. These results do not necessarily indicate lower seed bank resilience in shrubs and restioids as typically such longer-lived species have smaller seed banks than shorter-lived herbaceous species (Holmes, 2002). The longer-lived perennials will continue to augment their seed banks as the vegetation ages beyond 10 years. Seed bank abundance among focal species generally reflected their seed characteristics: the small-seeded species (*Erica*, *Metalasia* and *Restio*) had much larger soil-stored seed banks during the first restoration cycle than larger-seeded species, reflecting higher investment in seed quantity. Although long-lived perennial re-seeding species comprised a relatively small proportion of the soil seed bank during the first restoration cycle, this is fairly typical of fynbos and other Mediterranean-climate ecosystems (e.g. *Banksia* woodland, Rokich & Dixon, 2007). Seed densities of all focal species were sufficiently replenished to support regeneration following a future prescribed burn.

The large-seeded *Phylica* recorded the smallest seed bank, but this should still be large enough to ensure the persistence of this obligate reseeding species. This was corroborated in the second restoration cycle study post-fire, whereby sufficient *Phylica* recruits were documented to replace the previous adult population. However, size of seed bank is not the only important factor. These seed banks might be the longest lived, with seed viability of over 200 years in genera such as *Leucospermum* (Daws et al., 2007). This, coupled with hot fire germination cues, may result in significant carryover of seeds over several fire cycles, potentially as many as 12. *Phylica* is also ant-dispersed and because of this, seed banks will be clumped according to ant nest localities (Bond & Slingsby, 1983); hence, this study potentially under-estimated *Phylica* seed bank density. The wind-dispersed *Metalasia* was the most widespread seed bank species,

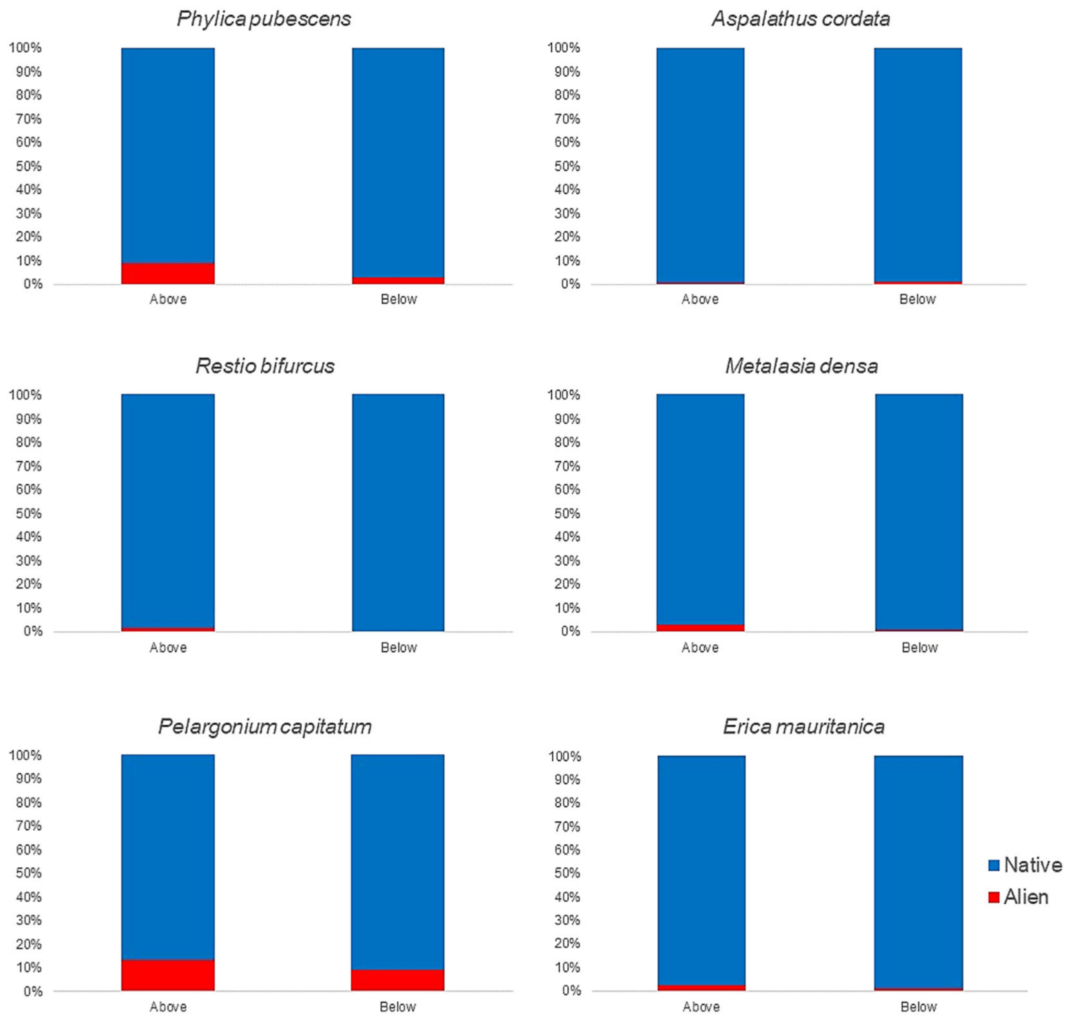

FIGURE 6 The proportion of alien compared to native species in each of the six focal species patches above and below ground 10 years post-fire at Tokai Park, South Africa.

occurring in all focal species patches sampled, whereas the larger, hard-seeded *Aspalathus* and *Phylica* with short-distance dispersal mechanisms, were only detected within their own patches and tended to show more clumped distributions within the restored below ground communities.

During ecosystem restoration, species with smaller distributions and short-distance dispersal mechanisms are likely to be less resilient than more widespread species owing to stochastic processes such as drought or inappropriate disturbances (e.g. prescribed fires in the wrong season). Such species should be monitored to ensure that populations recover sufficiently and do not decline. For the CFS Fynbos in Tokai Park, the second restoration cycle in the *Phylica* populations indicates a positive trajectory so far. Furthermore, these species tend to have long-lived seed banks, which may persist underground over several fire cycles, providing resilience to unfavourable fire events or post-fire weather. In the case of *Erica mauritanica*, which has a very small above ground population size, its seed bank presence provides hope for its persistence and potential population growth following a future prescribed burn.

The focal species patches were fairly distinctive except for the *Restio* and *Erica* patches which were similar, with *Restio bifurcus* prominent in both. These are spatially quite close to each other relative to the other patches. The *Pelargonium* focal species patch was located at the edge of its compartment close to the firebelt and had a largely herbaceous above ground community, with the highest cover of alien species. This was reflected by the seed bank too, which was the most depauperate in native species' densities of all the samples. It is likely that this patch has experienced edge-effects and is missing some longer-lived perennial species and could be a candidate for active restoration. However anecdotally, the entire northern edge of the park exhibits a similar trend. This is partly due to the firebelt, but could also be a shading effect from the alien gum trees which line the perimeter, a legacy of the plantation era. This shading effect could be promoting the alien grasses (annuals), but this could also be due to the lack of, or cool fire, due to the presence of the firebelt. If either of these effects are driving community composition, these pressures should be addressed prior to active restoration (e.g. removing the alien gum trees along the perimeter which are also a constant source of invasive

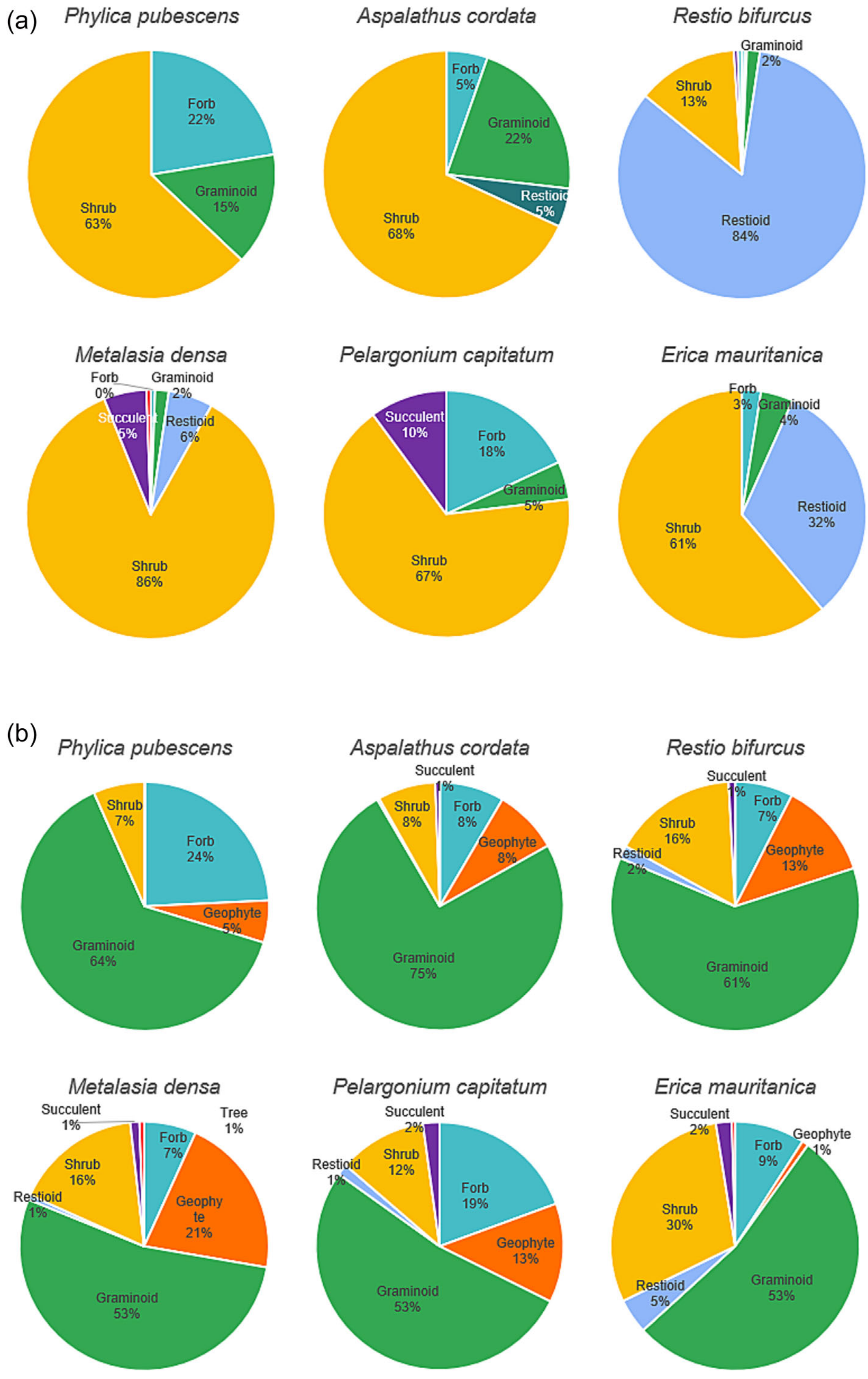

FIGURE 7 Growth forms characterising each of the six focal species patches (a) above and (b) below ground, 10 years post-fire at Tokai Park, South Africa.

alien propagules, and ensuring appropriate restoration burns). It is worth noting that *P. capitatum* is an opportunistic and potentially weedy species that tends to be more abundant in disturbed areas.

4.3 | Management recommendations

For most Cape Flats Sand (CFS) Fynbos species, soil-stored seed banks persist following pine plantation forestry and these species regenerate spontaneously post-fire, through a combination of passive and active restoration methods. This bodes well for passive restoration of CFS Fynbos. It stands to reason that invaded or planted pine stands should be removed and restoration initiated as a matter of urgency, especially where there is uncertainty as to the longevity of the soil seed banks. This is essential for South Africa's ability to achieve the biodiversity targets set forth in the Kunming-Montreal Global Biodiversity Framework, specifically targets 2 'Restore 30% of all Degraded Ecosystems' and 3 'Conserve 30% of Land, Waters and Seas'.

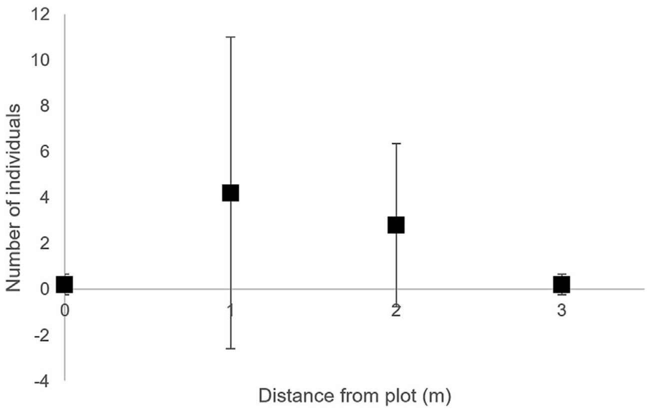

FIGURE 8 Number (mean ± standard deviation) of *Phylica pubescens* seedlings established in June 2023 following the March 2022 prescribed burn at Tokai Park, South Africa.

Required passive restoration treatment includes a prescribed burn following timber harvesting to clear the slash and provide the necessary germination cues to stimulate recruitment. Another study of CFS Fynbos at Milnerton Racecourse in Cape Town found that burning, followed by actively sowing seed and planting achieved the best and most cost-effective results (Retief et al., 2024).

The hypothesised granivore- and pathogen-free window in the first restoration cycle facilitates establishment and growth of the plant community as well as replenishment of the soil-stored seed banks. It is recommended that managers capitalize on, and extend, this window of opportunity by performing additional passive restoration treatments, including alien species control and ecological burns. The effectiveness and cost-efficiency of follow-up alien tree clearing in fynbos before the invasive alien trees are able to set seed cannot be overstated.

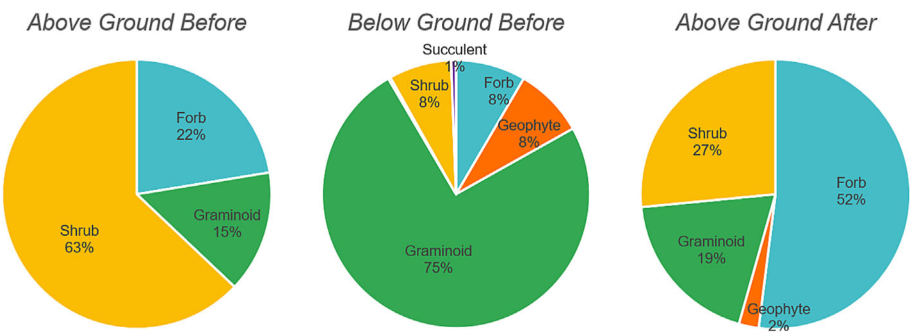

FIGURE 9 Growth form variation above and below ground for the *Phylica pubescens* focal species patch before and after the second prescribed burn in March 2022. Post-fire vegetation age was 10 years and 1 year respectively, at Tokai Park, South Africa.

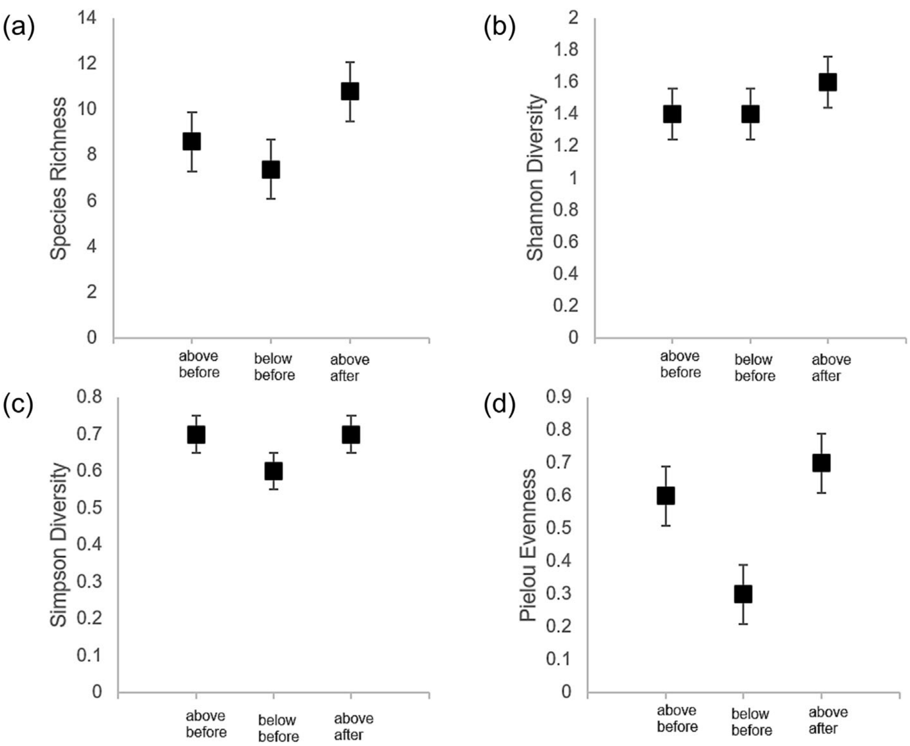

FIGURE 10 Diversity indices (mean ± standard deviation): (a) species richness, (b) Shannon-Weiner species diversity index, (c) Simpson diversity and (d) Pielou's measure of species evenness for above and below ground *Phylica pubescens* plots before (January 2021) and after (June 2023) the second prescribed burn in March 2022 at Tokai Park, South Africa. For values, see Table S3.

For this specific site, this is especially hand-pulling of pine seedlings which may seed into the area from remaining forestry compartments and alien acacias which were originally planted as companion species to the pines and left an alien seed bank legacy. Recommended active restoration treatments implemented at Tokai Park, include the re-introduction of serotinous overstorey Proteaceae, under-represented resprouter shrubs, and Red-listed threatened plant species (Hall et al., 2021; Ngwenya et al., 2023).

Monitoring of long-lived vegetation components should indicate whether any small populations are resilient or require augmentation, and a protocol for this should be developed. Rare and threatened species may benefit from the restored habitat and therefore augmentation of such species' populations should be considered, including re-introduction of 'extinct in the wild' threatened species (Hitchcock & Rebelo, 2017), provided that suitable microhabitats are present.

5 | CONCLUSION

The aim of this study was to assess fynbos vegetation resilience during the first restoration cycle after a century of pine plantations, following pine harvesting and a prescribed burn at Tokai Park, South Africa. Our results show that even for old forestry plantation areas, ecological restoration of fynbos to the historic vegetation community is feasible due to retained seed bank resilience, through a combination of passive and active restoration methods. Therefore, fynbos vegetation, specifically the obligate reseeders, demonstrated high resilience. Ecological restoration in cases where soil seed banks persist is therefore a viable and critically important method to attain 30% conservation and 30% restoration of ecosystems, as part of the Kunming-Montreal Global Biodiversity Framework. However, urgency is required, as it is unknown how much longer these fynbos seedbanks will continue to persist under remaining pine invasions and plantations.

AUTHOR CONTRIBUTIONS

AJR, PMH, KJE and AGR designed the research; AJR, PMH, KJE, AGR, SM, SHT and SHA did the research; PMH, KJE, SM and SHT collected the data; AJR did the data analysis; AJR, PMH, AGR and KJE interpreted results and AJR, PMH, KJE and AGR wrote the manuscript, while SM, SHT and SHA reviewed it and gave inputs.

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CONFLICT OF INTEREST STATEMENT

The authors have no conflicts of interest to declare.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in https://scholardata.sun.ac.za/ at 10.25413/sun.27660723. In addition, further data that support the findings of this study are available in the supplementary material of this article.

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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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