Impacts of an invasive alien Proteaceae on native plant species richness and vegetation structure

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A R T I C L E   I N F O

A B S T R A C T

The influence of invasive alien plants on plant community structure and above ground biomass in their novel range is poorly understood, as the magnitude and direction of these effects are often species and ecosystem specific. Here we compared community metrices of native plants and soil properties between study sites invaded by *Hakea drupacea*, uninvaded sites and cleared sites (sites formerly invaded by *H. drupacea*). A total of 129 plant species belonging to 75 genera were recorded across all study sites. Invasive *Acacia saligna, A. longifolia, A. cyclops* (Fabaceae) and *Leptospermum laevigatum* (Myrtaceae) co-occurred with *H. drupacea* in the invaded sites. Overall plant species richness, which constituted higher number of native plant species, was recorded in uninvaded sites compared to invaded and cleared sites. Plant species composition was similar between uninvaded and cleared sites, but species composition recorded in uninvaded and cleared sites were significantly different from species composition recorded at invaded sites. Litter depth was significantly higher in invaded sites compared to uninvaded and cleared sites. *Hakea drupacea* did not affect soil properties in invaded sites. Here we show that *H. drupacea* probably reduces the diversity of native plant species especially in invaded sites probably through the effect of litter production and canopy cover, pointing to a beneficial effect of removal of *H. drupacea*. We encourage active restoration of sites invaded by *H. drupacea* at early stages of invasion before the plants become established and suppress the growth of native species.

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1. Introduction

Biological invasion is one of the leading factors driving biodiversity loss through a direct effect on community structure and composition (Belnap and Philips 2001; Mangachena and Geerts 2017; Mangachena and Geerts 2019; Le Roux et al., 2020), as well as modification of ecosystem processes at various scales (Ehrenfeld 2003; Levine et al., 2003). Invasive alien plant species (IAPs) are often characterized by traits and ecophysiological functions such as high growth rate and deep roots (Liao et al., 2008; Morris et al., 2020), which aid the ability of IAPs to invade new ecosystems and out-compete native species. Since species traits may influence ecosystem processes (Hobbie 1992; Van Breemen and Finzi 1998), IAPs may alter soil properties and biogeochemical cycles (Ehrenfeld and Scott, 2001) as well as other abiotic conditions that typically impact the growth of both native and invasive alien species in invaded areas (Wilson et al. 2020).

Above ground biomass and ecosystem net primary productivity often increase in invaded versus uninvaded areas (Ehrenfeld 2003) due to altered nitrogen fixation rates and increased litter decomposition in invaded areas. While research has addressed changes in soil carbon and nitrogen, little attention has been paid to other soil elements (but see Blank and Young 2002; 2004; Stefanowicz et al., 2017) and how these influence the growth and development of native species. In a review by Hirsch et al. (2020), they indicated that while soil pH reduced significantly in areas invaded by *Eucalyptus camaldulensis* Dehnh., there was a significant increase in litter accumulation as well as changes in soil hydrological properties. These modifications to soil elements and other environmental components often result in a decline in the development and diversity of native species in invaded areas (Kerr and Ruwanza, 2016; Hirsch et al., 2020). In the Core Cape Floristic Region (CCFR) of South Africa, where the dominant native plant species are shrubs, the presence of invasive alien trees and shrubs may have a significant and varied impact on different soil elements as well as other abiotic conditions in different vegetation types in this region.

The CCFR − one of the richest biodiversity hotspots in the world − is home to over 9300 plant species (Linder 2005; Goldblatt and

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Manning 2002, Manning and Goldblatt 2012), 68% of which are endemic to the region (Manning and Goldblatt, 2012). Most of the flowering plants in the fynbos biome of the CCFR depend on fire at specific intervals for reproduction (Bond and van Wilgen, 1996). Also, fire is critical for the recycling of soil nutrients (Le Maitre and Midgley, 1992) and this partly influences species distribution in the CCFR. Biological invasion is one of the major threats to native plant diversity in the CCFR (Le Maitre et al., 2000) as up to 70% of the natural fynbos range is invaded by alien plants (Rouget et al., 2003). Invasive species of the genus *Hakea* Schrad. & J.C.Wendl. (*H. drupacea* (C.F. Gaertn.) Roem. & Schult., *H. gibbosa* Cav. and *H. sericea* Schrad. & J.C. Wendl.), are native to Australia and were introduced to South Africa between 1840 and 1860 (Shaughnessy, 1986; Richardson et al., 1987). Fire aids the spread of *Hakea* in this ecosystem as all three invasive *Hakea* species rely on fire for seed regeneration and dispersal (Richardson et al., 1987). In contrast, the spread of the naturalized *H. salicifolia* (Vent.) B.L.Burtt is not driven by fire (Moodley et al., 2014, Moodley et al., 2016). Invasive alien Proteaceae, especially *Hakea*, have larger seed banks and higher seed dispersal rates compared to native Proteaceae (Richardson et al., 1987). This contributes to the success of alien *Hakea* species in the CCFR and consequently this genus is the only Proteaceae genus overrepresented (Moodley et al., 2013). Also, invasive *Hakea* species are well adapted to the nutrient poor soil of the CCFR (Wilson et al., 2020), which also aid their persistence in this region.

Hakea drupacea, formerly known as *H. suaveolens* R.Br., was introduced to South Africa as a hedge plant to prevent animals from entering pine plantations and to stabilize sand dunes on the Cape Flats (Fugler, 1982). This invasive alien plant species is classified as a category 1b invader under the current NEM:BA regulations (NEM: BA 2016). It is a localized and abundant invader (Rouget et al., 2004) that forms dense, impenetrable stands that can suppress native vegetation (Fugler, 1982; Richardson and Van Wilgen, 2004; Erckie, 2014). *Hakea drupacea* is a granite specialist with a limited distribution range compared to the more widespread generalist congeners that occur mostly on the sandstone-derived soils (Wilson et al., 2020). *H. drupacea* is serotinous, has two-winged seeds that are covered in woody capsules and they are primarily dispersed by wind. Similar to *H. salicifolia* and unlike the more widespread *H. sericea* and *H. gibbosa* that have been studied extensively in this region (van Wilgen and Richardson, 1985; Richardson 1985; Richardson et al., 1987; Kluge and Neser, 1991, Gordon and Fourie 2011), *H. drupacea* has received little or no research attention, and the impact of this species on ecosystem soil properties and native vegetation structure is largely unknown. This may be because *H. drupacea* is the *Hakea* with the smallest distribution range in the CCFR (Richardson et al., 1987). However, fynbos generally occurs on low-nutrient soil (Wilson et al., 2020) and *H. drupacea* could expand its ecological range in low-nutrient soil if left unchecked.

Here we investigate whether the presence of *H. drupacea* affects native plant species richness, litter depth as well as the soil properties of invaded areas compared to uninvaded and cleared areas. Specifically, we aimed to determine whether: (1) *H. drupacea* abundance influences species richness and composition of native fynbos and other alien plant communities? (2) the height and canopy cover of *H. drupacea* influences leaf litter production; and (3) *H. drupacea* alters soil chemical and physical properties in invaded areas.

2. Materials and Methods

2.1. Study area

This study was conducted at 12 sites across the invasive range of *H. drupacea* within the Cape Peninsula and the Overberg region of the Western Cape Province, South Africa (Fig 1, Supplementary Table 1).

The area experiences a Mediterranean-type climate with hot dry summers and cold wet winters. Average annual rainfall is about 300 mm of which most falls during winter months (Lamprecht et al., 2006). The mean maximum temperature ranges between 15°C and 27°C for the cool and warm months, respectively. Soils of this region are classified as well-drained, acidic and nutrient-poor (Rebelo et al., 2006).

2.2. Experimental design

Twelve plots each measuring 5 × 5 m (25m²) were located in invaded and adjacent uninvaded sites (Supplementary Table 1). Due to low availability of cleared sites near invaded and uninvaded sites for comparative purposes, only three plots represented cleared sites, comprising a total of 27 study plots for invaded, uninvaded and cleared sites following Barney et al. (2015). Invaded sites referred to those predominantly invaded by *H. drupacea* with a cover of at least 50% *H. drupacea* and uninvaded sites constituted sites where *H. drupacea* was absent. Invaded sites considered were those with established invasions since impacts could be assessed with a higher level of confidence (Tererai et al., 2013). But due to lack of sites with established *H. drupacea* invasions, three more recently invaded sites were included. In cases where a site free of *H. drupacea* could not be obtained, few *H. drupacea* individuals were allowed to occur in uninvaded plots with low percentage cover (1-5 %), since IAPs at such low density have little or no effects upon native vegetation composition and structure (Hejda and Pyšek, 2006; Catford et al., 2012). Cleared sites referred to recovered sites where *H. drupacea* and other alien plants had been removed.

Sites had similar ecological conditions i.e. similar topography (altitude, slope, aspect), vegetation, soil type and land-use history (Hejda and Pyšek, 2006; Barney et al., 2015). A distance ranging between 20 m and 50 m was maintained between invaded and uninvaded plots. This ensured that uninvaded or cleared plots were not affected by impacts such as shade from the invader.

2.3. Vegetation survey

Vegetation surveys were conducted on all study sites between July and November 2016. For each site, plots of 5 × 5 m were temporarily demarcated using a measuring tape and plot corners marked with steel rods. The centroid of each plot was marked using a hand-held Global Positioning System (Garmin GPS map 60CSx).

All individual plant species encountered in each plot were counted and identified up to species level where possible (Supplementary Table 2). They were assigned to their origin status (alien or native) and growth forms (see Mangachena and Geerts, 2019). We classified both native and alien plant species as trees, shrubs, creepers, herbs, geophytes and graminoids (sedges, grasses and restioids (plants belonging to family Restionaceae)). Plant specimens that could not be identified in the field were pressed for identification at the Compton Herbarium, Kirstenbosch Botanical Gardens. A measuring tape was used to measure the height of all plant species and that of large trees were visually estimated. Woody plants found along plot margins were included if any of their parts fell inside the plot. In such cases, only the height of the part found in the plot was measured. For multi-stemmed plants, only the height of the tallest stem was recorded. Percentage canopy cover for each woody plant species was visually estimated and the level of invasion for each plot was characterized by the percentage cover of *H. drupacea*. Percentage cover for grasses was estimated according to Braun-Blanquet (1932) cover classes as follows: 5: 75-100%; 4: 50-75%; 3: 25-50%; 2: 5-25%; 1: 1-5% cover. We recorded the presence and absence of leaf litter and estimated the depth of accumulated leaf litter in five subsamples per plot (Barney et al., 2015).

2.4. Soil sampling

Soil sampling was done at the same time and on the same plots as the vegetation survey. Five soil samples from four edges and the center of each plot were collected. Soil was sampled following 48 hours without rain (Barney et al., 2015). Any surface litter present was removed, and the top 10 cm of the soil was collected with a standard soil auger. Soil samples from each plot were combined and mixed thoroughly to form a bulk sample for the plot. Soil was sieved with a 2 mm mesh to remove large particles and stones. Smaller fragments and debris were removed by hand. Representative soil samples of 500 g for each plot were placed in labelled, clean, air-proof polythene plastic bags.

Soil samples were analysed for soil texture, soil moisture, pH_{KCL}, organic carbon (C), nitrogen (N), phosphorus (P), potassium (K), calcium (Ca), magnesium (Mg) and sodium (Na). Nitrogen content was determined following the Kjeldahl method (Bremner & Mulvaney 1982). Phosphorus, K, Ca, Mg, Na and C were determined by using 1% citric acid. We weighed and oven-dried soil samples at 105° C for 48 hours and re-weighed to obtain percent soil moisture. The soil analysis was carried out at the Western Cape Department of Agriculture, Elsenburg Laboratory, following standard procedures used by member laboratories of the inter-laboratory control scheme Agri Laboratory Association of Southern Africa (AgriLASA) and methods of the Association of Official Analytical Chemists (AOAC).

2.5. Data analysis

The Shapiro-Wilk's test was performed on all data to test for normality assumptions. Species richness and composition, as well as litter depth were the main response variables with invasion as the main factor. Species richness was calculated as the number of plant species per sampling plot. The differences in plant species richness between invaded (n = 12), uninvaded (n = 12) and cleared (n = 3) sites was tested using one-way ANOVA as species richness conformed to normality assumptions. Species richness of alien plants and litter depth did not fit normal distributions and thus, we conducted a non-parametric Kruskal-Wallis test to determine differences in species richness of alien plant species between invaded, uninvaded and cleared sites. A Dunn's test was used to determine significance among paired study sites.

We also conducted a non-parametric Kruskal-Wallis test to determine differences in litter depth between invaded, uninvaded and cleared sites. The relationship between litter depth and canopy cover of *H. drupacea* in invaded sites was tested using a linear regression. To determine differences in percentage canopy cover between invaded and uninvaded sites, we conducted a Mann-Whitney U test. Similarly, a Mann-Whitney U test was used to determine differences in height of *H. drupacea* and dominant native species in uninvaded sites.

To assess differences in plant species composition among invaded, uninvaded and cleared sites, we used non-metric multi-dimensional
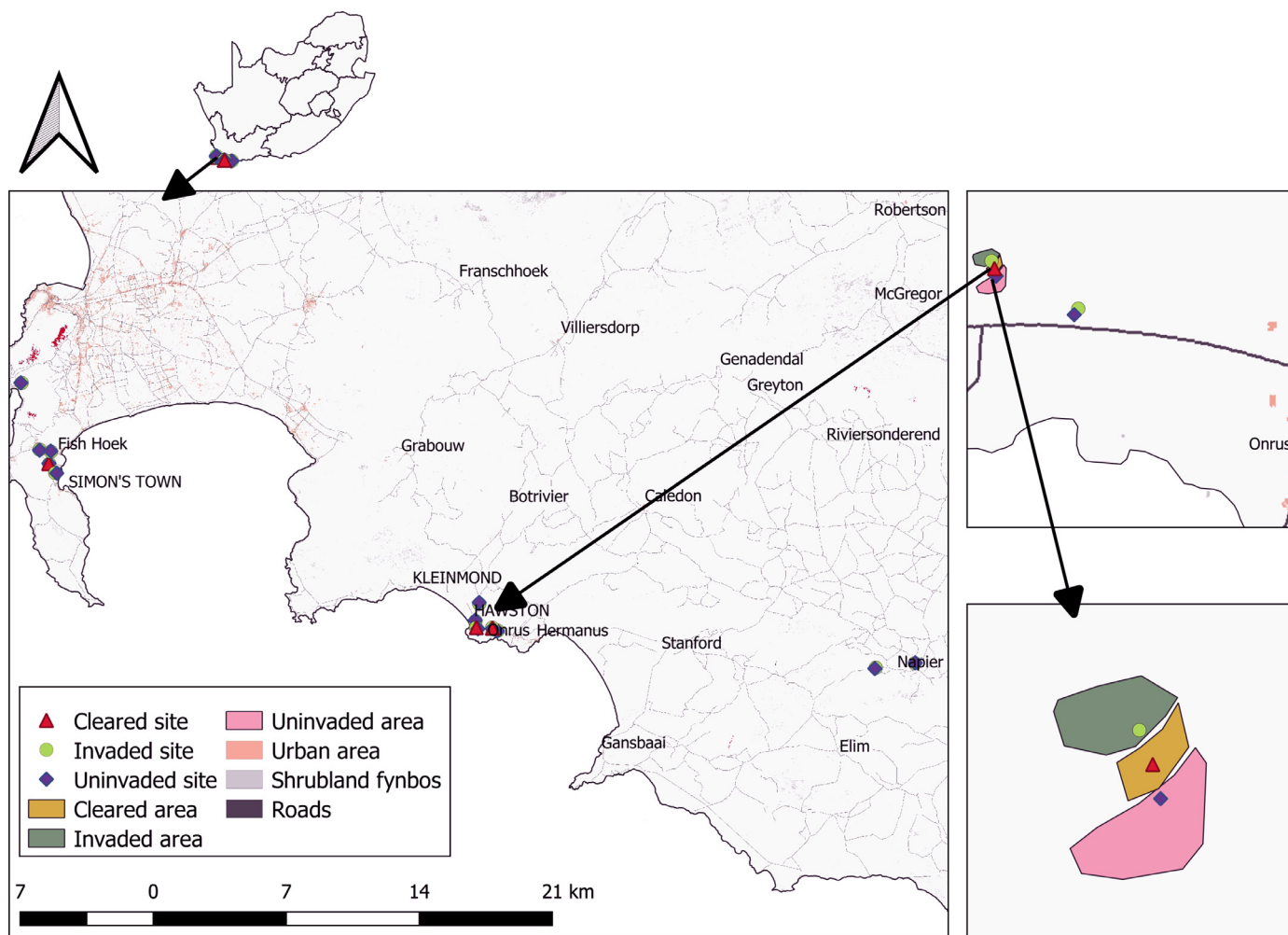

Fig 1. Study area and distribution of study sites with detailed example of invaded, uninvaded and cleared plot area

scaling ordination (nMDS) with the "vegan" package in R. Permutation Analysis of Variance (PERMANOVA) with 999 permutation was conducted to compare among-group similarities and assess significance by permutation. PERMANOVA was conducted using the Jaccard similarity index obtained from species presence/absence data. All analysis were conducted using R version 3.6.1 (R Core Team, 2017).

3. Results

A total of 129 plant species belonging to 35 families and 75 genera were recorded (Supplementary Table 2). 49 plant species were recorded in invaded sites, 94 plant species in the uninvaded sites and 27 species in the cleared sites. Species recorded in invaded sites comprised of 41 (84%) native and 8 (16%) alien, while 89 (95%) native and 5 (5%) alien were recorded in uninvaded sites and 26 (96%) native and 1 (4%) alien plant species were recorded in cleared sites. Percentage ground cover of native shrubs and creepers were higher in uninvaded sites, while alien trees dominated the invaded sites and native shrubs increased significantly in cleared sites (Fig. 2a).

The two most dominant plant species in uninvaded and cleared sites were *Passerina corymbosa* Eckl. ex C.H.Wright (Thymelaeaceae) and *Erica* L. species (Ericaceae) but were absent in sites with low invasion where *H. drupacea* (1- 5% cover) occurred. A native species, *Colpoon compressum* P.J. Bergius co-existed mostly with the invasive
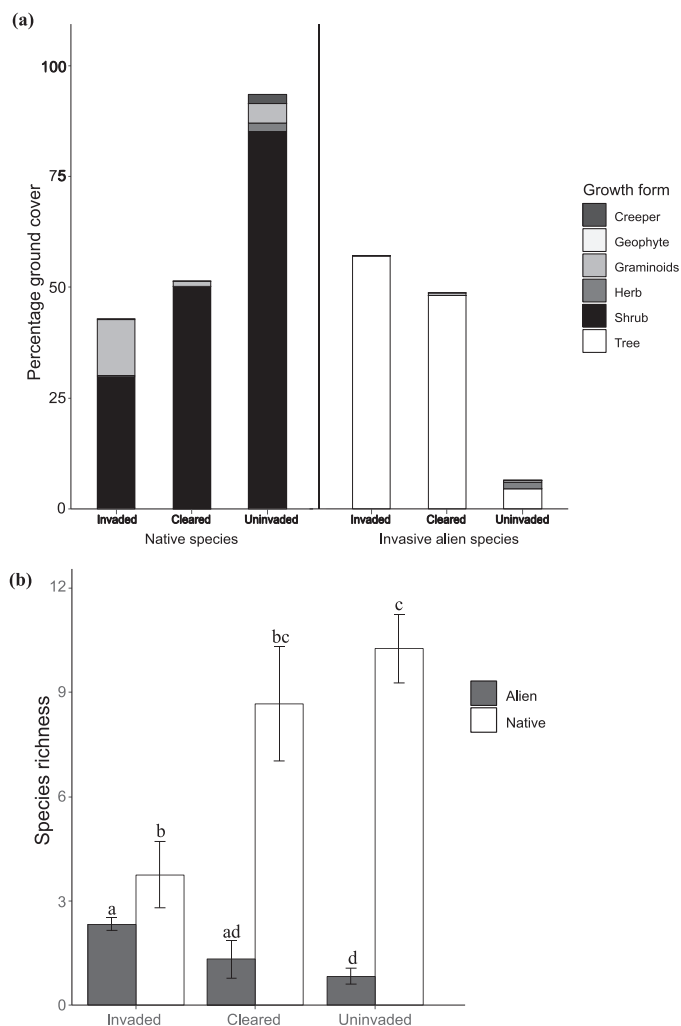
H. drupacea. Few stands of other IAPs including *Acacia saligna* (Labill.) H.L.Wendl., *A. longifolia* (Andr.) Willd., *A. cyclops* A.Cunn. ex G.Don (Fabaceae) and *Leptospermum laevigatum* (Gaertn.) F.Muell. (Myrtaceae) co-occurred with *H. drupacea* in the invaded sites.

There was a significant difference in plant species richness among the study sites ($F_{2,24}$ = 6.217, P = 0.007, Fig. 2b), specifically between the invaded and uninvaded sites (P = 0.006) following post-hoc test. Higher species richness of native plants was recorded in uninvaded sites compared to invaded sites ($F_{2,24}$ = 10.31, P = 0.0006). Also, higher species richness of IAPs was recorded in invaded sites compared to uninvaded and cleared sites (Kruskal-Wallis Chi squared = 12.701, P = 0.002, df = 2).

Litter depth was significantly lower in uninvaded sites (1.48 ± 0.1 cm) and cleared sites (0.27 ±0.05 cm) compared to invaded sites (11.55 ± 1.4 cm) where litter depth was almost 5 times that of uninvaded sites (Kruskal-Wallis Chi Square = 19.63, P<0.0001, df = 2, Fig. 3). There was no significant difference in litter depth between cleared and uninvaded sites.

When we compared the height of *H. drupacea* in invaded sites with the height of dominant native plant species in uninvaded sites, *H. drupacea* in invaded sites (mean (±SE) = 3.05 ± 0.34, 4.1 m-0.9 m) was significantly taller than dominant native plant species (mean (±SE) = 0.73 ± 0.11, 1.5 m-0.25 m) in uninvaded sites (Mann-Whitney U test = 138, P < 0.001). In invaded sites, there was a significant difference in the height of *H. drupacea* compared to other invasive alien plant species (mean (±SE) = 1.94 ± 0.39, 6.13 m-0.25 m), with *H. drupacea* dominating in height compared to other IAPs in invaded sites (t = 2.11, P = 0.045, df = 26).

There was a significant difference in canopy cover of *H. drupacea* in invaded sites compared to dominant native plant species in uninvaded sites (Mann-Whitney U test = 6, P = 0.0002), as the percentage canopy cover for *H. drupacea* (mean (±SE) = 63.33 ± 6.7, 90% - 20%) in invaded sites was significantly higher than canopy cover of dominant native species (mean (±SE) = 11.75 ± 3.04, 30% - 1%) in uninvaded sites.

There was a significant difference in plant species composition among the study sites (PERMANOVA $F_{2,24}$ = 3.698, P = 0.001), specifically between uninvaded and invaded sites (P = 0.003) as well as between invaded and cleared sites (P = 0.012). nMDS showed two

Fig 2. (a) Differences in growth forms and (b) mean ±(SE) species richness of native and invasive alien plants recorded among invaded, cleared and uninvaded sites. Bars with different alphabet are significantly different at P < 0.05.
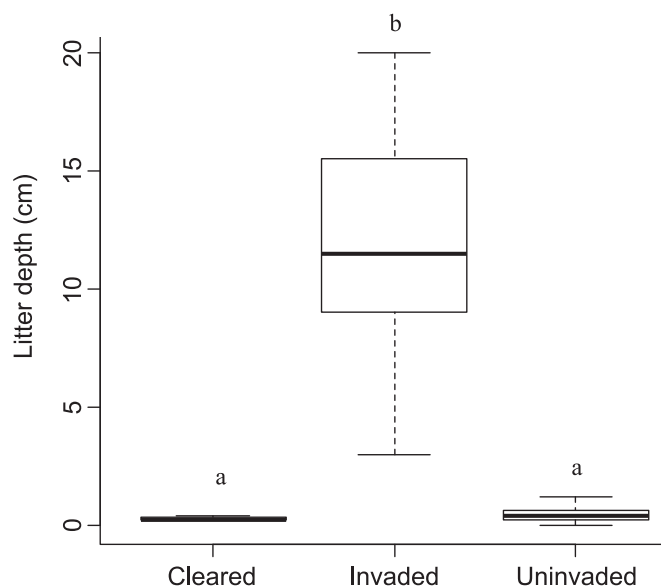
Fig 3. Differences in litter depth between invaded and uninvaded sites. Boxplots display the median with a solid line, 25th and 75th percentiles in the lower and upper boxes, respectively, and the data range is indicated by the whiskers. Bars with different alphabet are significantly different at P < 0.05.
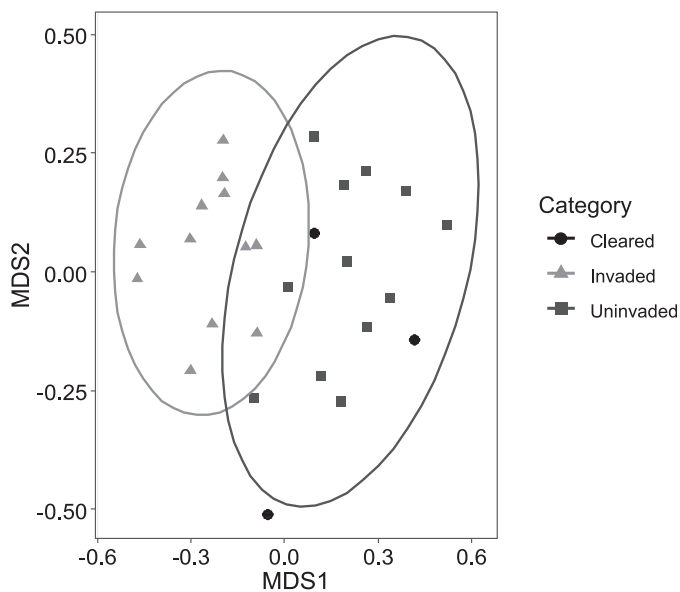
Fig 4. nMDS showing differences in species composition among invaded, uninvaded and cleared sites. Species presence/absence data was used to test for similarity (Jaccard index).

Table 1
Means ± (SE) of soil chemical properties in *Hakea drupacea* invaded sites and adjacent uninvaded sites.

Soil properties	Invaded	Uninvaded	df	t-value	P
Moisture	8.54 ± 2.19	6.23 ± 1.58	22	0.87	0.395
Acidity	1.22 ± 0.14	1.06 ± 0.07	13	1.02	0.328
pH	5.33 ± 0.32	5.39 ± 0.27	22	0.14	0.89
Carbon	2.33 ± 0.25	1.65 ± 0.22	22	2.008	0.057
Calcium	11.32 ± 5.00	8.66 ± 4.19	22	0.407	0.688
Magnesium	1.79 ± 0.23	1.45 ± 0.16	22	1.22	0.24
Phosphorus	9.5 ± 2.79	8.42 ± 1.76	22	0.89	0.38
Potassium	79.08 ± 10.88	59.08 ± 9.38	22	1.39	0.18
Sodium	136 ± 13.56	88.25 ± 29.84	22	1.32	0.2
Nitrogen	0.11 ± 0.02	0.09 ± 0.02	22	0.66	0.52

cleared sites grouped with uninvaded sites and a clear separation between uninvaded and invaded sites (Fig. 4).

3.1. Soil properties

There was no significant difference in soil properties between invaded and uninvaded sites (Table 1). Carbon was slightly higher in invaded compared to uninvaded sites, but this was not statistically significant.

4. Discussion

Here we show that *H. drupacea* significantly reduces native plant species richness in invaded sites, forms a denser canopy and increases litter depth. In a largely treeless ecosystem, like the CCFR, where the dominant native species are shrubs, the presence of invasive alien trees with dense canopies may reduce direct sunlight reaching the understory, impacting the growth and reproduction of understory native vegetation. In a review by Valladares et al. (2016), they highlighted mechanisms by which shade negatively impact the recruitment of plants, especially when reduced irradiance severely limits understory photosynthesis. Also, alien species from regions with similar climates have stronger impacts on native species in invaded areas (Gaertner et al., 2009). For example, the Australian *Acacia* Mill. species account for the highest decline in native plant species in South Africa (Gaertner et al., 2009). Since *H. drupacea* is native to

Australia − a Mediterranean type ecosystem with similar climate as the CCFR − it is therefore not surprising that native species richness declined significantly in *H. drupacea* invaded areas in the present study.

Habitat restoration through active clearing of *H. drupacea* improved the recovery of native species as plant species composition in cleared sites were similar to those in uninvaded sites, and species composition in cleared and uninvaded sites were significantly different from invaded sites. This suggests restoration of invaded sites can reduce the negative effect of *H. drupacea* on native plant species. Although we did not observe *H. drupacea* on any of the cleared sites, a few stands of *Acacia saligna* and *Leptospermum laevigatum* were recorded on one of the cleared sites as were a number of secondary invaders (Nsikani et al., 2020). Since *H. drupacea* spreads rapidly and alters abiotic conditions of invaded areas, changes in environmental condition such as precipitation, temperature, litter cover and soil nutrients may aid the development and spread of other IAPs in invaded areas. This will amplify the impacts of IAPs on native plant communities (Simberloff, 2006; O'Loughlin and Green, 2017), causing a further decline in the diversity and distribution of native species in invaded ecosystems.

Litter cover is one of the main factors hindering the growth of understory vegetation in areas with high canopies (Williams and Wardle, 2007; Mitchell et al., 2011; Dostál et al., 2013; Bravo-Monasterio et al., 2016). Olson and Wallander (2002) defined a litter depth of 5 − 10 cm as the limit for the recruitment of other species. In this study, a thick litter layer averaging 11.55 ± 1.4 cm was observed under *H. drupacea* stands, reaching up to 20 cm in some invaded sites. This is 2-4 times thicker than the defined limits for the recruitment of other plant species, especially in the fynbos. The accumulation of litter in the understory of *H. drupacea* could partly explain the declining plant species richness in invaded sites compared to uninvaded sites where litter depth is lower. A thick litter layer in the understory of IAPs reduces the access of understory vegetation to light and water, as well as reduces seed access to substrate for germination and growth (Olsen and Wallander, 2002; Hata et al., 2010). Also, litter depth increased with the height of *H. drupacea* in this study, which implies that litter depth is expected to increase with *H. drupacea* stand age. This may increase the biomass of flammable materials and accumulation of fuel loads in the invaded areas. The frequency and severity of wildfire is expected to increase in regions with Mediterranean climates due to predicted warmer and drier climates (Gitay et al., 2001). Increasing fuel loads from *H. drupacea* and other litter producing IAPs in the CCFR may further enhance fire frequency and severity in this region. This in turn might enhance the spread of *H. drupacea* and impact native species (Vlok and Yeaton, 2000; Geerts et al., 2013).

Litter cover also influences soil properties and other abiotic factors in areas invaded by alien trees or shrubs (Prescott 2002). Here, we found no significant difference in soil nutrient composition between invaded and uninvaded areas. This contrasts findings for some nitrogen-fixing alien trees like the Australian *Acacia* species, or creepers such as *Pueraria montana* (Thunb.) Merr. (kudzu vine) that change soil properties of the colonized range (Van Der Waal, 2009; Geerts et al., 2016). A recent meta-analysis by Zhang et al. (2018) showed that IAPs may support more decomposers that subsequently aid the release of nutrients through litter pathways, and also enhance nutrient uptake by forming more symbiosis in the rhizosphere. This process may take a considerable amount of time to develop and also depends on the quantity of litter produced that differ among IAPs (Medina-Villar et al., 2016). Invasion of *H. drupacea* in our study sites may be too early to cause significant effects on soil nutrients, as some invaded sites were only recently invaded by *H. drupacea*. We observed a slight increase in soil carbon in invaded sites compared to uninvaded sites in this study, although this was not statistically significant. Other studies have also reported higher soil organic carbon

in the understory of invaded sites compared to open uninvaded sites (Mugunga and Mugumo, 2013; Zhang et al., 2018). This is mostly attributed to the influence of shade from the canopy of IAPs stimulating the decomposition of litter and release of soil carbon and other soil chemical components (Prescott, 2002). A longer invasion period of *H. drupacea* will increase canopy cover and litter production in invaded areas, and will most likely enhance the magnitude of the effects of *H. drupacea* on soil properties.

In conclusion, *H. drupacea* significantly reduced the diversity of native plant species in invaded sites. This is one of the few studies that have assessed the effects of *H. drupacea* on above ground community structure and soil properties (Cilliers et al., 2004). While active clearing may restore native species in previously invaded areas, *H. drupacea* may facilitate the growth of other IAPs that may be more resilient to habitat restoration. Therefore, we encourage active removal of invasive *H. drupacea* at an early stage of invasion before they become established where they facilitate other IAPs and produce a thick litter layer to suppress the development of native species in their colonized range.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.sajb.2021.09.017.

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