Restoration Potential of Invaded Abandoned Agricultural Fields: What Does the Seed Bank Tell Us?

Running head: Seed bank contribution to rangeland restoration

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NH, CD, KM, PLR, VK conceived and designed the research; CD, KM performed the fieldwork and experiments; PLR analyzed the data; NH, PLR, VK wrote and edited the manuscript

Abstract

Soil seed banks can play an important role in the restoration of degraded ecosystems, especially where indigenous species are well represented in, and invasive species are largely absent from the seed bank. Here, we studied the potential contribution of the soil seed bank to the restoration of invaded, abandoned agricultural fields in the Eastern Cape, South Africa. We recorded the aboveground cover and belowground abundance of all vascular plant species from 120 quadrats that differ in cover of the extralimital woody invader, *Pteronia incana*. Our results show that higher cover of *P. incana* is associated with lower species richness, aboveground cover and belowground seed abundance. Furthermore, community similarity between the above- and belowground component was low, with the seed bank and standing vegetation having only 15 species in common and 49 species being recorded only from the seed bank. We suggest that this large number of seed bank-only species is a relic of previous vegetation, prior to large-scale invasion by *P. incana*. The most important finding from our study is the absence of *P. incana* from the soil seed bank. This finding, combined with the large number of mostly native species from the seed bank, holds promise from a restoration perspective. However, given the susceptibility of the invaded systems to erosion, coupled with the low grazing value of the seed bank species, we suggest that *P. incana* removal should be accompanied by both erosion control measures and reseeding with palatable grass species, to secure the livelihoods of local communities.

Keywords: above-belowground similarity, ecological disturbance, environmental degradation, *Pteronia incana*, rangeland restoration, shrub invasion

Implications for practice:

- Management of non-desired species should account for whether species have persistent seed banks. Restoration management actions against unwanted species with transient seed banks (including the extralimital woody invader, *Pteronia incana*) should be timed when the species is absent from (or least abundant in) the seed bank.
- In situations where species of low grazing value are abundant in the seed bank, such as in our study, reseeding by palatable species may additionally be required.
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Introduction

The soil seed bank provides an indication of the regeneration potential of an ecosystem and can contribute towards the restoration of degraded systems if the seeds of preferred species are well-represented and persistent (Skoglund 1992; Warr et al. 1993). Thus, in degraded systems where desired species have been lost from the vegetation, but survive in the seed bank, conservation efforts could focus on regeneration of the standing vegetation from the belowground seed bank (Van der Valk & Pederson 1989; Skoglund 1992; Török 2018). In contrast, soil disruptions, which could stimulate germination from the seed bank, should be avoided as far as possible during restoration efforts if undesired species are abundant belowground (Thompson & Grime 1979; Jefferson & Usher 1987; Skowronek et al. 2014). Understanding the impact of habitat degradation on the soil seed bank is therefore important from a conservation perspective as seed bank characteristics can constrain the suitability of restoration techniques.

The effects of habitat degradation, particularly via different types of disturbances, on soil seed bank characteristics have been well studied (e.g. Metsoja et al. 2014; Pol et al. 2014; Clause et al. 2015; Franzese et al. 2015), but inconsistent seed bank responses have been observed. For example, overgrazing in Argentinian grasslands can both increase (Pol et al. 2014) and decrease (Franzese et al. 2015) seed density in the soil. Similarly, disturbances associated with wild boar rooting in Spain have inconsistent effects on seed bank species richness (Bueno et al. 2011).

One of the most frequently used metrics to study the effect of disturbance on seed banks is the similarity between seed bank and standing vegetation composition, i.e. comparing above- and belowground plant species composition (Hopfensperger 2007). The effect of disturbances on above-belowground similarity appear to be dependent on disturbance type. For example, fire may increase above-belowground similarity in Iranian grassland systems (Naghipour et al. 2015), while nitrogen deposition decreases similarity between the standing vegetation and the seed bank in grasslands of the UK (Basto et al. 2015). Furthermore, time since disturbance also plays a role in determining above-belowground similarity, with species similarity generally decreasing with time since disturbance in forests and wetlands, but, in contrast, increasing with time since disturbance in grasslands (Hopfensperger 2007). Therefore, the compositional similarity between aboveground vegetation and the associated soil seed bank is likely to vary both spatially (between areas affected by different disturbances) and temporally.

The establishment of invasive species (i.e. non-indigenous species that successfully reproduce and disperse from their site of introduction) can be an important driver of habitat degradation, although the presence of alien species may also be a response to habitat degradation (MacDougall & Turkington 2005). The effects of invasive plant species on seed banks range from suppressing the emergence of native species and hampering vegetation recovery (Williams-Linera et al. 2016), to reducing native seed bank species richness, density (see Gioria et al. 2014) and diversity (Hager et al. 2015). From a restoration perspective, determining the contribution of an invasive species' propagules to the seed bank can help assess the local persistence of the species (Gioria et al. 2014), while quantifying the abundance and composition of indigenous species within the seed bank provides an indication of the potential for the original (i.e. pre-invasion) species to re-establish.

Biological invasions are a continuous process, like many other ecological disturbances (Lee & Chown 2009). Therefore, although the introduction of an invasive species might be a single, discrete event (Lee & Chown 2009), the spread of the invader and the resulting transformation of local systems is a more gradual, continuous process, resulting in a continuum of changes to community structure, as opposed to an abrupt transition from an uninvaded to an invaded state. Furthermore, in general, alien species' impacts worsen as the invasion process continues and the cover of the alien species increases (Meiners et al. 2001). Despite this, many studies of the effects of biological invasions simply compare sites where the invader is present with undisturbed control sites (see review by Gioria et al. 2014). However, given the continuum of increasing ecological impacts as a biological invasion intensifies, we propose that there is merit in studying invasion impacts along a gradient of invasion (*sensu* Dresseno et al. 2018), as estimated from the cover, abundance and/or biomass of the invading species (see Meiners et al. 2001).

The aim of this research was therefore to study plant community characteristics along a gradient of invasion caused by increasing cover of the woody shrub, *Pteronia incana* (Asteraceae), in degraded areas of the Eastern Cape Province, South Africa. This species is indigenous to South Africa, but has undergone extralimital range expansion from drier regions, facilitated by anthropogenic habitat disturbances. The invasion is dominant on abandoned lands, which are a widespread phenomenon in the province. Two main research questions were examined: 1) what are the changes in both above- and belowground species richness and abundance along a gradient of increasing invasion? and 2) does floristic similarity between the seed bank and standing vegetation change as invasion intensifies?

These questions will be addressed in an effort to understand whether the restoration potential of the soil seed bank is affected by increasing levels of invasion. Our results could have important implications for rangeland rehabilitation and restoration, and securing sustainable livelihoods for local communities.

Methods

Study Area

This study was conducted in the Ngqushwa Municipality of the Eastern Cape Province, close to Mgwalana Village, on the east coast of South Africa (33.402° S, 27.270° E). On average, the area receives an annual rainfall of c. 500 mm (2007 – 2017 data from the two closest weather stations; Bisho and Grahamstown, 55 km north-east and 55 km west of Mgwalana respectively). Summers are warm (December to March: average daily maximum of 26°C) and winters are mild (June to August: average daily minimum of 7.5°C). Red mudstones and shale underlie the area (Manjoro et al. 2012), resulting in soils which are shallow and rocky, and high in swelling hydrous mica clays (Kakembo 2009). Additionally, the soils are highly dispersive and low in organic matter, often resulting in surface crusting and erosion (Kakembo et al. 2009). The study area lies within the Thicket biome (Mucina & Rutherford 2010).

Historically, the communal lands of the study area were used for both cattle grazing and the cultivation of crops (Kakembo 2001). Aerial photographs show that cultivation has been abandoned since at least 1975, with early *Pteronia incana* colonization visible on orthophoto maps of 1988 (Kakembo 2001). Following crop abandonment, cattle grazing is now the main land use on the communal lands. The increased cover of *P. incana* has reduced grazing availability, placing higher pressure on palatable grasses (Kakembo et al. 2007). Currently there are no livestock control systems in place, with continued grazing by free-roaming cattle, sheep and goats across the landscape (Palmer 2010).

Study Species

Pteronia incana is an unpalatable dwarf woody shrub indigenous to the dry Nama Karoo biome of South Africa (Odindi & Kakembo 2011). However, subsequent to the changes in land use, the shrub expanded its range in the Eastern Cape. The species can create a landscape characterized by an alternating mosaic of bare soil and shrub patches as it replaces grasses over time (see Fig. 1) (Kakembo 2009).

Fig. 1. *Pteronia incana* invasion (low-growing grey-blue shrubs) on abandoned cultivated lands near Mgwalana Village

Pteronia incana spreads when fire is infrequent, and when intense soil disturbance (such as livestock trampling or termite activity) creates gaps for seedling establishment (Palmer 2010). A number of catchments in the Ngqushwa District have been colonized, most notably amongst communal settlements (Kakembo et al. 2009). *Pteronia incana's* adaptations to drier conditions gives the species a strong advantage over native grasses (Kakembo 2009; Palmer 2010), making it a successful invader, particularly during times of drought in the Eastern Cape (Kakembo 2009).

Sampling Design and Data Collection

Two sites of 288 m x 120 m were chosen in the study area. These were located approximately 2 km apart. Both sites showed signs of overgrazing and soil erosion in the form of rills and extensive gullies present at the bases of numerous slopes. *Pteronia incana* cover at the sites ranged from 0% to 90%. In addition, one of the sites had formed part of previous studies on the hydrological and slope characteristics associated with *P. incana* (Kakembo et al. 2007; Kakembo 2009).

Each site was divided into 60 quadrats (five columns by 12 rows) of 24 m x 24 m each. Data were collected in January 2017 from a 4 m x 4 m sub-quadrat located in the north-western corner of each of the larger quadrats. At each sub-quadrat the top 10 cm of soil was sampled, after the soil surface was cleared of litter and plant material, to obtain a 300 g sample for quantifying the seed bank using the emergence method. In addition, all vascular plant species of the standing vegetation, including *P. incana*, were identified to species level where possible (otherwise to genus level) and the aerial cover of each species estimated to the nearest 5%. Additionally, within each quadrat soil compaction was determined using a handheld penetrometer (Model H-4139, Proctor Penetrometer), and soil texture was estimated to one of three categories (coarse, intermediate, fine).

Seed Germination

To determine seed bank composition and size, a seedling emergence approach was used (Thompson & Grime 1979). Each soil sample was passed through a 2.8 mm sieve to break up large soil aggregates, after which samples were checked for seeds > 2.8 mm. The 120 sieved soil samples were subsequently transferred into pots onto a layer of clean quartz sand. These were placed under a clear roof, keeping rain water from entering the pots, but allowing the pots to receive full sun. The pots were then watered every second to third day (depending on weather conditions) with 200 ml stored rainwater. Every second week the position of the pots was randomly re-arranged. The emerging seedlings were identified up to species level where possible (otherwise to genus- or family level). Seedling emergence was recorded for a period of six months (February to August 2017).

Data Analyses

The relationship between *P. incana* cover and species richness (and seed abundance) was modelled with generalized linear models (GLZs; assuming a Poisson distribution), using site identity (Site 1 or Site 2), soil compaction and soil texture as covariates. Cover data were square-root-transformed prior to analysis, and were analyzed using a GLZ with a Gaussian distribution. Above- vs. belowground similarity scores (calculated using the Sørenson's index) were also modelled using GLZs (assuming a binomial distribution) and the same predictor variables. As soil compaction and soil texture did not contribute significantly to explaining variation in most response variables, these predictors were excluded from final models when their inclusion did not improve model performance significantly, i.e. when nested models were compared using the likelihood ratio statistic. The statistical interaction between *P. incana* cover and site identity was tested in all models, but was only reported in final models where the inclusion of the interaction term significantly improved the model, based on the likelihood ratio statistic.

The influence of *P. incana* cover (and the other predictor variables) on above- and belowground species composition was analyzed using Permutational Multivariate ANOVA (PERMANOVA) tests, with these relationships visualized using Non-metric Multidimensional Scaling (NMDS). Only samples containing at least one species were included in analyses. Additionally, one quadrat was excluded from the aboveground vegetation dataset (comprising only 5% cover of a single species) and one from the seed bank dataset (one occurrence of a single species) as these samples were outliers that prevented convergence of the algorithm. The influence of all four predictor variables on species composition was initially assessed, but as soil compaction and texture had no significant effect, these variables were excluded from the final models. All analyses were conducted in R (R Core Team, 2016), implementing functions from the vegan (Oksanen et al. 2016) packages.

Results

Thirty-two vascular plant species were recorded during the vegetation survey (excluding *Pteronia incana*), while 64 species were identified from the seedlings germinating from the soil samples. The seed bank and standing vegetation had only 15 species in common and 49 species were identified only from the seed bank (Table S1). *Pteronia incana* occurred in 91% of vegetation samples (218 of 240 quadrats) with a mean cover of 41% (± 1 SD = 28%), but no *P. incana* seedlings germinated from the soil samples.

The cover of *P. incana* was negatively related to above- and belowground species richness (Table S2; Fig. 2). This was most prominent for the aboveground component, where the mean number of species per quadrat declined from seven to four species at Site 1 and from five to two species at Site 2, as *P. incana* cover increased. Species richness, both above- and belowground, also differed between sites. *Pteronia incana* cover was significantly negatively correlated with aboveground vegetation cover at both sites, although the slope of the relationship differed between sites, being steeper at Site 2 than Site 1 (Fig. 2).

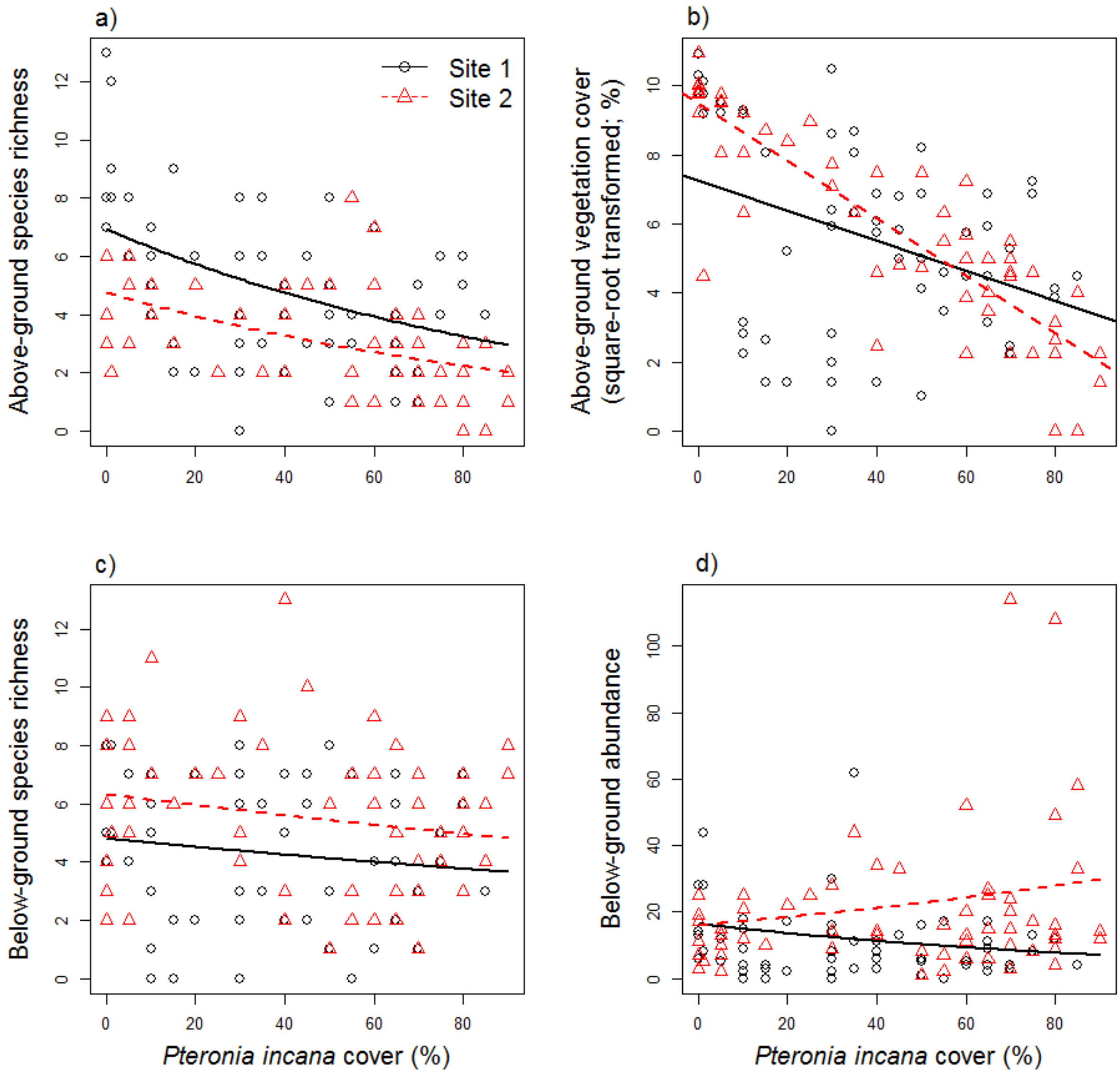

Fig. 2. The relationship between *Pteronia incana* cover and a) aboveground species richness, b) total vegetation cover, c) below-ground species richness, and d) seedling abundance, split by site. The regression lines plotted in (d) are for soils with a fine texture (the modal texture class) and mean compaction values. See Table S2 for detailed statistical results.

Specifically, mean species cover was reduced from 50 – 100 % in uninvaded quadrats to 5 – 15 % in the most highly invaded samples. In general, a similar negative relationship between *P. incana* and species richness and cover was also observed when grouping species according to their longevity, life history or growth form (Fig. S1 and S2, Table S3). *Pteronia incana* cover was also related to the abundance of seedlings, but the nature of this relationship differed between sites, being negative at Site 1 and positive at Site 2 (Fig. 2). Seedling abundance was additionally related to soil compaction, with fewer seedlings in more compacted soils, and soil texture, with both fine and course soils having a higher seedling abundance than soils of an intermediate texture.

Both above- and belowground species composition were significantly related to *P. incana* cover (Table S4, see also Figs S3 and S4), with this variable explaining 6 – 12% of variation in species composition. Species composition also differed significantly between Site 1 and Site 2, although site only had a small effect (r^2 = 3%) on aboveground composition. The similarity between above- and belowground species composition was on average low (mean = 0.12, range = 0 – 0.6) with only 15 species in common (Fig. 3). Similarity scores were not significantly related to any predictor variables (all predictors $p > 0.13$).

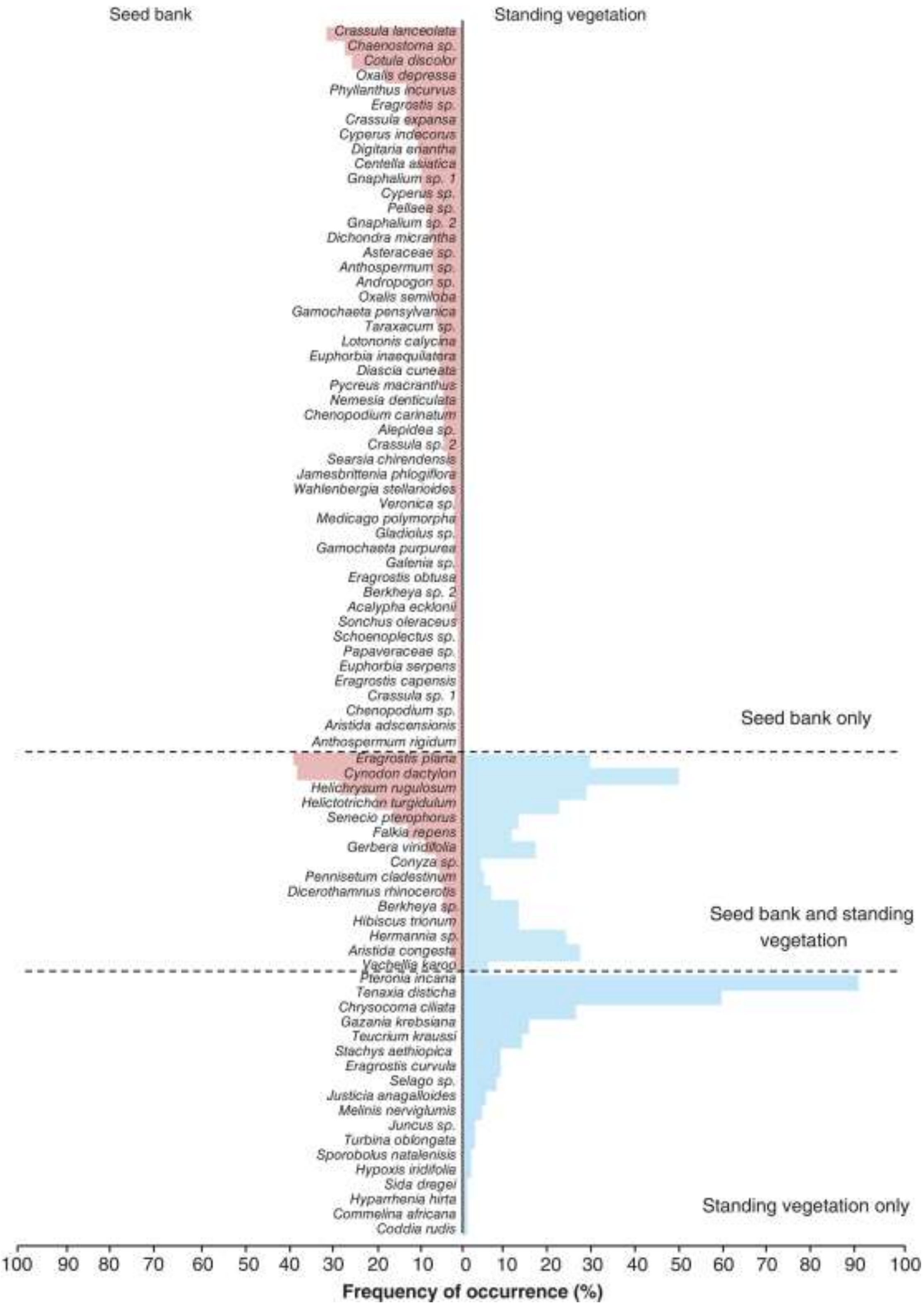

Fig. 3. Percentage of samples that contained each of the species from the belowground assemblage (seed bank, left) and aboveground assemblage (standing vegetation, right), split by species unique to the seed bank, unique to standing vegetation, or common to both the seed bank and the standing vegetation.

Discussion

Higher cover of the extralimital woody invader, *Pteronia incana*, was, in general, associated with negative changes to both above- and belowground vegetation characteristics, although these negative impacts were not consistently observed, nor equally robust at the two sites. In general, the aboveground effects were clearest. The impacts of invasive plants on native plant species are well-reviewed (Ehrenfeld 2010; Vilà et al. 2011; Pyšek et al. 2012). In line with our results, the majority of these studies show significant declines in native species richness and abundance in invaded sites (Gaertner et al. 2009; Hejda et al. 2009), which is generally attributed to the ability of many exotics to outcompete native species under disturbed conditions (Daehler 2003; Vila & Weiner 2004), such as those associated with abandoned agricultural activity (Meiners et al. 2001). In the case of *P. incana* in the Eastern Cape, clearing of the land may have reduced competition with native species and, upon land abandonment, facilitated the establishment of *P. incana*. Once established, *P. incana* tends to form dense stands, reducing both space and light for lower-growing vegetation, and consequently hindering the re-establishment of native species. Furthermore, the deep root system of this invader, gives it a competitive advantage during times of prolonged drought (Kakembo 2009).

In addition to the declines in species richness and cover of the standing vegetation, species composition changed along the gradient of increasing cover of the invader. Thus, not only do fewer species grow alongside *P. incana* in quadrats with higher invasion, but the identity of these species also changes. As none of the most common species were completely absent from quadrats with higher invasion (results not shown), changes in the occurrence of rare species are probably driving changes in species richness and composition. Therefore, instead of specific species disappearing altogether under increased *P. incana* cover, some species occur less frequently, lowering the overall species richness and changing vegetation composition per quadrat.

In contrast to the aboveground trends, belowground impacts of *P. incana* were less consistent and weaker. For example, although significant, the decline in seed bank species richness with increasing *P. incana* cover was substantially smaller than the aboveground declines (coefficient of -0.003 vs -0.009 for belowground and aboveground species richness respectively). In addition, increasing *P. incana* cover had opposite, albeit weak, effects on seed abundance at the two sites, decreasing the number of individual seedlings at Site 1 and increasing these at Site 2. Broadly, these results are in line with studies that have compared invaded and non-invaded sites, mostly reporting declines in native seed bank richness and abundance following invasion (Fisher et al. 2009; Gioria & Osborne 2009; but see also Vilà & Gimeno 2007). Such reductions have been attributed to corresponding aboveground declines in richness and cover, especially where propagules from uninvaded sites cannot reach invaded sites (Witbooi 2002; Gioria et al. 2014). However, alien plant invasion may also result in increased biomass production driven by one or two highly productive species, despite declines in overall species diversity (Vilà et al. 2011). This appears to be happening at Site 2, where the increase in seedling abundance is driven by two *Crassula* species, with one of these species contributing more than 100 seedlings at one of the more heavily invaded quadrats.

Similarity between the above- and belowground components of the vegetation was low (see Hopfensperger 2007 for a comparison) and a large number of seed bank-only species was recorded. These seed-bank only species were largely indigenous, non-weedy perennial species, as opposed to the weedy annuals that one would expect to dominate in the seed banks of abandoned fields. We therefore suggest that this dominance of seed bank-only species is possibly a relic of previous communities (Warr et al. 1993), reflecting the vegetation prior to large-scale abandonment. It therefore appears that while species were lost from the aboveground component as the sites systematically degraded, their seeds remained viable belowground (Thompson 1978). Importantly, above-belowground similarity does not change as the cover of *P. incana* increases, possibly pointing towards advanced stages of degradation across both sites, where the standing vegetation of the site as a whole has been affected and species have been lost from the aboveground component even in quadrats with no obvious impact from *P. incana* cover.

Given the ecological changes associated with increasing *P. incana* cover reported in this study, the negative changes to site hydrology and erosion reported elsewhere (Kakembo 2009; Manjoro et al. 2012), and the possible consequences that these changes hold for livelihoods and the economic development of the area, we advocate that active restoration is needed. Previous efforts to eradicate *P. incana* from the area have proven expensive and partly ineffective, because of substantial re-growth from the seed bank (Palmer 2010). This is in stark contrast to the results from our study, where *P. incana* was completely absent from the seed bank. During laboratory trials, Witbooi (2002) found that 57% of *P. incana* seeds were viable and more than 30% of sowed seeds germinated, even at relatively low temperatures. We therefore consider it unlikely that viable *P. incana* seeds were present in our samples, but that none of them had germinated. Instead, in agreement with Esler (1993), we suggest that the species does not maintain a persistent, soil-stored seed bank. Studies on the phenology of *P. incana* are warranted to provide insight into the seasonality of seed bank dynamics.

From an ecological restoration perspective, the absence of a persistent *P. incana* seed bank is promising and suggests that viable *P. incana* seeds are not present in the seed bank year-round. Indeed, a seasonal absence of viable seeds has been recorded for this genus elsewhere in South Africa, with viable seeds being present in summer, after dispersal, but absent from soil samples the following winter (Esler 1993). If timed correctly, the physical removal of *P. incana* from the aboveground component of the vegetation could therefore successfully eliminate the species from these sites and potentially allow the re-establishment of indigenous species from the seed bank. Our results suggest that mid-summer is an appropriate time for *P. incana* removal. However, given that Palmer (2010) noticed seeds on the soil surface underneath shrubs in late-summer and regrowth following removal a few months later, we advocate that further phenological studies are warranted. Furthermore, *P. incana* removal should be applied with caution for two reasons. First, although the seed bank was dominated by non-weedy, perennial species, the perennials with the highest abundance in the seed bank were disturbance-tolerant species (e.g. *Cynodon dactylon*), often with little grazing value (e.g. *Crassula* species). In line with other studies that test the seed bank potential for restoration (Godefroid et al. 2018; Klaus et al. 2018), we therefore suggest that reseeding with target species might be necessary to restore rangeland potential. Second, *P. incana* invasion tends to result in a patchy landscape, with bare-soil inter-patches prone to erosion. *Pteronia incana* shrubs provide at least some degree of erosion protection in these landscapes (Kakembo 2009), and we therefore concur with Kakembo (2003) that *P. incana* shrubs should be systematically removed, with concurrent implementation of effective erosion control measures, to allow native species to gradually re-establish.

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Supplementary Material

Table S1. Traits of the species observed only in the soil seed bank. Biennial species are lumped with annuals. Life history was known from the literature (primarily Bromilow 2010). Alien species are indicated with an asterisk.

Species	Longevity	Life history	Growth form
Acalypha ecklonii	Perennial	Not weedy	Forb
Alepidea sp.	Perennial	Not weedy	Forb
Andropogon sp.	Perennial	Not weedy	Graminoid
Anthospermum rigidum	Perennial	Not weedy	Forb
Anthospermum sp.	Perennial	Not weedy	Forb
Aristida adscensionis	Annual	Weedy	Graminoid
Asteraceae sp.	[unknown]	Not weedy	Forb
Berkheya sp.	Perennial	Not weedy	Forb
Centella asiatica	Perennial	Weedy	Forb
Chaenostoma sp.	[unknown]	Not weedy	Forb
*Chenopodium carinatum**	Annual	Weedy	Forb
Chenopodium sp.	Annual	Weedy	Forb
Cotula discolour	Perennial	Not weedy	Forb
Crassula expansa	Annual	Not weedy	Forb
Crassula lanceolata	Perennial	Not weedy	Forb
Crassula sp. 1	[unknown]	Not weedy	Forb
Crassula sp. 2	[unknown]	Not weedy	Forb
Cyperus indecorus	Perennial	Not weedy	Graminoid
Cyperus sp.	Perennial	Not weedy	Graminoid
Diascia cuneata	Annual	Not weedy	Forb
*Dichondra micrantha**	Perennial	Weedy	Forb
Digitaria eriantha	Perennial	Not weedy	Graminoid
Eragrostis capensis	Perennial	Not weedy	Graminoid
Eragrostis obtusa	Annual	Not weedy	Graminoid
Eragrostis sp.	Perennial	Not weedy	Graminoid
Euphorbia inaequilatera	Annual	Weedy	Forb
*Euphorbia serpens**	Annual	Weedy	Forb
Galenia sp.	Perennial	Not weedy	Forb
*Gamochaeta pensylvanica**	Annual	Weedy	Forb
*Gamochaeta purpurea**	Annual	Weedy	Forb
Gladiolus sp.	Perennial	Not weedy	Forb
Gnaphalium sp. 1	[unknown]	Weedy	Forb
Gnaphalium sp. 2	[unknown]	Weedy	Forb
Jamesbrittenia phlogiflora	Perennial	Not weedy	Shrub
Lotononis calycina	Perennial	Not weedy	Forb
*Medicago polymorpha**	Annual	Weedy	Forb
Nemesia denticulata	Perennial	Not weedy	Forb

Oxalis depressa	Perennial	Not weedy	Forb
Oxalis semiloba	Perennial	Not weedy	Forb
Papaveraceae sp.*	Annual	Weedy	Forb
Pellaea sp.	Perennial	Not weedy	Forb
Phyllanthus incurvus	Perennial	Not weedy	Shrub
Pycreus macranthus	Perennial	Not weedy	Graminoid
Schoenoplectus sp.	Perennial	Not weedy	Graminoid
Searsia chirendensis	Perennial	Not weedy	Tree
*Sonchus oleraceus**	Annual	Weedy	Forb
Taraxacum sp.*	Annual	Weedy	Forb
Veronica sp.	[unknown]	Not weedy	Forb
Wahlenbergia stellarioides	Perennial	Not weedy	Forb

Table S2. Best-fit models for aboveground species richness and cover, and belowground species richness and abundance. %DE = percentage of deviance explained by the model.

Response variable	**Model p**	**%DE**	**Predictor variables**	**Factor level**	**Estimate ± SE**	**Predictor variable *p***
Aboveground species richness	< 0.001	32.7	*Pteronia incana* cover	-	-0.0094 ± 0.0016	< 0.001
			Site	Site 2	-0.3726 ± 0.0922	< 0.001
Aboveground vegetation cover (square-root-transformed)	< 0.001	45.22	*Pteronia incana* cover	-	-0.0434 ± 0.0113	< 0.001
			Site	Site 2	2.2378 ± 0.7106	0.115
			Pteronia cover * Site	-	-0.0400 ± 0.0146	0.006
Belowground species richness	0.001	7.37	*Pteronia incana* cover	-	-0.0030 ± 0.0015	0.038
			Site	Site 2	0.2762 ± 0.0837	< 0.001
Belowground total abundance	< 0.001	21.94	*Pteronia incana* cover	-	-0.0094 ± 0.0017	0.0546
			Site	Site 2	-0.0184 ± 0.1028	< 0.001
			Soil compaction	-	-0.0001 ± 0.0001	0.0494
			Soil texture	Fine	0.0781 ± 0.0857	< 0.001
				Intermediate	-0.3332 ± 0.0904	
			Pteronia cover * Site	-	0.0163 ± 0.0020	< 0.001

Table S3. Relationship between the richness and cover of different functional groups of vascular plant species and the cover of *Pteronia incana*. Results are from univariate generalized linear models, using a Poisson distribution for species richness and a binomial distribution for species cover (cover data were converted to proportions prior to analyses, and the coefficients reported are for the transformed data; for the six samples where cover exceeded 100%, cover was rounded down to 100% prior to analyses). All measures of species richenss and cover exclude *P. incana*. %D.E. = percentage deviance explained.

Response variable		**Species group**	**Mean richness**	**%D.E.**	**Estimate ± S.E.**	**Model p**
Species richness	Above-ground	Perennials	3.96	23.9	-0.010 ± 0.002	**< 0.001**
		Annuals	0.15	0.9	-0.007 ± 0.009	0.420
	Below-ground	Perennials	3.83	3.7	-0.004 ± 0.002	**0.007**
		Annuals	0.53	0.2	0.003 ± 0.004	0.563
	Above-ground	Non-weedy	2.14	4.1	-0.006 ± 0.002	**0.010**
		Weedy	2.00	29.4	-0.015 ± 0.002	**< 0.001**
	Below-ground	Non-weedy	3.24	0.1	0.001 ± 0.001	0.995
		Weedy	1.68	7.0	-0.007 ± 0.003	**0.006**
	Above-ground	Woody	0.44	1.3	-0.006 ± 0.005	0.238
		Forbs	1.62	7.4	-0.010 ± 0.003	**< 0.001**
		Graminoids	2.08	23.3	-0.011 ± 0.002	**< 0.001**
	Below-ground	Woody	0.22	1.0	-0.006 ± 0.007	0.360
		Forbs	3.08	0.3	-0.001 ± 0.002	0.473
		Graminoids	1.62	1.5	-0.004 ± 0.003	0.133
			Mean cover			

Cover	Above-ground	Perennials	40.2	44.5	-0.039 ± 0.008	**< 0.001**
		Annuals	0.5	2.4	-0.013 ± 0.050	0.783
		Non-weedy	15.6	5.7	-0.010 ± 0.009	0.256
		Weedy	25.2	51.0	-0.046 ± 0.010	**< 0.001**
		Woody	2.1	1.2	-0.007 ± 0.023	0.767
		Forbs	6.6	14.5	-0.019 ± 0.014	0.171
		Graminoids	32.1	44.6	-0.038 ± 0.009	**< 0.001**

Table S4. PERMANOVA results, testing for an effect of *P. incana* cover on species composition.

Species composition	**Predictor variable**	***df***	***F* statistic**	r^2	***p***
Aboveground	Site	1	4.45	0.033	< 0.001
	P. incana cover	1	16.67	0.124	< 0.001
Belowground	Site	1	8.83	0.069	< 0.001
	P. incana cover	1	7.89	0.061	< 0.001

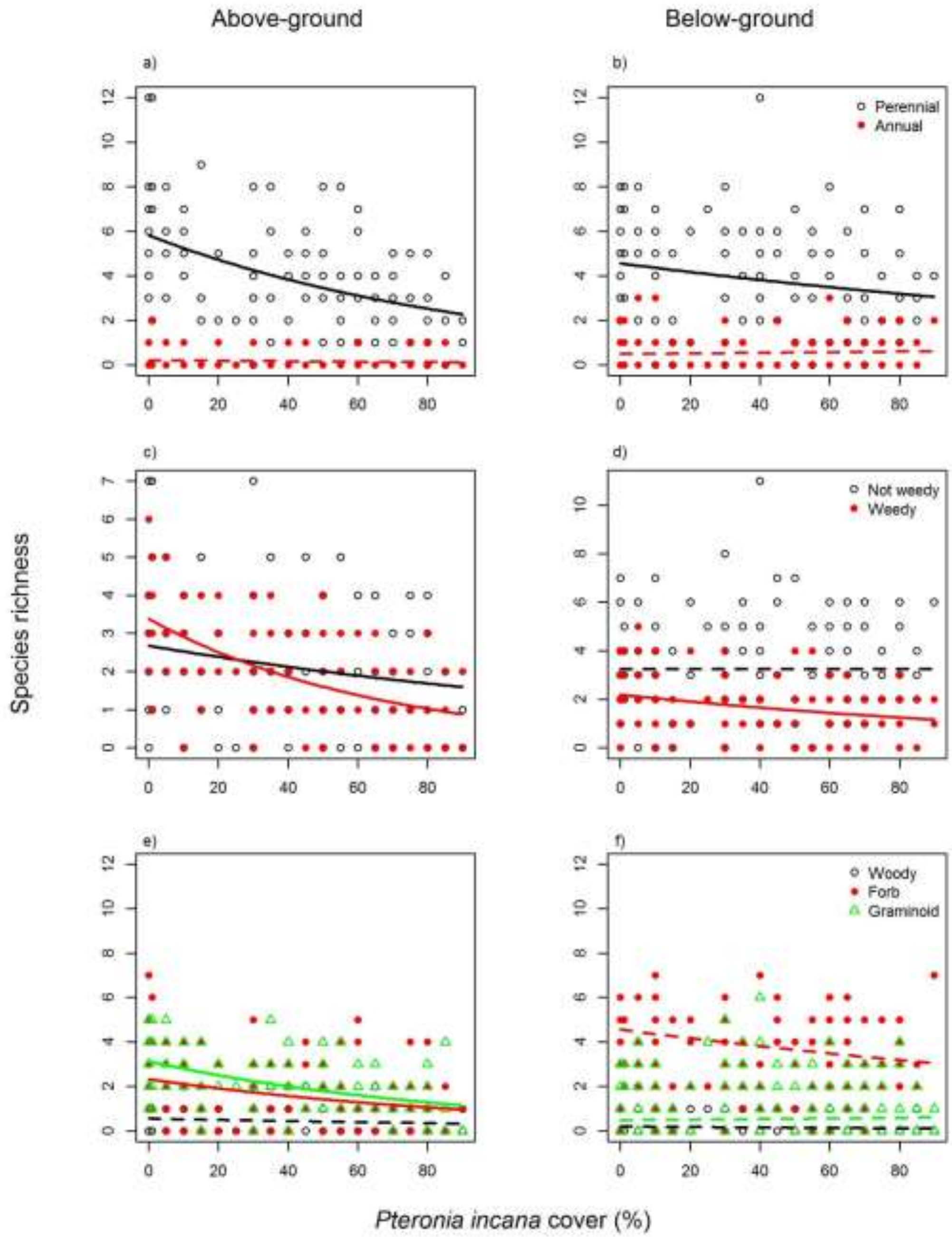

Fig. S1. Variation in the species richness of (a) and (b) perennial and annual (including biennial) species, (c) and (d) weedy (i.e. ruderal and/or pioneer species, including all alien species) and non-weedy species, and (e) and (f) woody (trees, shrubs and dwarf shrubs), forb (including geophytes) and graminoid species in relation to the cover of *Pteronia incana*. Analyses are repeated for above ground (left-column) and above-ground (right column) data. Best fit regression lines based on Poisson regression shown for each species group, with a solid (or dashed) line indicating a significant (or non-significant) relationship between richness of a group and P. incana cover. Detailed statistics are provided in Table S3.

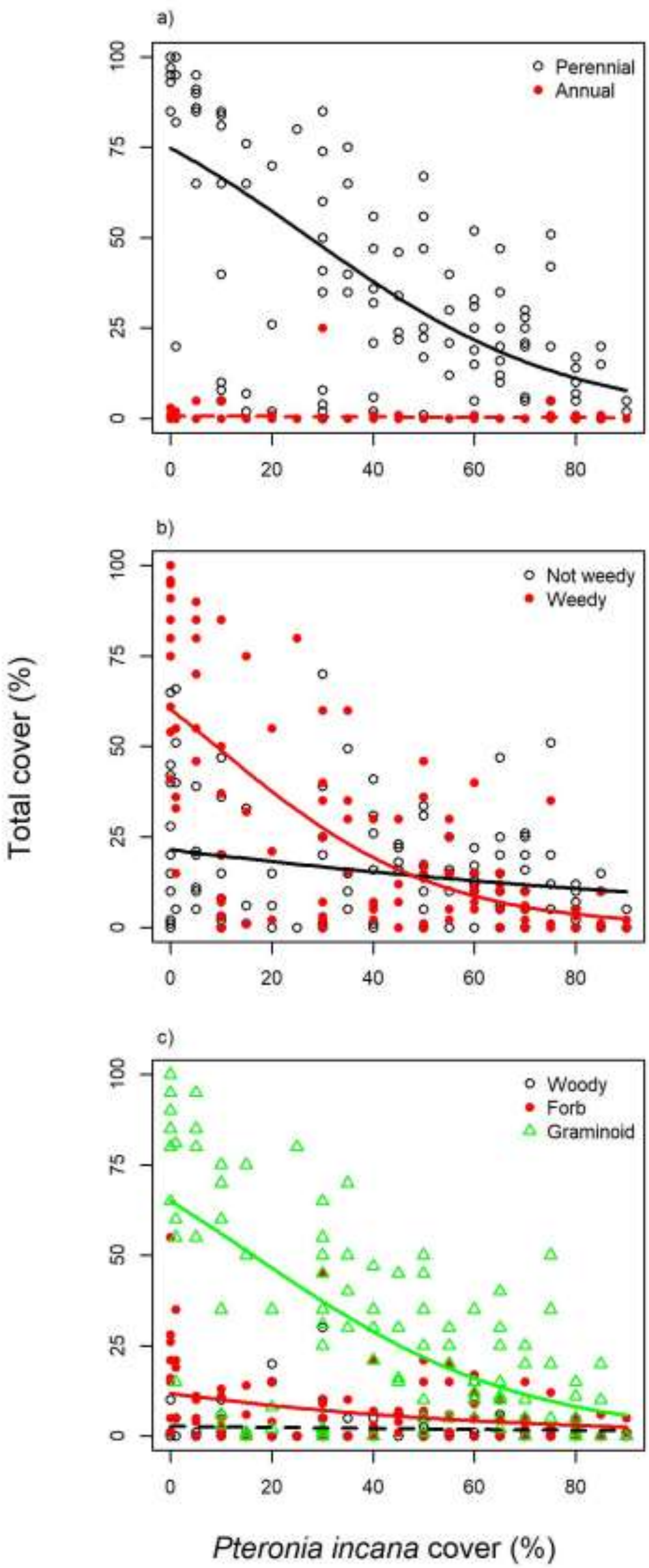
a)
Perennial
Annual
b)
Not weedy
Weedy
c)
Woody
Forb
Graminoid
Total cover (%)
Pteronia incana cover (%)

Fig. S2. Variation in the species cover of (a) perennial and annual (including biennial) species, (b) weedy (i.e. ruderal and/or pioneer species, including all alien species) and non-weedy species, and (c) woody (trees, shrubs and dwarf shrubs), forb (including geophytes) and graminoid species in relation to the cover of *Pteronia incana*. Best fit regression lines based on Poisson regression shown for each species group, with a solid (or dashed) line indicating a significant (or non-significant) relationship between richness of a group and *P. incana* cover.

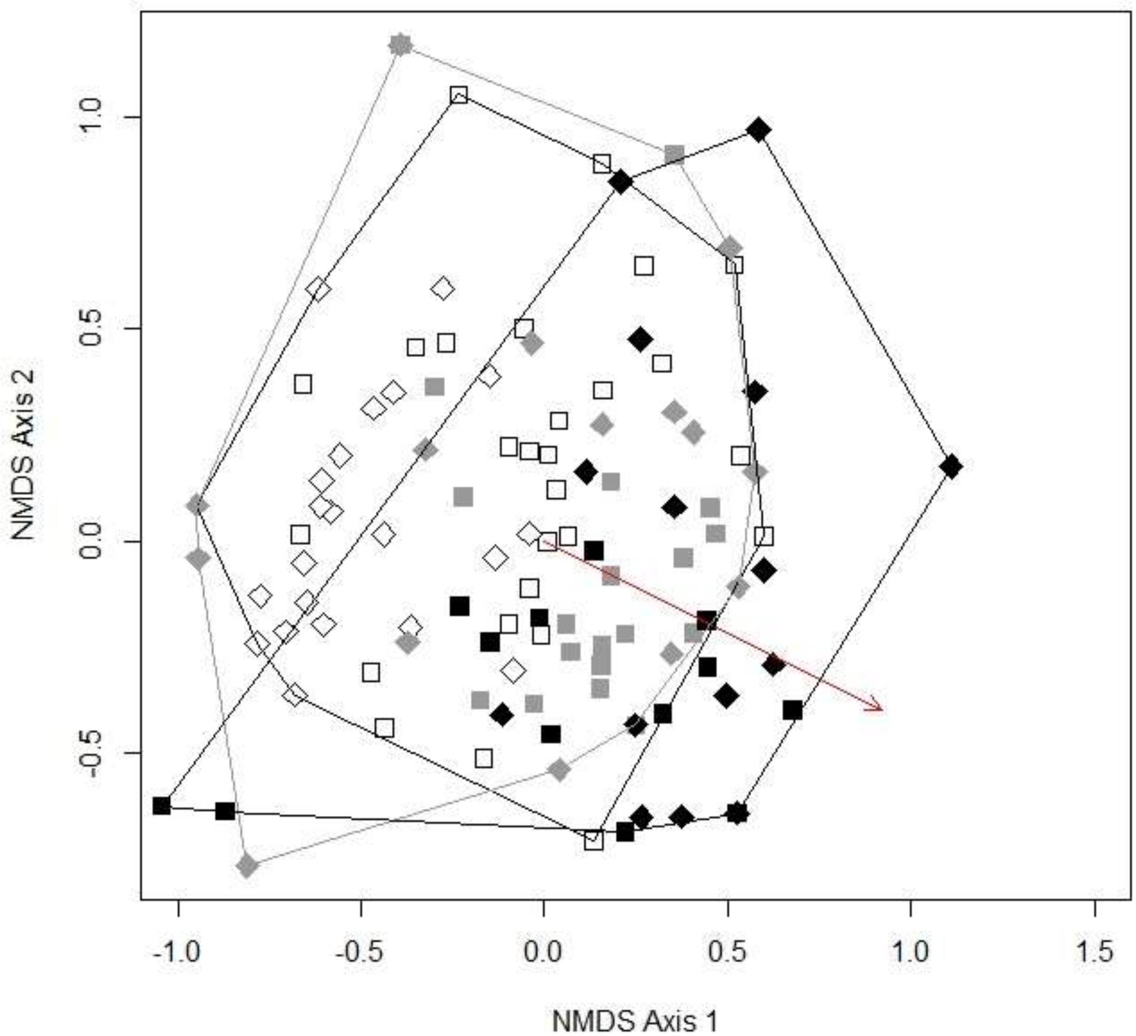

Fig. S3. Non-metric multidimensional scaling ordination of aboveground species composition (based on Bray-Curtis dissimilarity scores, after Wisconsin double standardization). Symbol types indicate the two sites, and symbol color indicates *P. incana* cover (black: *P. incana* cover > 60%, grey: cover 30 – 60%, white: cover < 30%). Convex polygons are drawn for each of the three *P. incana* cover categories to illustrate the variation in species composition observed under low, mid and high *P. incana* cover. The arrow indicates increasing *P. incana* cover. Stress = 20.1 %.

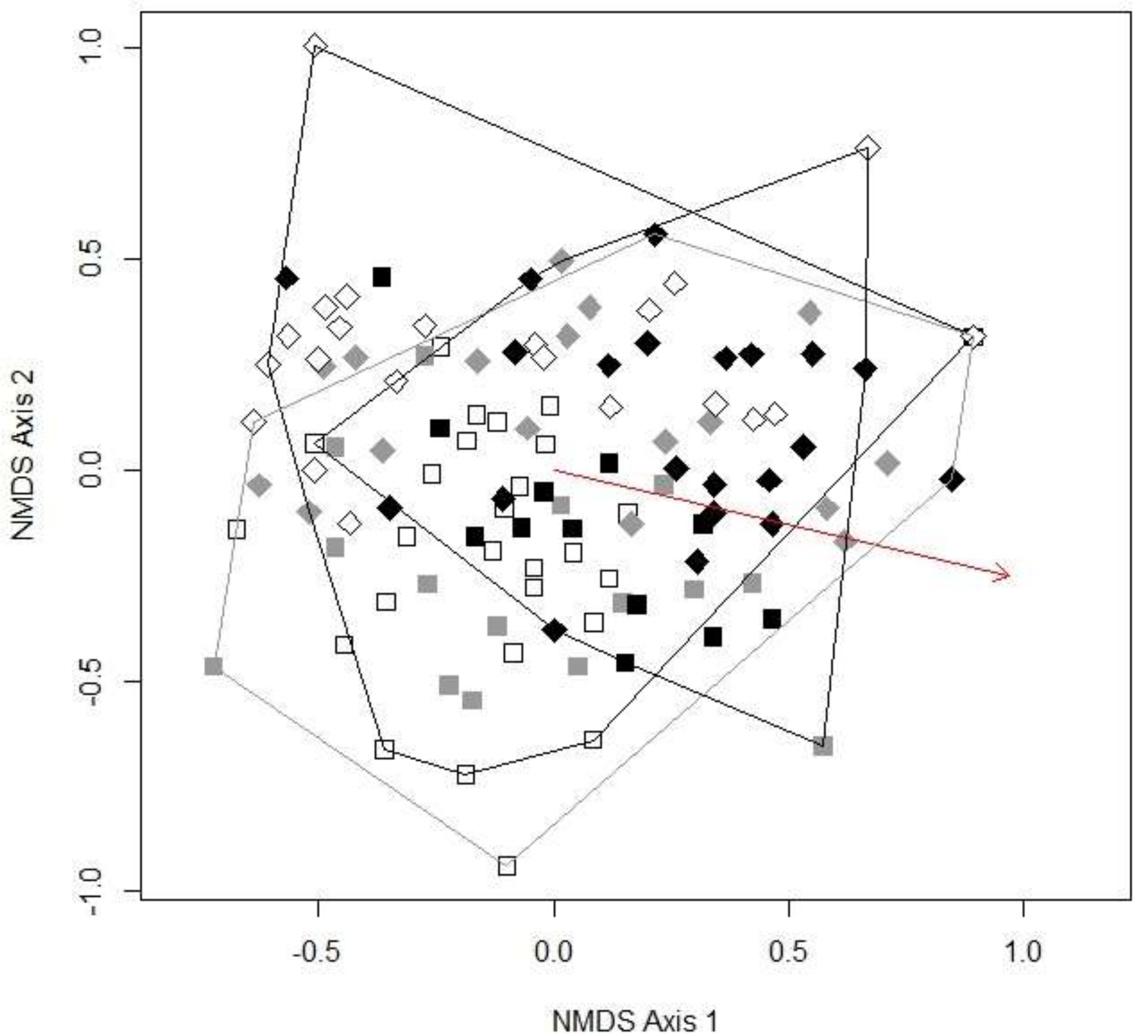

Fig. S4. As for Fig. A1 except for belowground species composition. Stress = 26.1 %.

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