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The impact of pine plantations on fynbos above-ground vegetation and soil seed bank composition

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ABSTRACT

Pine plantations and pine invasions have numerous impacts on native ecosystems in the Fynbos biome of South Africa. The severity of these impacts greatly determines the extent of potential ecosystem recovery after the pines are felled. The recovery potential of fynbos after felling of pine plantations of varying longevity and the subsequent application of ecological burns was investigated in the Helderberg Nature Reserve, Western Cape Province, South Africa. Above-ground vegetation, soil seed bank and abiotic variables were sampled across three treatments (reference fynbos and sites that had been under pines for 30 and 50 years respectively) using 1 m^2 quadrats placed along 50 m line transects. The soil seed bank samples were smoke treated and then monitored in a greenhouse to determine the soil seed bank species and growth form composition. Areas previously under 30 year old pine plantations had high native species and growth form density (number of species/growth forms per unit area) and similar plant density (number of individuals per unit area) to the reference fynbos areas. Conversely, areas previously under 50 year old pine plantations had significantly lower native species and growth form density and plant density than the reference fynbos and were dominated by alien species. In addition, areas previously under 50 year old pine plantations had lower species diversity than the reference fynbos areas and areas previously under 30 year old pine plantations which were found to be similar to one another. Felled pine plantations were shown to minimally impact on soil abiotic variables, with only soil temperature and pH showing significant differences. Therefore, areas previously under 30 year old pine plantations have higher recovery potential following pine removal than 50 year old plantations, owing to the depleted native soil seed bank in the latter. Consequently, active restoration may be needed to re-introduce the missing long-lived growth forms and to prevent soil erosion. Pine plantation and invasion management in the Fynbos biome should aim to fell pines before the native seed bank is depleted to maintain the recovery potential of fynbos and prevent the need for active restoration.

1. Introduction

Pine species are renowned invaders in the southern hemisphere having been introduced by humans for timber and other uses such as wind breaks (Richardson et al., 1994; Richardson and Higgins, 1998). Pines have invaded from these initial plantations (Richardson et al., 1994; Richardson, 1998; Richardson and Higgins, 1998; McConnachie et al., 2015). Alien tree invasions in South Africa, specifically across the Fynbos biome, are a serious problem that threatens both native biodiversity and water security (Le Maitre et al., 1996, 2002; Latimer et al., 2004; Richardson and Van Wilgen, 2004; Van Wilgen et al., 2008).

Invasive alien plants, including some pine species, can reduce ecosystem resilience of the invaded area by causing biotic and/or abiotic thresholds to recovery to be passed that may lead to a biotic/abiotic feedback threshold where the invader dominates the ecosystem (Gaertner et al., 2012, 2014). Pines can have a significant impact on abiotic variables such as fire severity and soil pH (Gaertner et al., 2012; Van Wilgen and Richardson, 2012; Mostert et al., 2016; Taylor et al., 2017). Pines can form dense stands which can survive for many years whilst excluding native plant species; this may also result in the native seed bank declining over time (Richardson and Higgins, 1998; Holmes and Marais, 2000; Gaertner et al., 2012). Pine trees are able to outcompete native vegetation for sunlight due to their large stature which leads to the gradual exclusion of native plant species beneath the pine tree canopy over time (Richardson and Van Wilgen, 1986; Maccherini and De Dominicis, 2003; Gaertner et al., 2012). Leaf litter produced by mature pine trees is far higher than that produced by fynbos which

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also contributes to the suppression of vegetation surviving in the understorey (Richardson and Van Wilgen, 1986; Gaertner et al., 2014). However, these pine-related impacts on the ecosystem are considered less severe compared with other invasive alien trees (e.g. *Acacia* species) and therefore areas invaded by pine species are believed to be easier to restore (Mostert et al., 2016).

When pine trees are cut down and the area burnt, these bare sites are often left to restore passively which can potentially result in soil erosion and reinvasion by alien plants (Holmes and Richardson, 1999; Holmes et al., 2000). Restoration of these bare sites depends on the presence of native seeds which have been naturally dispersed and persisted in the soil seed bank (Holmes and Newton, 2004; Heelemann et al., 2013). If these two sources of plant propagules are insufficient to restore the native species richness and functioning of the native ecosystem then these sites will need active restoration to re-introduce crucial native plant functional types (Holmes and Richardson, 1999; Montoya et al., 2012).

Much research has been undertaken on the impacts of other alien invaders (e.g. *Acacia saligna*) in the Fynbos biome on the species/guild richness of fynbos vegetation and seed banks. Pine tree effects on fynbos above-ground vegetation have been studied, but there has been little research concerning their effects on fynbos soil-stored seed banks (Richardson and Van Wilgen, 1986; Holmes et al., 2000). As current restoration practices mostly rely upon soil seed bank recruitment, it is crucial to understand when an area invaded by pines or under a pine plantation can be successfully restored passively and when active intervention (i.e. re-introduction of native species through either sowing or planting) is needed. This is especially important in the Western Cape where many pine plantations are being phased out as economically unviable, and the forestry industry is progressing towards more sustainable pine plantation management (Van Wilgen, 2015; Stehle, 2016). Mountain catchments are also extensively invaded by pines which need to be felled and the areas restored.

The overall aim of this study was to determine the recovery potential of fynbos when subjected to extended periods under pine plantations. The key study questions, which entail comparing fynbos sites and sites that were under pine plantations, were:

- Are there differences in native and alien species diversity, diversity by growth form and density among sites?
- Are there differences in surface cover and abiotic variables among sites?
- Are there differences in species and plant density between the above-ground vegetation and the soil seed banks among sites?

2. Materials and methods

2.1. Study area and sites

The study area was in the lower portion of the Helderberg Nature Reserve in the City of Cape Town, Western Cape, South Africa (34° 03′ 54.35″ S, 18° 52′17.79″ E; see supplementary material – Fig. S1). The vegetation type of the study area is endangered Cape Winelands Shale Fynbos (Rebelo et al., 2006). Fynbos is a fire-driven ecosystem that relies on fire for stimulating seedling recruitment (Kraaij and Van Wilgen, 2014). Fires in the southwestern Cape usually take place during the hot and dry summer months (Kraaij and Van Wilgen, 2014). An area that included fynbos and sites previously under pine (*Pinus radiata*) plantations were chosen for this study. The only recorded incidence of alien trees in the reference fynbos sites were small patches of *Eucalyptus* which were felled between 1992 and 1994. The pine plantations were planted in the 1960s with some sites being felled 30 years later between 1992 and 1994. These sites have subsequently had 20 years of recovery time whilst other sites were only felled in the winter of 2014 and thus were under pine plantations for about 50 years. All of the sites (reference fynbos and the sites previously under pines for 30 and 50 years) were burnt a year before the study, during the autumn of 2015. Scattered invasive alien species such as wattles, hakeas and pines are under maintenance control.

At each site, native and alien species composition was measured by sampling the above-ground vegetation and soil seed bank together with the abiotic variables. Possible edge effects were avoided by sampling more than 5 m away from the edge of each site. Field work was performed during January 2016 (mid-summer in South Africa) so that the condition of the stored soil samples could imitate the dry topsoil conditions experienced in the field during summer (Holmes and Cowling, 1997). The post-fire age of the vegetation was 8 months.

Each treatment (reference fynbos and the sites previously under pines for 30 and 50 years respectively) was replicated at 3 sites each. At each of the 9 sites, three parallel 50 m line transects (approximately 5 m apart) were used to position quadrats for sampling of the above-ground vegetation and soil seed bank. Three 1 m^2 quadrats were randomly positioned along each transect. To sample abiotic variables at each site, two transects were used, with 3 quadrats along the first transect and 2 quadrats along the second. The direction of each transect was arranged in accordance with the longest edge of each area sampled. Random numbers from a random number table were used to determine the distance among the quadrats that were placed along each transect (Holmes and Cowling, 1997). Google Earth was used to randomly pinpoint the starting points for each of the transects, with each of the end points being placed 50 m away conforming with the shape of the site. The areas sampled at each site were chosen to ensure that the sampling areas were between 150 m and 200 m apart to maintain independence among the sites.

2.2. Above-ground vegetation survey

Each quadrat was used to determine the above-ground species and growth form density and plant density, and projected canopy cover (Pierce and Cowling, 1991; Heelemann et al., 2013). Plant taxonomy followed that of Manning and Goldblatt (2012). The different species in each quadrat were identified and number of individuals counted. Each new plant species encountered was sampled and pressed in the field for identification using relevant field guides (Bean and Johns, 2005; Manning and Paterson-Jones, 2007; Bromilow, 2010; Manning and Goldblatt, 2012; Fish et al., 2015). In each quadrat, the projected plant cover for each species and the proportion of bare ground, rock, litter and pine debris was recorded using the Braun-Blanquet scale (Braun-Blanquet, 1964). Due to the logistics of this study, sampling took place during the dry summer months which may have resulted in an underestimate of annual plant species which usually emerge during the wetter winter months – these species were subsequently identified in the soil seed bank analysis.

2.3. Soil seed bank sampling

Using a manual metal soil corer, four soil core samples (50 mm in diameter and 100 mm in depth) were taken from each of the corners of the 1 m^2 quadrats and bulked together to cater for patchy seed distributions and to minimise variation (Vosse et al., 2008). The bulked soil cores from each quadrat were individually stored in a brown paper bag in a dry place at ambient temperatures for two months until mid-March 2016. As fynbos seedling recruitment occurs naturally during the wet winter months, the soil seed bank was assessed using the seedling emergence approach over this same time period.

These soil samples were then transported to a greenhouse with transparent roofing and shade-netting sides at the Department of Forest and Wood Science at Stellenbosch University. A basal layer of newspaper and then river-washed sand was placed into 81 seedling trays (27 cm long × 31 cm wide) with the bulked soil samples placed on top and spread to a depth of approximately 5 cm. An additional three seedling trays were filled with river-washed sand only to serve as control trays to detect any wind-borne seeds that may have germinated from the sand. A smoke treatment was then applied to promote germination of the seeds in the soil as it is known that the chemicals in smoke can stimulate fynbos seeds to germinate (Brown, 1993). Smoke was produced by burning freshly-cut fynbos biomass in a metal drum that was then pumped into a tent which contained the seedling trays with the soil samples (Dixon et al., 1995; Holmes, 2002). Once the seedling trays were exposed to the smoke for 2 h they were removed, placed within the greenhouse and then lightly watered to wash the smoke chemicals into the soil.

Using an automated irrigation system, the seedling trays were then watered every day for seven months. Emergent seedlings were counted and positively identified to species and growth form level as above. Monitoring of the seedlings occurred once a week for seven months from mid-March until mid-October of 2016.

2.4. Abiotic variable sampling

The soil abiotic conditions were measured to determine differences among the three treatment types (reference fynbos and sites previously under pines for 30 and 50 years respectively) in terms of soil temperature, soil moisture, soil pH and soil infiltration rate. The abiotic data for each variable were measured across all sites in one day to reduce small scale temporal variation.

Soil temperature and soil moisture for each quadrat were measured and recorded in summer by placing an electronic thermometer and a soil moisture device (Hydrosense™) respectively 10 cm deep into the soil at the centre of each quadrat.

During winter, a soil sample from the top 10 cm of soil was removed from each of the corner areas of each quadrat and bulked together, taken to a laboratory at Stellenbosch University, mixed with distilled water in a small cylinder and its pH tested using a pH meter (HANNA instruments®). Soil infiltration rate was also measured during winter by timing how fast 175 ml of water percolated into the soil from a cylinder placed 5 cm into the undisturbed soil surface.

2.5. Data analysis

The programme *Statistica* 12.0 (StatSoft Inc., 2004) was used to perform all statistical analyses. One-Way ANOVAs were used followed by Bootstrap post hoc tests to determine significant differences ($p < 0.05$) among treatments in species and growth form density and plant density, and abiotic variables. Bootstrapping was chosen as it was seen to have higher accuracy than other post hoc tests available (D. Nel, pers. comm.; Efron and Tibshirani, 1993). Sørensen's Similarity Index (%) and Simpson's Diversity Index (1-D value) were used to determine differences in similarity and diversity among treatments, (Vosse et al., 2008). Surface cover differences among treatments were assessed through the conversion of Braun-Blanquet scores to percentage values (Agenbag et al., 2008). To determine significant differences in species and plant density between the above-ground vegetation and seed bank of each treatment, Wilcoxon matched pairs tests were used.

3. Results

The total number of plant species found in the above-ground vegetation was 84, of which 70 were native. Of these native species, 8 were unique to the reference fynbos, 21 to the areas previously under 30 year old pines and 10 to the areas previously under 50 year old pines. Fourteen native species were found in all 3 treatments. In comparison, the total number of plant species found in the soil seed bank was 78 and consisted of 47 native species. Of these native species, 10 were unique to the reference fynbos, 11 to the areas previously under 30 year old pines and 2 to the areas previously under 50 year old pines. Nine native species were found in all 3 treatments. As the four alien species that emerged from the control seedling trays were also observed in the field, they were included in the soil seed bank analysis.

3.1. Native and alien species composition

A greater proportion of native species was found in the above-ground vegetation composition of the reference fynbos and areas previously under 30 year old pines compared to the areas previously under 50 year old pines. Above-ground vegetation in the reference fynbos was dominated by native species (99.2% of individuals and 91.6% of species recorded). There was also a high proportion of native species recorded in the areas previously under 30 year old pines (86.8% of individuals and 81.7% of species) whereas the areas previously under 50 year old pines had the lowest proportion of native species (51.1% of individuals and 77.5% of species).

The proportion of native species found in the seed bank composition of the reference fynbos and areas previously under 30 year old pines was higher than the areas previously under 50 year old pines. The highest proportion of native species was recorded in the reference fynbos (72.4% of individuals and 60% of species) and areas previously under 30 year old pines (68.3% of individuals and 62.7% of species). The seed bank of the areas previously under 50 year old pines had the lowest proportion of native species (34.9% of individuals and 38.5% of species).

3.2. Differences in species diversity

Above-ground vegetation native species density (number of species per unit area) in the reference fynbos and areas previously under 30 year old pines was significantly higher than in the areas previously under 50 year old pines, as was the native species density of the areas previously under 30 year old pines compared with the reference fynbos ($F_{2,78} = 50.52$, $p < 0.01$; Fig. 1a; see supplementary material – Fig. S2). Alien species density of the above-ground vegetation in the areas previously under 30 and 50 year old pines were significantly higher than in the reference fynbos ($F_{2,78} = 3.96$, $p < 0.05$; Fig. 1a; see supplementary material – Fig. S2).

Seed bank native species density in the reference fynbos and areas previously under 30 year old pines were significantly higher than in the areas previously under 50 year old pines ($F_{2,78} = 37.58$, $p < 0.01$; Fig. 1b; see supplementary material – Fig. S2).

Above-ground native vegetation plant density (number of individuals per unit area) in the reference fynbos and areas previously under 30 year old pines was significantly higher than in the areas previously under 50 year old pines ($F_{2,78} = 26.02$, $p < 0.01$; Fig. 1c). Similarly, native seed bank plant density in the reference fynbos and areas previously under 30 year old pines was significantly higher than in the areas previously under 50 year old pines ($F_{2,78} = 9.82$, $p < 0.01$; Fig. 1d).

The number of native individuals in the above-ground vegetation and seed bank mostly comprised of an even spread and higher abundance of native species with certain natives dominating in the reference fynbos and areas previously under 30 year old pines (e.g. *Metalasia densa*, *Cliffortia ruscifolia* and *Anthospermum aethiopicum*) (see supplementary material – Fig. S3). In comparison, certain alien species in the above-ground vegetation and seed bank dominated the areas previously under 50 year old pines.

The native and alien above-ground vegetation species diversity was similar across treatments (Table 1). However, the Simpson diversity indices showed that native and alien seed bank species diversity of the areas previously under 50 year old pines was lower compared to the reference fynbos and areas previously under 30 year old pines, which again were similar (Table 1).

The Sørensen similarity index (%) showed that the highest similarity for native species of the above-ground vegetation and seed bank was between the reference fynbos and areas previously under 30 year old pines (Table 1). Conversely, similarity was lowest between either the reference fynbos and areas previously under 50 year old pines or the areas previously under 30 and 50 year old pines (Table 1).

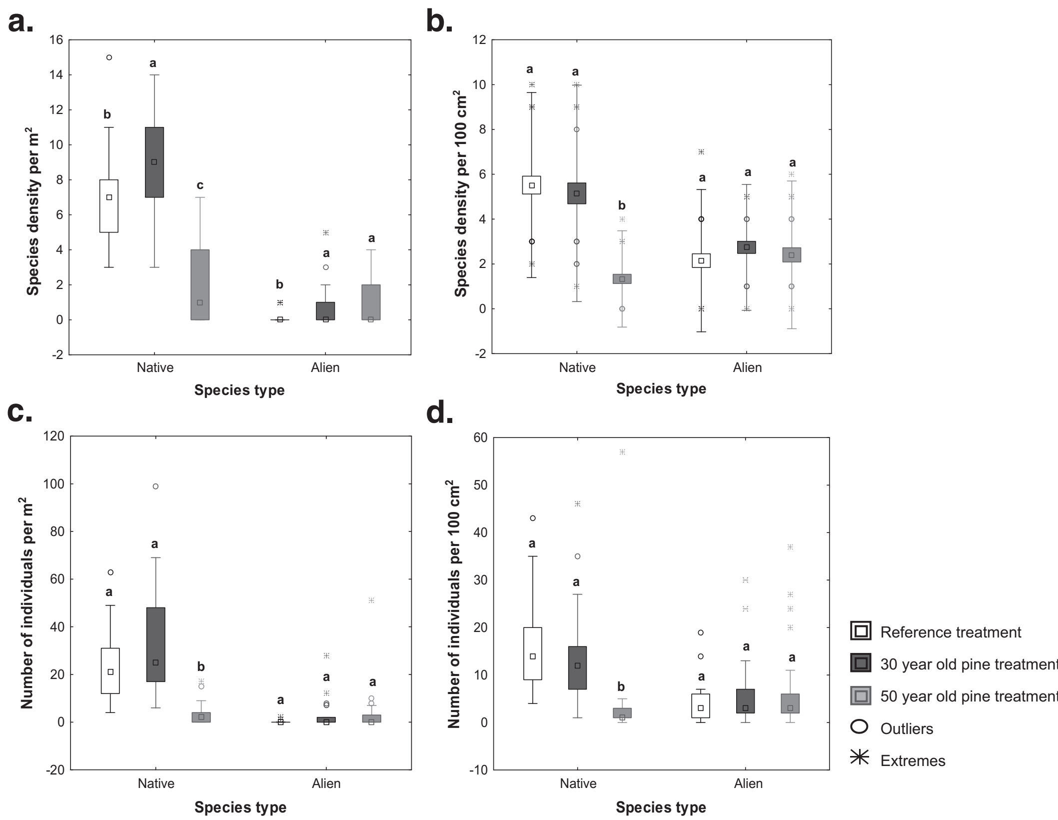

Fig. 1. The species density of the native and alien species for each treatment in the (a) above-ground vegetation (median ± quartiles) and (b) seed bank (mean ± SD), and the plant density of the native and alien species for each treatment in the (c) above-ground vegetation and (d) seed bank (median ± quartiles). The alphabetical letters a, b and c indicate significant differences recorded using a One-way ANOVA followed by a Bootstrap post hoc test.

The areas previously under 30 year old pines consistently had the highest number of unique native species in both the above-ground vegetation and seed bank (see supplementary material – Fig. S4; Appendix A). The greatest number of native species shared was between reference fynbos and areas previously under 30 year old pines in both the above-ground vegetation and seed bank (see supplementary material – Fig. S4; Appendix A). The areas previously under 50 year old pines had the highest number of unique alien species in the seed bank (see supplementary material – Fig. S4).

Relative seed bank native species density was significantly higher than the above-ground vegetation for the areas previously under 50 year old pines ($Z = 2.03$, $p = 0.042$). Conversely, relative seed bank native species density was significantly lower than the above-ground vegetation of the areas previously under 30 year old pines ($Z = 4.24$, $p < 0.01$). Relative seed bank alien species density was significantly higher than the above-ground vegetation across all three treatments (reference fynbos: $Z = 4.11$, $p < 0.01$; 30 year pine: $Z = 3.94$, $p < 0.01$; 50 year pine: $Z = 4.65$, $p < 0.01$). The relative plant density followed a similar pattern to relative species density across all three treatments.

Table 1
The differences in native and alien species diversity and similarity among the three different treatments of the above-ground vegetation and soil seed bank.

	Above-ground vegetation		Seed bank	
	Native	Alien	Native	Alien
Treatment:	Simpson Diversity Index			
Reference	0.92	0.67	0.91	0.87
30 year old pine	0.94	0.66	0.93	0.89
50 year old pine	0.95	0.7	0.78	0.73
Treatment:	Sørensen Similarity Index (%)			
Reference vs 30 year old pine	60.5	16.7	61.5	75.7
Reference vs 50 year old pine	47.8	40	46.8	61.9
30 year old pine vs 50 year old pine	46.9	44.4	45.8	58.5

3.3. Differences in diversity by growth form

Across treatments, above-ground vegetation was dominated by long-lived perennial shrub species (Fig. 2a,c; Appendix A). In contrast, the seed bank was dominated mostly by short-lived annual herbs and geophytes, and long-lived perennial shrubs and perennial graminoids (Fig. 2b,d; Appendix A). Similar patterns in growth form density (number of growth forms per unit area) were observed for above-ground vegetation and seed bank growth form plant density (see supplementary material – Fig. S5).

Above-ground vegetation growth form density in the reference fynbos and areas previously under 30 year old pines was significantly higher than in the areas previously under 50 year old pines for native perennial shrub, annual graminoid, annual herb and geophyte growth forms (Table 2). Alien growth form density in the above-ground vegetation was significantly higher in the areas previously under 30 and 50 year old pines for the perennial shrub and annual graminoid growth forms (Table 2).

Seed bank growth form density in the reference fynbos and areas previously under 30 year old pines was significantly higher than in the areas previously under 50 year old pines for the native perennial shrub, annual herb, perennial graminoid and geophyte growth forms (Table 3). Conversely, alien perennial shrub growth form density in the areas previously under 50 year old pines was significantly higher than in the reference fynbos and areas previously under 30 year old pines ($F_{2,78} = 9.3$, $p < 0.01$; Fig. 2d).

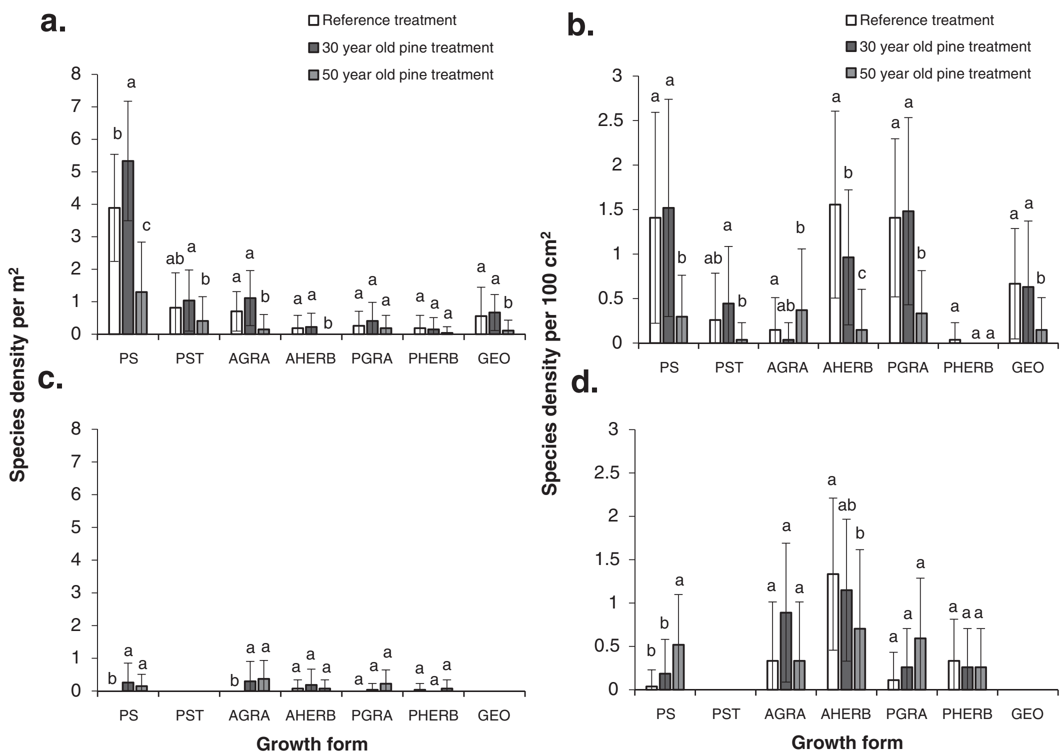

Fig. 2. The average species density of native species in (a) above-ground vegetation and (b) seed bank; alien species in the (c) above-ground vegetation and (d) seed bank. Error bars indicate 1 standard deviation. The alphabetical letters a, b and c indicate significant differences recorded using a One-way ANOVA followed by a Bootstrap post hoc test. PS = Perennial shrub, PST = Perennial shrublet, AGRA = Annual graminoid, AHERB = Annual herb, PGRA = Perennial graminoid, PHERB = Perennial herb, GEO = Geophyte.

3.4. Abiotic differences

In all three treatments, the total surface cover was dominated by bare ground and rock, typical of the first year post-fire. The reference fynbos and areas previously under 30 year old pines had a higher proportion of plant litter and vegetation cover compared to the areas previously under 50 year old pines (Fig. 3). The areas previously under 50 year old pines however had a much higher proportion of pine debris remaining compared to the areas previously under 30 year old pines.

There were few significant differences for the abiotic variables recorded among the three treatments (Table 4). The areas previously under 30 year old pines had significantly higher pH compared to the reference fynbos and areas previously under 50 year old pines ($F_{2,42}$ = 3.35, $p < 0.05$; Table 4). Soil temperature (°C) was significantly higher in the areas previously under 30 and 50 year old pines than in the reference fynbos ($F_{2,42}$ = 9.27, $p < 0.01$; Table 4).

4. Discussion

This study contributes to the growing body of literature on the impacts of alien plants on the flora of the Cape Floristic Region, and shows that duration under pine plantations can significantly impact the recovery potential of fynbos. The fynbos previously under pine plantations for 30 years was shown to have similar species diversity and diversity by growth form to the reference fynbos areas. Contrarily, the fynbos previously under 50 year pine plantations showed a dramatic decrease in species diversity and diversity by growth form, indicating that a biotic threshold to recovery had been crossed (Gaertner et al., 2012; Downey and Richardson, 2016). Few abiotic variables differed among treatments suggesting that an abiotic threshold had not been crossed by either pine treatment (Gaertner et al., 2012; Mostert et al., 2016). The higher relative number of alien species in the soil seed bank compared to the above-ground vegetation could be attributed to

Table 2
Growth forms with at least two treatments having significantly greater above-ground vegetation growth form density among the three treatments. REF – reference fynbos treatment, 30YP – 30 year old pine treatment, 50YP – 50 year old pine treatment.

Growth form	Native species			Alien species		
	REF	30YP	50YP	REF	30YP	50YP
PS	40**	40**	–	–	5.06*	5.06**
PST	–	–	–	–	–	–
AGRA	14.6*	14.6**	–	–	4.32*	4.32**
AHERB	3.42*	3.42*	–	–	–	–
PGRA	–	–	–	–	–	–
PHERB	–	–	–	–	–	–
GEO	5.81*	5.81**	–	–	–	–

Significant F values were recorded using a One-way ANOVA followed by a Bootstrap post hoc test (*$p < 0.05$, **$p < 0.01$). Non-significant values as well as where only one treatment had a significantly greater growth form richness (–). PS = Perennial shrub, PST = Perennial shrublet, AGRA = Annual graminoid, AHERB = Annual herb, PGRA = Perennial graminoid, PHERB = Perennial herb, GEO = Geophyte.

Table 3
Growth forms with at least two treatments having significantly greater seed bank growth form density among the three treatments. REF – reference fynbos treatment, 30YP – 30 year old pine treatment, 50YP – 50 year old pine treatment.

Growth form	Native species			Alien species		
	REF	30YP	50YP	REF	30YP	50YP
PS	11.89**	11.89**	–	–	–	–
PST	–	–	–	–	–	–
AGRA	–	–	–	–	–	–
AHERB	21.44**	21.44**	–	–	–	–
PGRA	9.45**	9.45**	–	–	–	–
PHERB	–	–	–	–	–	–
GEO	6.36**	6.36**	–	–	–	–

Significant F values were recorded using a One-way ANOVA followed by a Bootstrap post hoc test (*$p < 0.05$, **$p < 0.01$). Non-significant values as well as where only one treatment had a significantly greater growth form richness (–). PS = Perennial shrub, PST = Perennial shrublet, AGRA = Annual graminoid, AHERB = Annual herb, PGRA = Perennial graminoid, PHERB = Perennial herb, GEO = Geophyte.

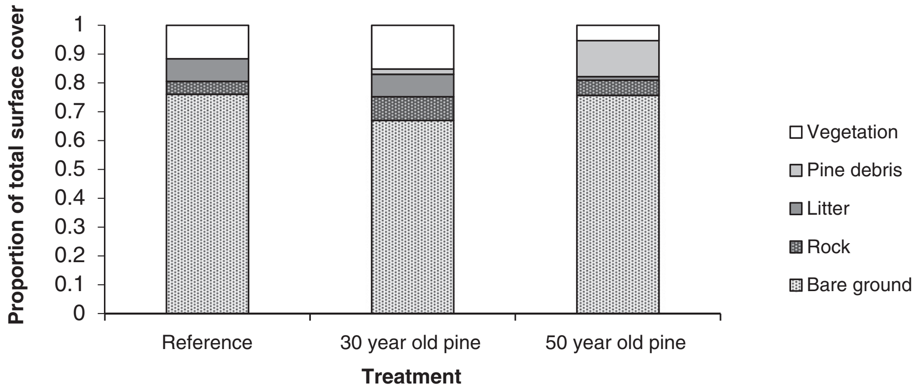

Fig. 3. The relative contribution of total vegetation, pine debris, litter, rock and bare ground to the total soil surface cover of each treatment. The low contribution of vegetation to total surface cover is due to the recent occurrence of a fire that burnt through all three treatments in summer 2015.

the high proportion of short-lived alien species which thrive briefly following disturbance events.

In areas previously under 30 year old pine plantations, it appears that there were sufficient long-lived native species recruited from the seed bank to outcompete alien species. In areas previously under pine plantations for 50 years, however, short-lived alien species were able to dominate due to low numbers of long-lived native species in the depleted soil seed bank (Richardson and Van Wilgen, 1986). This indicates the possible crossing of a biotic threshold (Gaertner et al., 2012; Downey and Richardson, 2016). These areas are vulnerable to both soil erosion and further invasion by alien species, therefore preventative and control measures should be implemented for restoration (Holmes and Richardson, 1999; Petersen et al., 2007).

Higher relative alien species and plant density in the soil seed bank compared to the above-ground vegetation across all three treatment areas further illustrates that the alien species composition was dominated by short-lived species. Higher relative native species and plant density in the above-ground vegetation compared to the soil seed bank in areas previously under 30 year old pine plantations illustrates that the native species composition was dominated by longer-lived species.

With the presence of some native species in the seed bank, areas previously under pine plantations for 30 years have the potential to recover both species diversity and diversity by growth form. These findings concur with a study by Holmes (2001) which showed that following the clearing of 30 year old pine-invaded areas, a native seed bank with high recovery potential remained. As pine plantation duration increased to 50 years, however, recovery potential was drastically reduced. As the vegetation matures post-fire, the similarity between restored pine plantation areas and natural vegetation areas is likely to increase (Holmes and Marais, 2000). Areas impacted by longer pine rotations (40–50 years) may take longer to recover along this trajectory without active restoration interventions.

Native perennial shrub, shrublet and graminoid species density and plant density was drastically reduced in the areas previously under 50 year-old pine plantations. Included in these reduced growth forms are species that either do not rely on the soil seed bank for recruitment (e.g. serotinous species) or do so minimally (e.g. resprouter species) (Richardson and Van Wilgen, 1986; Holmes and Richardson, 1999). Serotinous species, such as proteas, store their seeds in fire-proof cones in the canopy, with the seeds only released following fire events (Kraaij and Van Wilgen, 2014). Resprouter species usually do not produce as many seeds as do reseeder species as their survival strategy allows them to both resprout from storage organs as well as recruit from the seed bank following disturbances (Kraaij and Van Wilgen, 2014).

Table 4
A comparison of the abiotic variables recorded among treatments in the field (mean ± SD).

Abiotic variable	Reference treatment	30 year old pine treatment	50 year old pine treatment
Infiltration rate (cm/min)	1.06 ± 1.42^a	1.91 ± 2.34^a	0.39 ± 0.27^a
pH	5.24 ± 0.28^b	5.49 ± 0.3^a	5.12 ± 0.57^b
Soil temperature (°C)	29.75 ± 0.93^b	32.54 ± 2.54^a	31.49 ± 1.52^a
Volumetric water content (%)	4 ± 1.25^a	4.8 ± 3.36^a	5.33 ± 2.32^a

a & b indicate significant differences recorded using a One-way ANOVA analysis followed by a Bootstrap post hoc test.

Felled pine plantations were shown to have minimal impact on soil abiotic variables, with only soil temperature and pH showing significant differences. This concurs with a study in the renosterveld shrublands of the Cape Floristic Region by Heelemann et al. (2013) that showed felled pine plantations usually do not have a significant effect on soil abiotic variables. Felled pine plantations usually maintain the acidic soil pH found in uninvaded areas, giving fynbos species a good chance of successfully recovering (Heelemann et al., 2013). In this study, the differences observed in soil temperature and pH did not appear to affect the patterns in species and growth form composition. Soil temperatures in both areas previously under 30 and 50 year old pine plantations were higher than the reference fynbos but they showed different levels of recovery. Areas previously under 30 year old pine plantations had the highest pH but showed greater recovery than those under 50. Further analyses are needed to confirm the relationship between the soil chemistry (e.g. nutrient differences) and species composition.

Older pine plantations have been shown to substantially reduce native species diversity and diversity by growth form as well as native plant density (Richardson and Van Wilgen, 1986; Richardson et al., 1989; Holmes and Foden, 2001). Active restoration, i.e. re-introductions, are required to return the missing long-lived growth forms and species without soil stored seed banks to areas previously under plantations for extended periods (over 30 years) (Holmes and Foden, 2001; Hitchcock et al., 2012). If biotic and potentially abiotic barriers in longer duration pine plantations are too significant and impede restoration efforts, alternative management goals (such as rehabilitation) may be needed instead (Suding et al., 2004; Gaertner et al., 2012). At Helderberg Nature Reserve, progress has already been made in the areas previously under 50 year old pine plantations as the management teams have successfully re-introduced locally sourced serotinous protea species (O. Wittridge, pers. comm.). The active re-introduction efforts will help to restore the structural and functional heterogeneity to the recovering ecosystem which is needed to maximise the return of biodiversity as well as ecosystem function and resilience (Holmes and Richardson, 1999).

In comparison to pines, alien *Acacia* invasions also negatively impact on native species and growth form composition, however they additionally have a substantial impact on the abiotic conditions (e.g. through soil nutrient enrichment by nitrogen fixation) and build up dense soil seed banks of their own (Holmes and Cowling, 1997; Holmes, 2002; Richardson and Kluge, 2008; Gaertner et al., 2012; Mostert et al., 2016). As duration of invasion increases, the *Acacia*'s ability to shift the ecosystem into alternative states (via both biotic and abiotic thresholds) results in invaded areas becoming very difficult to restore due to positive feedback systems which maintain invaded areas in degraded states (Gaertner et al., 2012; Mostert et al., 2016). However, as with pine species, if the trees are cleared before the biotic thresholds are passed, these areas retain a high recovery potential via the native soil seed banks (Holmes and Cowling, 1997; Fourie, 2008; Gaertner et al., 2012).

In terms of the closing of future plantations in the Western Cape as well as removal of invading pines, emphasis should be placed on felling pines before the 40–50 year age limit during which the native seed bank subsequently becomes depleted (Richardson and Van Wilgen, 1986; Richardson et al., 1989; Holmes and Foden, 2001; Van Wilgen, 2015). The presence of a substantial native seed bank greatly improves the recovery potential of fynbos and averts the need for intensive active restoration, which is costly and time-consuming. Long term follow-up control of alien species will also need to be implemented so as to deplete the alien seed bank and maximise the survival of restored native species.

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