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Fine-scale variables associated with the presence of native forbs in natural temperate grassland.

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Abstract

Broad-scale threats to floristic diversity in native temperate grasslands are well-documented and include elevated soil nutrients, changes in disturbance regimes and exotic species. However, fine-scale variables associated with the presence of native forbs, such as gap size and biomass cover, have received relatively little attention. We conducted a case-control study to determine the relative influence of physical structural dimensions and other fine-scale variables associated with the presence of native forbs in a modified temperate grassland previously used for domestic grazing. We matched 145 case plots centred on 27 different species of native forb with 290 control plots not centred on a native forb. For each percentage increase in ground litter cover, dead biomass cover, grass cover or exotic forb cover, or the area of bare ground within 30 cm, the relative odds that a native forb was present vs absent declined by a mean of 10-13%. Living and dead biomass reduces light availability and the former can also reduce nutrient and water availability. Declines in the presence of native forbs associated with increasing total bare ground may suggest that gap sizes were too small or the soil surface condition too degraded. Our results add to a body of evidence suggesting that native forbs in temperate native grassland are likely to benefit from periodic removal of living and dead grass biomass and a reduction in the cover of exotic forbs.

Keywords: Biomass; Competition; Grassland diversity; Stabilising mechanisms; Temperate grassland

Introduction

Biodiversity has declined in native grasslands as a result of agriculture, urbanisation, and altered disturbance regimes (Howe 1994; Kiehl *et al.* 2006; McDougall and Morgan 2005; McIntyre 2011; Öster *et al.* 2009). Native forbs have declined considerably in grassland ecosystems as a result of these changes (Brandt and Seabloom 2012; Stevens *et al.* 2010; Tremont and Mcintyre 1994). Native forbs are an important component of species and functional diversity in grasslands (Lavorel *et al.* 2011; McCain *et al.* 2010; Pallett *et al.* 2016; Tremont and Mcintyre 1994). They contribute to a range of ecosystem services such as water infiltration and invasion resistance, have aesthetic value (Tilman *et al.* 2006; Tscharntke *et al.* 2005; Wratten *et al.* 2012) and can influence fire behaviour (Wragg *et al.* 2018). Native forbs are more likely than exotic forbs to be well adapted to historic conditions (Brandt and Seabloom 2011; Flores-Moreno *et al.* 2016) and to provide habitat resources required by native fauna (Antos and Williams 2015), including some which perform ecosystem services such as pollination and biological pest control (Isaacs *et al.* 2009; Schmidt-Entling and Döbeli 2009; Williams *et al.* 2015; Wratten *et al.* 2012). Thus, the conservation and restoration of native forb diversity has garnered considerable interest (Foley *et al.* 2005; Hobbs *et al.* 2013; Suding 2011).

Understanding the habitat requirements of subordinate species such as grassland forbs (Tremont and Mcintyre 1994) requires an understanding of the conditions that enable coexistence with other grassland species (Roxburgh *et al.* 2004). On-going coexistence on a fine scale requires stabilizing mechanisms that prevent over-abundance of individual species and allows recovery after decline (Fox 2013; Levine and HilleRisLambers 2009; Scherrer *et al.* 2019; Sears and Chesson 2007). Stabilizing mechanisms on a fine scale may include spatial partitioning of resources, which influences the spatial arrangement of plants according to heterogeneity in species traits and distribution of available resources, and limiting similarity, which influences the spatial arrangement of functionally similar plants according to fine-scale competition (Chesson 2000; Price *et al.* 2017; Price *et al.* 2013; Scherrer *et al.* 2019).

Grassland species composition is influenced by competition and the physical structure defined by the dominant grass species (Morgan and Williams 2015; Tremont and Mcintyre 1994). Functional differences and spatial partitioning allow sub-dominant species (e.g. forbs and smaller grasses) to coexist with the dominant grasses, and each other, within the gaps between grass tussocks (McIntyre *et al.* 1995). The size and shape of gaps and the surrounding vegetation influence the conditions provided for germination (e.g. light, diurnal temperature fluctuations, moisture) and later survival (e.g. available light, moisture and nutrients) (Isselstein *et al.* 2002; Jiménez-Alfaro *et al.* 2016), and the amount of shelter from adverse environmental conditions and grazing (Diaz *et al.* 2007; Morgan 1998b). Thus, physical structure and gap characteristics can influence the range of species able to use the gap (Bullock *et al.* 1995; Fibich *et al.* 2013; Liao *et al.* 2015) and the stabilizing mechanisms allowing their coexistence (mainly limiting similarity) (Price *et al.* 2017). Morgan (1998b) found that seedling survival of five native forb species in natural temperate grassland declined in gaps with radii less than 18 cm due to reduced light availability at ground level. McIntyre (2005) suggests that grassland swards with a physical/gap structure defined by tall tussock-forming species are likely to support greater overall biodiversity than short-statured swards.

In productive grasslands, the benefit of gaps can be lost due to excessive accumulation of biomass. Gaps can be filled-in or reduced in size by an accumulation of grass litter if the decomposition rate is lower than the production rate (O'Halloran *et al.* 2013), or by vegetative expansion of the dominant perennial grasses (Fibich *et al.* 2013; Saiz *et al.* 2016). The amount, and size, of available gap space may also be affected by altered fire regimes, which can influence the identity of the dominant grass species (Prober *et al.* 2007) and the amount of accumulated biomass (grass litter and standing dead biomass) occupying the gaps. Domestic grazing also reduces biomass, and at medium intensity or higher can lead to an overall reduction in the size-range of grass species, smaller or larger gap sizes (if grazed at medium or high intensity, respectively) and reduced water infiltration and nutrient cycling, due to soil compaction (McIntyre and Tongway 2005; Travers *et al.* 2018). Hence, the ongoing presence of native forbs may be threatened under changed land use and modified disturbance regimes (Lunt and Morgan 1999; McIntyre and Lavorel 2007).

Vast areas of grassland in south-eastern Australia have been modified by agricultural practices such as domestic livestock grazing of native pastures, pasture improvement, and cropping (Prober and Thiele 2005). Yet we have little understanding of the likelihood or time needed for recovery to a pre-European state (McIntyre *et al.* 2017) or how to manage grasslands after agriculture ceases. According to the intermediate disturbance hypothesis (Roxburgh *et al.* 2004), we might expect a transition following the removal of grazing to a more heterogeneous physical structure and species composition, including the return of tall and/or grazing-intolerant species for example. However, this trajectory may eventually be reversed if there is a lack of alternative management to control biomass (e.g. fire, mowing) (McIntyre and Lavorel 2007; Prober *et al.* 2013). Previous examples of agricultural sites re-purposed for conservation, aided by treatments such as reduced kangaroo grazing and burning, have had mixed success (e.g. due to exotic forb invasion) (Lunt 1999) and suggest lengthy timeframes to achieve a resemblance of their pre-agricultural state, if at all (McIntyre and Lavorel 2007; McIntyre *et al.* 2017).

The aim of our study was to identify fine-scale variables associated with the occupancy of forbs in a modified grassland following the removal of grazing, without alternate types of disturbance to control biomass. Existing studies, such as the one conducted by Kelemen et al (2013), have compared the relative influence of above-ground biotic components, such as functional plant groups (grasses and exotic forbs), standing dead biomass and ground litter, on species richness, but we are not aware of other studies of the fine-scale variables associated with native forb occupancy within Australian temperate grassland. While observations at larger scales are appropriate for studying the influences of site-scale environmental conditions (eg. soil type, climate, elevation) (Whittaker *et al.* 2001), a fine-scale approach is needed to capture variables that influence the ability of a forb to coexist with neighbouring grassland species (Liao *et al.* 2015; Miller *et al.* 2009; Saiz *et al.* 2016; Scherrer *et al.* 2019; Sears and Chesson 2007; Spotswood *et al.* 2017).

Methods

Study area

Our study was undertaken in an area of modified natural temperate grassland within approximately 70 hectares of grassy woodland within a recently declared nature reserve in the Australian Capital Territory (ACT) in south-eastern Australia (35.270562° S, 149.026425° E). Prior to its declaration as a nature reserve in 2010, the site had a history of grazing by sheep and then cattle. Grazing ceased in 2005. The study area is approximately 580 m above sea level, has a median annual rainfall of 650 mm and a mean minimum and maximum daily temperature of 7.0° and 20.8° Celsius (http://www.bom.gov.au/climate/data/index.shtml). Soils in the study area have low to moderate fertility (King, 1996), except where super-phosphate was applied with *Avena sativa* and *Trifolium subterraneum* seed sown from as early as 1947 (ACT Govt. Environment and Planning Directorate, TL2432#01 - Department of the Interior - Property and Survey Branch. Block 21 Belconnen - O.H. Dixon). Vegetation in the ground-layer ranges from areas dominated by exotic grasses and forbs to areas dominated by native species. There is on-going low intensity grazing by the eastern grey kangaroo (*Macropus giganteus*) and European rabbit (*Oryctolagus cuniculus*), with both species managed by occasional population control. A portion of the site was affected by fire in 2003, and areas of St John's Wort (*Hypericum perforatum*) infestation were boom-sprayed with a non-residual selective broadleaf herbicide (fluroxypyr) in 2011 and 2012.

Data collection

We employed a case-control design—a method originally developed to identify causes of rare diseases (Mann 2003)—to examine fine-scale variables associated with the presence of individual native forbs within temperate grassland. The case-control approach was preferred to random sampling due to the tendency of native forbs to be sparsely distributed in modified grasslands (Keating *et al.* 2004). To our knowledge this method has not been previously used in studies of grassland forbs.

The response variable is forb presence/absence. The explanatory variables include environmental indicators that can vary over a short distance, and apart from rock and log cover, are associated with mechanisms that may influence the ability of forbs to coexist with other grassland species. We measured the physical structure and spatial arrangement of large grass tussocks (tussock size, gap size) to capture the level of competition a gap-dwelling species might experience from large tussocks, as well as the amount of shelter tussocks provide for seedling and adult forbs from climatic conditions and grazing (Fibich *et al.* 2013; Morgan 1998b). Soil surface condition (moisture, temperature, hardness) are likely to affect germination (Harper *et al.* 1965; Zhao *et al.* 2007) and may affect infiltration and nutrient cycling rates (McIntyre and Tongway 2005). Living biomass (grass cover, exotic forb cover) indicates the overall level of competition for space and resources (light, moisture and nutrients) (Fibich *et al.* 2013; Hellström *et al.* 2009; Lindsay and Cunningham 2012). Dead biomass cover (standing and ground litter) may impede establishment by physical obstruction of seed arrival (Ruprecht and Szabó 2012) or seedling emergence and survival (Loydi *et al.* 2013); which can affect native forb species more severely than exotic forb species (Johnson *et al.* 2018).

We identified 145 case plots, each with two associated control plots (Fig. 1). The key difference between case and control plots being the presence of a native forb at the centre of case plots (control plots contained no native forbs). To identify case plots, we searched for native forbs of any species within a matrix of circular search zones with radii of 20 m at 60 m intervals along parallel transects 60 m apart. We commenced zone searches in the centre and spiralled outwards until a native forb was encountered or the radius distance of 20 m from the centre was reached. If a native forb was located, we marked its location as the centre of a circular case plot. For each case plot, we located two control plots with centres at random distances (within 1-5 m) and compass bearings from the case plot centre. Control plots contained no native forb species within a radius of 30 cm; all other plant species, including exotic forbs, were allowed. The proximity of each case plot and paired control plots minimises between-plot variation in land-use history, soil properties (texture and fertility), landscape position, distance to (and population size of) forb propagule sources (native and exotic) and climatic variables.

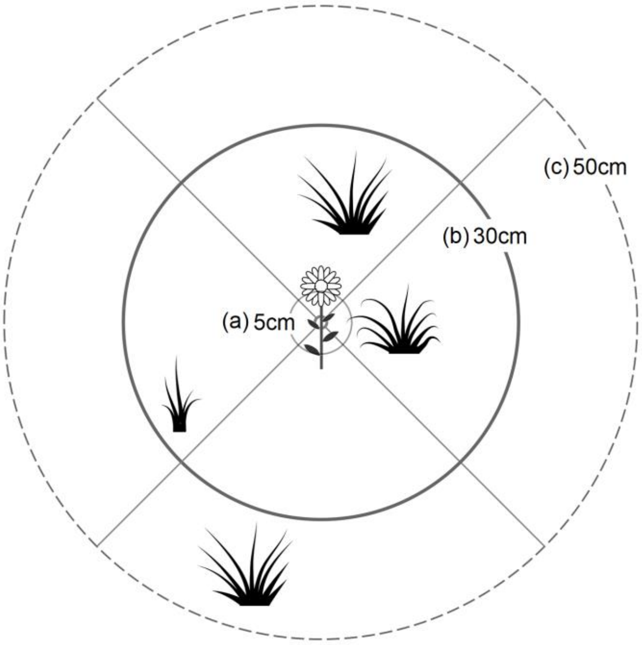

Fig. 1. The dimensions of case and control plots used in this study. Case plots were centred on a native forb. Control plots were centred on a point located randomly within 1-5 m of each case provided they did not contain a native forb. For each case and control plot we measured: (a) soil surface condition (moisture, temperature, hardness) within 5 cm of the centre; (b) grass and exotic forb cover, litter depth and cover, standing dead biomass height and cover, and cover of rocks, coarse woody debris and cryptogams within the 30 cm of the centre; and (c) the distance to, height and canopy width of the nearest grass tussock of minimum size (height and/or canopy width ≥10 cm) within 50 cm of the centre (in each of four quadrants).

All fieldwork was undertaken during austral late spring/early summer of 2014. We acknowledge that differences in phenology (growing season) may influence the competitive pressure influenced individual grass species, depending on the time of year. We conducted the survey during spring/summer because the majority of grassland species are actively growing, and total competitive pressure is high.

We measured abiotic and biotic variables that may influence the regeneration niche for native forbs (soil moisture, temperature and hardness, light penetration, %bare ground, %cover of rocks, logs, ground litter and standing dead biomass, litter depth and standing dead biomass height) or survival at any life stage (grass and exotic forb cover, distance to tussocks, canopy width and height of tussocks, cryptogam cover, including lichens, mosses, liverworts, fungi and algae) (Fig. 1, Table 1). Table S1 (Appendix S1) explains variable selection in more detail.

194 **Table 1**. Definition and collection method of potential explanatory variables measured in this study.

Explanatory variable	Definition	Collection method
%Soil moisture	Percentage soil moisture by volume to a depth of 6 cm	Measured with Delta-T Theta Probe ML2X in a gap between plants within 5 cm of the plot centre
Soil temperature	Soil temperature 6cm deep (Celsius)	Measured with Milwaukee TH310 temperature probe in a gap within 5 cm of the plot centre
Soil hardness	Soil surface hardness (0-5 kgf.cm^2)	Measured with Controls brand 16-T0171 hand-held soil penetrometer in an undisturbed gap within 5 cm of the plot centre
%Light to ground	Percentage of the above-canopy photosynthetically active radiation (PAR) reaching the ground	Calculated from PAR above the canopy, using a LI-COR LI-191 line quantum sensor, divided by PAR at ground level
%Bare ground	Percentage area of bare ground	Visual estimation within a circular plot with 30 cm radius
%Rocks	Percentage of area covered by rocks	Visual estimation within a circular plot with 30 cm radius
%Logs	Percentage of area covered by course woody debris	Visual estimation within a circular plot with 30 cm radius
%Litter cover	Percentage of area covered by dead plant material lying on the ground	Visual estimation within a circular plot with 30 cm radius
Litter depth	Litter depth (cm)	Average of 3 random measurements within a circular plot with 30 cm radius
%Dead biomass cover	Percentage of area covered by dead plant material still standing	Visual estimation within a circular plot with 30 cm radius
Dead biomass height	Height of standing dead biomass in cm	Average of 3 random measurements within a circular plot with 30 cm radius
%Grass cover	Percentage of area covered by living grasses	Calculated based on visual cover estimations of each species in a circular plot with 30 cm radius
%Exotic forb cover	Percentage of area covered by exotic forb species	Calculated based on visual cover estimations of each species in the plot
Tussock distance	Average distance to nearest tussocks in 4 quadrants	Average distance from the central native forb (case plots) or plot centre (control plots) to the nearest tussock greater than 10 cm in canopy diameter and/or height in 4 point-centred quadrants (PCQs) within 50 cm of the plot centre
Tussock height	Average height of nearest tussocks in 4 quadrants	Average leaf height of the nearest tussock in 4 quadrants within 50 cm of the plot centre
Tussock diameter	Average canopy diameter of nearest tussocks in 4 quadrants	Average canopy diameter of the nearest tussock in 4 quadrants within 50 cm of the plot centre
%Cryptogams	Percentage of area covered by cryptogams	Calculated based on visual estimations within a circular plot with 30 cm radius

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Most variables (except distance to and size of tussocks) represent observations within a circular quadrat of radius 30 cm (area 0.28 m^2) from the identified plot centres (Fig. 1). We used a modified point-centred quadrant technique (Dix 1961) to derive metrics representing the average distance to, size of, and gap between grass tussocks within 50 cm from the plot centre (Fig. 1). A tussock was any grass with a height and/or canopy width ≥10 cm. If no tussocks existed within 50 cm in a quadrant we assumed a default tussock distance of 60 cm; the use of a larger default distance was preferred instead of possibly calculating the average over less than four quadrants (which would disproportionately weight the importance of tussock distance in the quadrants containing tussocks). Sensitivity testing of alternate default tussock distances of 80 and 100 cm had negligible effect on the results. All surveying (including physical measurements and cover estimations) were carried out by one person to minimize the variation in data that may occur.

Data analysis

We examined associations between the occurrence of individual native forbs and the potential explanatory variables (Table 1) using conditional logistic regression (Keating et al. 2004) implemented by the “clogit” function within the “survival” package (Therneau 2015) in R (R Core Team 2016). We included the 15 non-correlated variables ($r < 0.6$) (all variables in Table 1 except %Light to ground and Dead biomass height) to identify significant terms ($p < 0.05$) and their odds ratios. The parameter coefficients for the explanatory variables are logarithms of odds ratios, which when exponentiated, represent the change in the relative odds (or odds ratios, hereafter “odds”) if an explanatory variable increases by one unit (Monahan et al. 2007). We calculated the change in odds of a native forb being present (i.e. the probability of native forb presence divided by the probability of native forb absence) associated with a unit increase in each significant explanatory variable (Table 3). For example, an odds ratio for the variable *%Litter cover* of 0.88 means that the odds of a native forb being present is expected to fall, on average, by 12% with every percentage increase in litter cover.

Note: The magnitude of the change in terms of probability depends on the background probability (in average conditions). For example, if the background probability of native forb presence is $p = 0.1$, the revised probability would be $p = 0.088$. That is, a fall of 12% reduces the odds ratio (OR) from OR = 0.111 [i.e. $0.1/(1-0.1)$], to $0.88*0.111 = 0.097$. Reversing the calculation using the revised odds ratio [i.e. $p = 0.097/(0.097+1)$] gives $p = 0.088$ (Liberman 2005).

Similarly, a hypothetical odds ratio for *%Litter depth* of 1.12 would mean that the odds of a native forb being present is expected to increase by 12% with every percentage increase in litter cover (e.g. a probability of $p = 0.1$ would increase to $p = 0.11$). Potential models were ranked using the “dredge” function from the “MuMIn” package (Barton 2017) and selected according to the Bayesian Information Criterion (BIC).

Results

We surveyed 145 case plots, centred on 27 different species of native forbs (Table S2 in Appendix S2) and 290 associated control plots. The mean distance between the centres of case plots and their matched pair of control plots was 2.89 m (± SD 1.05 m). The species list for case and control plots included eight exotic grass species, 10 native grass species, 22 exotic forb species, 31 native forb species, and five other species, mainly sedges and rushes (Table S2 in Appendix S2). In addition to these, two exotic grasses, two native grasses, and two native forbs were identified at genus level. The case and control plots contained means of 31% native grass cover, 6% exotic grass cover and 5% exotic forb cover. Summary statistics for all potential explanatory variables and significant correlations are in Table 2. Relative differences between variable means in case plots and controls plots are in Fig. 2.

Table 2. Summary statistics of all data variables. Variables with the same superscript letter are significantly correlated ($|r| > 0.6$).

	Variable	Mean	Std Dev	Min	Max
	%Soil moisture	7.16	4.10	0.2	24
	Soil temperature	24.69	4.10	4.80	38.6
	Soil hardness	3.03	1.36	0.25	5.1
	%Light to ground ^{a,b}	40	30	0	100
	%Bare ground	1.54	6.36	0	75
	%Rock cover	0.17	1.65	0	25
	%Logs cover	0.17	1.43	0	20
	%Litter cover	33.50	19.83	0	90
	Litter depth ^{a}	2.05	1.32	0	6
	%Dead Biomass cover ^{b,c}	10.30	16.46	0	85
	Dead Biomass height ^{c}	5.52	5.59	0	38
	%Grass cover	36.84	20.93	0	100
	%Exotic Forb cover	5.19	9.55	0	60
	Tussock distance	28.72	13.64	4	60
	Tussock height	11.82	5.83	0	55
	Tussock diameter	13.78	5.22	0	49
	%Cryptogam cover	0.15	1.00	0	12
#	*%Native Forb cover*	18.42	18.00	1	80
*	*Total vegetation cover*	90.90	12.32	17	100

Case plots only, * Total cover of grasses (dead and alive) and forbs

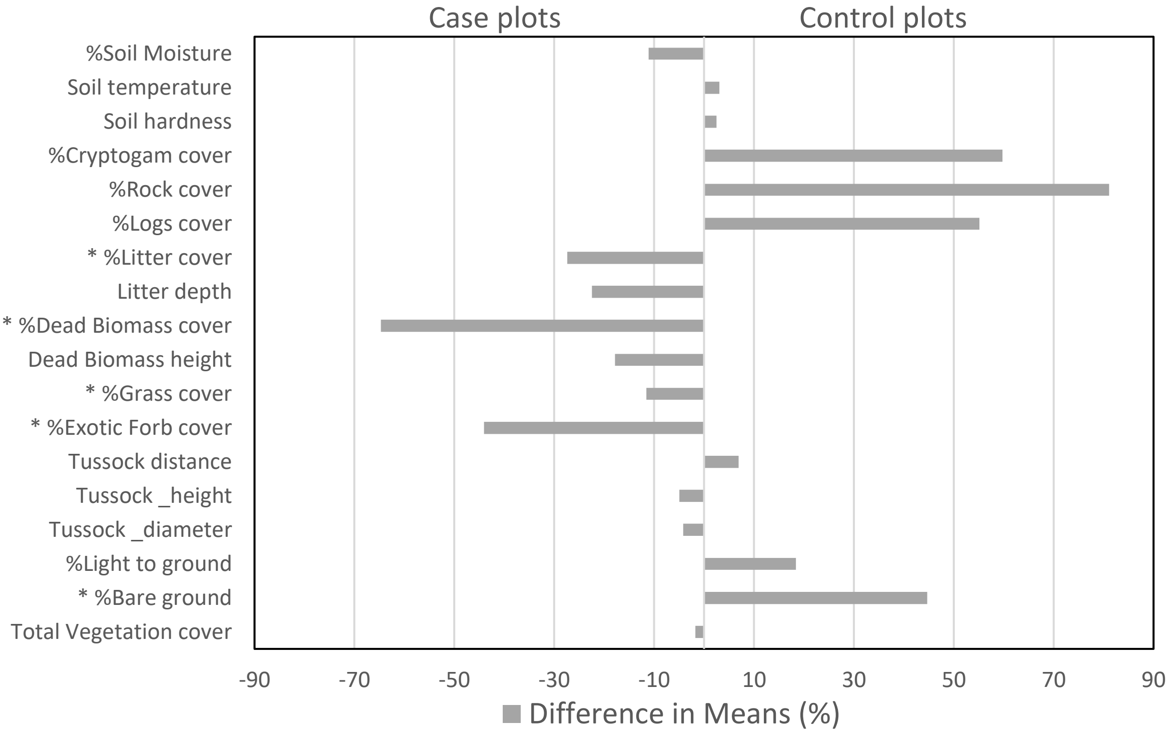

Fig. 2. The difference between the means in case and control plots as a percentage of the Case means – i.e. (Case – Control)/Case * 100 – for all explanatory variables. Significant variables are indicated by an Asterix.

The best conditional logistic model (lowest BIC) selected to predict the odds of a native forb being present included: %Bare ground area, %Ground litter cover, %Dead biomass cover, %Grass cover and %Exotic forb cover (Table 3). The selected model indicated that, for each percentage increase in the area of bare ground, ground litter cover, dead biomass cover, grass cover or exotic forb cover, the odds that a native forb will be present declined by a mean of 10-13% (Table 3).

Table 3. Terms in the best conditional logistic regression model used to predict the odds that a native forb is present. Estimates for each variable, standard errors, statistical significance, odds ratio with 95% confidence interval and model BIC. Delta-BICs (relative to best-model, including all these variables, with BIC = 217.7) indicates the change in BIC that would occur if a single variable is omitted from the model.

Variable	Estimate	Std Error	P-value	Odds ratio	95% confidence interval for odds ratio	Delta-BIC

%Bare ground	-0.104	0.026	< 0.001	0.901	0.878 - 0.925	+ 7
%Litter cover	-0.122	0.018	< 0.001	0.885	0.869 - 0.901	+ 92
%Dead biomass cover	-0.125	0.020	< 0.001	0.883	0.865 - 0.901	+ 70
%Grass cover	-0.101	0.016	< 0.001	0.904	0.890 - 0.918	+ 68
%Exotic Forb cover	-0.135	0.028	< 0.001	0.874	0.850 - 0.898	+ 36

Discussion

We found that, nine years after domestic livestock grazing was removed, the likelihood of a native forb being present was inversely associated with the cover of grasses and exotic forbs, and bare ground, with little influence from the physical structure and spatial configuration of larger tussock species.

The negative influence of vegetation cover (litter cover, dead biomass cover, grass cover and exotic forb cover) agrees with research conducted at plot-scale and larger (> 1m^2), regarding the effects of competition from dominant grasses (Ceulemans *et al.* 2013; Daehler 2003; Dorrough and Scroggie 2008; Hobbs and Huenneke 1992; Seabloom *et al.* 2015) and exotic species have on other species (Dawson *et al.* 2012; Scharfy *et al.* 2011), and seedling restriction by litter (Johnson *et al.* 2018; Loydi *et al.* 2013). Consistent with Scherrer (2019), these results suggest that native forb occupancy was more sensitive to variation in biotic interactions with grasses and exotic forbs (grass cover, forb cover, standing dead biomass, litter) and the area of bare ground over a short distance (1-5 m) than physical structure (average tussock height and diameter, distance to tussock) or other abiotic conditions (eg. soil moisture, temperature and hardness). Note that (total) area of bare ground does not imply gap size or physical structure.

Ground litter and standing dead biomass were negatively associated with native forb occupancy, and had the greatest influence on the accuracy of the model (Delta-BIC = 92 and 70, respectfully) most likely due to their effects on the regeneration niche (recruitment conditions) (Kelemen *et al.* 2013; O'Halloran *et al.* 2013). Ground litter affects the regeneration niche by obstructing the arrival of seed (Ruprecht and Szabó 2012) and seedling emergence (Johnson *et al.* 2018; Letts *et al.* 2015). Negative correlations between light reaching the ground, and litter depth and percentage dead biomass cover (r = -0.68 and -0.61 respectively) suggests that the reduction of light may be one mechanism for the negative effects of litter and dead biomass on native forbs. Light affects germination of some native forb species (Morgan 1998a), and early survival (Borer *et al.* 2014; Hautier *et al.* 2009) of forbs. Litter and standing dead biomass can also have a positive effect on seedling survival through the retention of soil moisture (Loydi *et al.* 2013), but available soil moisture can also increase the likelihood that native forbs are replaced by species in other functional groups

(Tzialla *et al.* 2006), such as exotic plant species. We suggest that light restriction from litter and standing dead biomass interferes with the stabilizing mechanisms needed for coexistence of forbs and grasses on a small scale (Chesson 2000; Scherrer *et al.* 2019).

The cover of living grass and exotic forbs were also negatively associated with native forb occupancy. Living grasses can affect native forbs by competing with them for space and resources (light, moisture, nutrients) (Goldberg and Barton 1992; Johnson *et al.* 2018; Staples *et al.* 2016). However, light and moisture availability may also depend on the height and openness of the canopy (Borer *et al.* 2014), which influence light penetration and evaporation. Our finding that the cover of living and dead biomass (from grasses and exotic forbs) is negatively associated with native forb occupancy agrees with others who recommend biomass management in productive grasslands (e.g., burning, mowing and raking, light grazing) (Driscoll 2017; Morgan 2015; Prober *et al.* 2007).

The negative influence of gap-dwelling exotic forbs on native forb occupancy supports previous research associating the arrival of exotic species with a decline in native species richness on a fine scale (Brandt and Seabloom 2012; Lunt and Morgan 1999; McIntyre and Tongway 2005). By studying native forb occupancy in relation to exotic forb cover we were able to observe the effects of competition between functionally similar plants at neighbourhood level. Our results showed a decline in native forb occupancy with increasing cover of exotic forbs, supporting Price and Pärtel (2013) who found that limiting similarity alone does not protect established native forbs in natural communities from being replaced by functionally similar exotic species. This suggests that, in addition to the restriction resulting from limiting similarity on the level of coexistence between native and exotic forbs, the exotic forb species present may have an overall competitive advantage over the native forb species. The two groups are coexisting on a broader scale, but we can only speculate on the relative extents of native and exotic forb cover prior to the removal of grazing, and since then, whether either group has been gaining space previously occupied by the other group.

The negative influence that (total) area of bare ground had on native forb occupancy is counter-intuitive, as gaps between tussocks can provide habitat for subordinate species (Hellström *et al.* 2009; Morgan 1998b), and implies that habitat quality within some gaps may not be suitable for forbs. We propose two reasons why forbs may not have found suitable habitat conditions in gaps: average gaps sizes were too small, or the soil surface was unsuitable for establishment. Total bare ground area could potentially increase if gaps become greater in number while remaining small enough to affect adult forb survival or too small to isolate seedlings from competition (Fibich *et al.* 2013; Morgan 1998b). Even though the average gap radius between larger tussocks (28.72 cm) was much greater than 18 cm (the threshold below which Morgan (1998b) suggests native forb seedling survival may be affected), the gaps between smaller grasses (not measured in our study) generally appeared much smaller than 18 cm. It is also possible that years of compaction from grazing have degraded soil surface condition and led to lower rates of infiltration and nutrient cycling (McIntyre and Tongway 2005), affecting seed germination in some bare ground patches. However, soil hardness was not a significant influence and the mean total vegetation cover of 90.9% (Table 2) suggests generally non-hostile soil conditions.

The relative importance of competitive biotic interactions identified in our results are consistent with predictions for productive grassland (Scherrer *et al.* 2019). We would expect fewer negative effects of litter and dead biomass in unproductive areas (Morgan 1998b; Williams *et al.* 2007) where there is less biomass produced, less competition from dominant species (Price and Morgan 2010), and greater filtering by abiotic conditions relative to biotic interactions (the stress gradient hypothesis) (Spotswood *et al.* 2017). We acknowledge that forb occurrence in the study site may have been slightly affected by grazing by kangaroos and rabbits, even though populations of both are managed, indirectly because these wild grazers consume grass biomass, and directly because forbs are a part of the normal diet of rabbits (Travers *et al.* 2018).

We do not have data to represent the site prior to the removal of grazing by livestock and therefore cannot draw conclusions about the combined influence of previous grazing and subsequent biomass accumulation on the trajectory of recovery (or degradation) towards a pre-modified physical structure or forb diversity. However, our study suggests that many forb species persisted through the grazed period, during which grazing intensity was reportedly low (King, 1996), and survived nine years of unmanaged biomass levels, although abundance for many species was low (average 4.8 plots per species, of 145 case plots, Table S2 in Appendix S2). We did not find evidence of renewed influence from a recovering physical structure, but our results add to existing evidence suggesting that the abundance and diversity of native forbs in temperate grasslands will benefit from management to control grass biomass and reduce the cover of exotic forbs.

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Supporting Information

Appendix S1: Explanatory variables

Appendix S2: Plant species

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Appendix S1: Explanatory variables

Table S1. Potential explanatory variables and reasons/comments regarding their selection.

Explanatory variable	Selection reason/comments
%Soil moisture *Soil temperature* *Soil hardness*	Soil conditions influence forb germination and seedling survival (Fay and Schultz 2009; Harper *et al.* 1965; Morgan 1998a; Pennington *et al.* 2017; Prober *et al.* 2014) as well as resource availability for gap dwelling species. May be affected by physical tussock structure and the presence of rocks, logs (Goldin and Hutchinson 2015) and cryptogams (Eldridge 1993). Landscape position (e.g. high or low, drainage or ridge) may also influence soil moisture and temperature and may have greater influence on the spatial distribution of plant species composition and abundance.
%Light to ground *%Bare ground*	Light penetration and bare ground influence microsite suitability for germination and young seedlings, and provide alternate metrics associated with gap size and grass cover (Morgan 1998b).
%Rocks *%Logs*	Rock and log cover preclude forbs from occupying that space.
%Litter cover *Litter depth*	Litter influences the regeneration niche, through interference during seed dispersal (Ruprecht and Szabó 2012), and seedling emergence (Loydi *et al.* 2013). Cover and depth may influence forbs in different ways.
%Dead biomass cover *Dead biomass height*	Standing dead biomass affects seedling survival primarily through light restriction (Carson and Peterson 1990). Cover and height may influence forbs in different ways.
%Grass cover *%Exotic forb cover*	Grass and exotic forb cover influence the regeneration niche through light restriction and the competition from these plant groups affects native forbs throughout their life (Adler and HilleRisLambers 2008; Gunton and Kunin 2007; Staples *et al.* 2016). Potential for additional biotic interactions between native and functionally similarity exotic forbs.
Tussock distance *Tussock height* *Tussock diameter*	The average distance to and size of grass tussocks influence the regeneration niche through their influence on shelter they provide to forb seedlings, and competition they exert on forbs of any age (Goldberg and Werner 1983; Morgan 1998b).
%Cryptogams	Cryptogam cover can also influence seedling recruitment by altering soil surface conditions, and the on-going growth and survival of seedlings by competing for resources (Chamizo *et al.* 2012).

Appendix S2: Plant species

Table S2. Species list of recorded plants, including longevity, the number of plots and average cover.

Species	Longevity	Plots	Avg Cover	Species	Longevity	Plots	Avg Cover
Grasses - Exotic				Grasses - Native			
Aira spp	Annual	31	7	*Austrostipa bigeniculata*	Perennial	44	15
Avena sativa	Annual	46	17	*Austrostipa scabra*	Perennial	44	12
Briza minor	Annual	13	5	*Bothriochloa macra*	Perennial	18	14
Bromus diandrus	Annual	30	14	*Dichelachne spp*	Perennial	1	25
Bromus hordaceous	Annual	108	4	*Elymus scaber*	Perennial	25	3
Cynosurus echinatus	Annual	2	1	*Eragrostis brownii*	Perennial	4	5
Holcus lanatus	Annual	5	3	*Microleana stipoides*	Perennial	107	18
Vulpia spp	Annual	59	7	*Panicum effusum*	Perennial	4	4
Lolium perenne	Perennial	8	2	*Poa labilladieri*	Perennial	1	5
Phalaris aquatica	Perennial	6	21	*Poa sieberiana*	Perennial	22	13
				Rytidosperma spp	Perennial	59	8
				Themeda australis	Perennial	311	30
Forbs - Exotic				Forbs - Native (Case plots)			
Centaurium erythraea	Annual	1	1	*Euchiton sphaericus*	Annual	1	40
Conyza bonariensis	Annual	18	3	*Triptilodiscus pygmaeus*	Annual	5	3
Echium plantagineum	Annual	2	3	*Hypericum gramineum*	Either	5	4
Hypochaeris glabra	Annual	38	4	*Vittadinia cuneata*	Either	6	29
Lactuca serriola	Annual	14	5	*Acaena ovina*	Perennial	7	20
Petrorhagia nanteuilii	Annual	28	5	*Asperula conferta*	Perennial	3	8
Plantago lanceolata	Annual	30	6	*Bulbine bulbosa*	Perennial	11	8
Sonchus oleraceus	Annual	2	1	*Cheilanthes spp*	Perennial	6	15
Tolpis barbata	Annual	8	2	*Chrysocephalum apiculatum*	Perennial	14	29
Tragopogon dubias	Annual	6	3	*Convolvulus erubescens*	Perennial	3	5
Trifolium angustifolium	Annual	1	1	*Cymbonotus preissianus*	Perennial	9	9
Trifolium arvense	Annual	9	7	*Desmodium varians*	Perennial	1	3
Trifolium glomeratum	Annual	2	1	*Dichondra repens*	Perennial	4	25
Trifolium subterranean	Annual	10	11	*Dichopogon fimbriatus*	Perennial	3	10
Carthamus lanatus	Annual	4	3	*Eryngium ovinum*	Perennial	6	12
Cirsium vulgare	Annual	24	8	*Euchiton gymnocephalus*	Perennial	1	20
Acetosella vulgaris	Perennial	33	11	*Gonocarpus tetragynus*	Perennial	1	4
Chondrilla juncea	Perennial	5	6	*Haloragis heterophylla*	Perennial	5	44
Hypericum perforatum	Perennial	75	10	*Hydrocotyle laxiflora*	Perennial	6	23
Hypochaeris radicata	Perennial	28	9	*Leptorhynchos squamatus*	Perennial	11	7
Paronychia brasiliana	Perennial	7	9	*Oxalis perennans*	Perennial	2	23
Sanguisorba minor	Perennial	1	20	*Plantago varia*	Perennial	11	20
				Senecio quadridentatus	Perennial	2	9
Rushes & Sedges				*Solenogyne dominii*	Perennial	2	20
Lomandra filiformis	Perennial	24	8	*Tricoryne elatior*	Perennial	6	6
Lomandra longifolia	Perennial	1	15	*Vittadinia meulleri*	Perennial	2	6
Carex inversa	Perennial	11	8	*Wahlenbergia stricta*	Perennial	12	6

Juncus filicaulis	Perennial	2	2
Other sedge		14	4
Other			
Rubus spp	Perennial	1	8

Forbs - Native (Control plots only)			
Erodium crinitum	Annual	1	5
Euchiton involucratis	Perennial	1	5
Geranium solanderi	Perennial	2	3
Rumex brownii	Perennial	2	16