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# 1 Fine-scale variables associated with the presence of native forbs in 2 natural temperate grassland.

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4 Authors: David P. Johnson, Don A. Driscoll, Jane A. Catford, Philip Gibbons

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6 Johnson, D. P. (Corresponding author, david.johnson@anu.edu.au)<sup>1</sup>

7 Driscoll, D. A. (d.driscoll@deakin.edu.au)<sup>5</sup>

8 Catford, J. A. (jane.catford@kcl.ac.uk)<sup>1,2,3,4</sup>

9 Gibbons, P. (philip.gibbons@anu.edu.au)<sup>1</sup>

10

11 <sup>1</sup>The Fenner School of Environment and Society, The Australian National University, Building 43,  
12 Canberra, ACT 0200, Australia

13 <sup>2</sup>Department of Geography, King's College London, London, WC2B 4BG, UK

14 <sup>3</sup>Biological Sciences, University of Southampton, Southampton SO17 1BJ, UK

15 <sup>4</sup>School of BioSciences, The University of Melbourne, Vic 3010, Australia

16 <sup>5</sup>School of Life and Environmental Sciences, Centre for Integrative Ecology, Deakin University,  
17 Burwood, Vic 3125, Australia

18

## 19 Corresponding Author details

20 Email: david.johnson@anu.edu.au

21 Phone: +61 (0)438 310679

22 Postal address: 177 Morrison Rd, Bywong, NSW 2621

23

## 24 **Abstract**

25 Broad-scale threats to floristic diversity in native temperate grasslands are well-documented and  
26 include elevated soil nutrients, changes in disturbance regimes and exotic species. However, fine-scale  
27 variables associated with the presence of native forbs, such as gap size and biomass cover, have  
28 received relatively little attention. We conducted a case-control study to determine the relative  
29 influence of physical structural dimensions and other fine-scale variables associated with the presence  
30 of native forbs in a modified temperate grassland previously used for domestic grazing. We matched  
31 145 case plots centred on 27 different species of native forb with 290 control plots not centred on a  
32 native forb. For each percentage increase in ground litter cover, dead biomass cover, grass cover or  
33 exotic forb cover, or the area of bare ground within 30 cm, the relative odds that a native forb was  
34 present vs absent declined by a mean of 10-13%. Living and dead biomass reduces light availability and  
35 the former can also reduce nutrient and water availability. Declines in the presence of native forbs

36 associated with increasing total bare ground may suggest that gap sizes were too small or the soil  
37 surface condition too degraded. Our results add to a body of evidence suggesting that native forbs in  
38 temperate native grassland are likely to benefit from periodic removal of living and dead grass biomass  
39 and a reduction in the cover of exotic forbs.

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

41

## 42 Introduction

43 Biodiversity has declined in native grasslands as a result of agriculture, urbanisation, and altered  
44 disturbance regimes (Howe 1994; Kiehl *et al.* 2006; McDougall and Morgan 2005; McIntyre 2011;  
45 Öster *et al.* 2009). Native forbs have declined considerably in grassland ecosystems as a result of these  
46 changes (Brandt and Seabloom 2012; Stevens *et al.* 2010; Tremont and McIntyre 1994). Native forbs  
47 are an important component of species and functional diversity in grasslands (Lavorel *et al.* 2011;  
48 McCain *et al.* 2010; Pallett *et al.* 2016; Tremont and McIntyre 1994). They contribute to a range of  
49 ecosystem services such as water infiltration and invasion resistance, have aesthetic value (Tilman *et al.*  
50 2006; Tschardt *et al.* 2005; Wratten *et al.* 2012) and can influence fire behaviour (Wragg *et al.*  
51 2018). Native forbs are more likely than exotic forbs to be well adapted to historic conditions (Brandt  
52 and Seabloom 2011; Flores-Moreno *et al.* 2016) and to provide habitat resources required by native  
53 fauna (Antos and Williams 2015), including some which perform ecosystem services such as pollination  
54 and biological pest control (Isaacs *et al.* 2009; Schmidt-Entling and Döbeli 2009; Williams *et al.* 2015;  
55 Wratten *et al.* 2012). Thus, the conservation and restoration of native forb diversity has garnered  
56 considerable interest (Foley *et al.* 2005; Hobbs *et al.* 2013; Suding 2011).

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

67 Grassland species composition is influenced by competition and the physical structure defined  
68 by the dominant grass species (Morgan and Williams 2015; Tremont and McIntyre 1994). Functional  
69 differences and spatial partitioning allow sub-dominant species (e.g. forbs and smaller grasses) to

70 coexist with the dominant grasses, and each other, within the gaps between grass tussocks (McIntyre  
71 *et al.* 1995). The size and shape of gaps and the surrounding vegetation influence the conditions  
72 provided for germination (e.g. light, diurnal temperature fluctuations, moisture) and later survival (e.g.  
73 available light, moisture and nutrients) (Isselstein *et al.* 2002; Jiménez-Alfaro *et al.* 2016), and the  
74 amount of shelter from adverse environmental conditions and grazing (Diaz *et al.* 2007; Morgan  
75 1998b). Thus, physical structure and gap characteristics can influence the range of species able to use  
76 the gap (Bullock *et al.* 1995; Fibich *et al.* 2013; Liao *et al.* 2015) and the stabilizing mechanisms  
77 allowing their coexistence (mainly limiting similarity) (Price *et al.* 2017). Morgan (1998b) found that  
78 seedling survival of five native forb species in natural temperate grassland declined in gaps with radii  
79 less than 18 cm due to reduced light availability at ground level. McIntyre (2005) suggests that  
80 grassland swards with a physical/gap structure defined by tall tussock-forming species are likely to  
81 support greater overall biodiversity than short-statured swards.

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

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

105 achieve a resemblance of their pre-agricultural state, if at all (McIntyre and Lavorel 2007; McIntyre *et*  
106 *al.* 2017).

107 The aim of our study was to identify fine-scale variables associated with the occupancy of  
108 forbs in a modified grassland following the removal of grazing, without alternate types of disturbance  
109 to control biomass. Existing studies, such as the one conducted by Kelemen *et al* (2013), have  
110 compared the relative influence of above-ground biotic components, such as functional plant groups  
111 (grasses and exotic forbs), standing dead biomass and ground litter, on species richness, but we are  
112 not aware of other studies of the fine-scale variables associated with native forb occupancy within  
113 Australian temperate grassland. While observations at larger scales are appropriate for studying the  
114 influences of site-scale environmental conditions (eg. soil type, climate, elevation) (Whittaker *et al.*  
115 2001), a fine-scale approach is needed to capture variables that influence the ability of a forb to  
116 coexist with neighbouring grassland species (Liao *et al.* 2015; Miller *et al.* 2009; Saiz *et al.* 2016;  
117 Scherrer *et al.* 2019; Sears and Chesson 2007; Spotswood *et al.* 2017).

118

## 119 **Methods**

### 120 Study area

121 Our study was undertaken in an area of modified natural temperate grassland within approximately 70  
122 hectares of grassy woodland within a recently declared nature reserve in the Australian Capital  
123 Territory (ACT) in south-eastern Australia (35.270562°S, 149.026425° E). Prior to its declaration as a  
124 nature reserve in 2010, the site had a history of grazing by sheep and then cattle. Grazing ceased in  
125 2005. The study area is approximately 580 m above sea level, has a median annual rainfall of 650 mm  
126 and a mean minimum and maximum daily temperature of 7.0° and 20.8° Celsius  
127 (<http://www.bom.gov.au/climate/data/index.shtml>). Soils in the study area have low to moderate  
128 fertility (King, 1996), except where super-phosphate was applied with *Avena sativa* and *Trifolium*  
129 *subterraneum* seed sown from as early as 1947 (ACT Govt. Environment and Planning Directorate,  
130 TL2432#01 - Department of the Interior - Property and Survey Branch. Block 21 Belconnen - O.H.  
131 Dixon). Vegetation in the ground-layer ranges from areas dominated by exotic grasses and forbs to  
132 areas dominated by native species. There is on-going low intensity grazing by the eastern grey  
133 kangaroo (*Macropus giganteus*) and European rabbit (*Oryctolagus cuniculus*), with both species  
134 managed by occasional population control. A portion of the site was affected by fire in 2003, and areas  
135 of St John's Wort (*Hypericum perforatum*) infestation were boom-sprayed with a non-residual  
136 selective broadleaf herbicide (fluroxypyr) in 2011 and 2012.

137

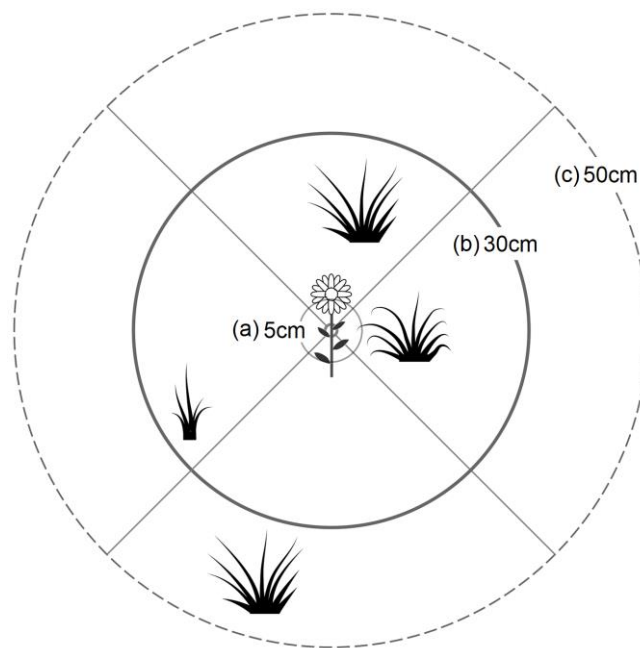
138

## 139 Data collection

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

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

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



172

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

181

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

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

193

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

Explanatory variable	Definition	Collection method
<i>%Soil moisture</i>	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
<i>Soil temperature</i>	Soil temperature 6cm deep (Celsius)	Measured with Milwaukee TH310 temperature probe in a gap within 5 cm of the plot centre
<i>Soil hardness</i>	Soil surface hardness (0-5 kgf.cm <sup>2</sup> )	Measured with Controls brand 16-T0171 hand-held soil penetrometer in an undisturbed gap within 5 cm of the plot centre
<i>%Light to ground</i>	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
<i>%Bare ground</i>	Percentage area of bare ground	Visual estimation within a circular plot with 30 cm radius
<i>%Rocks</i>	Percentage of area covered by rocks	Visual estimation within a circular plot with 30 cm radius
<i>%Logs</i>	Percentage of area covered by coarse woody debris	Visual estimation within a circular plot with 30 cm radius
<i>%Litter cover</i>	Percentage of area covered by dead plant material lying on the ground	Visual estimation within a circular plot with 30 cm radius
<i>Litter depth</i>	Litter depth (cm)	Average of 3 random measurements within a circular plot with 30 cm radius
<i>%Dead biomass cover</i>	Percentage of area covered by dead plant material still standing	Visual estimation within a circular plot with 30 cm radius
<i>Dead biomass height</i>	Height of standing dead biomass in cm	Average of 3 random measurements within a circular plot with 30 cm radius
<i>%Grass cover</i>	Percentage of area covered by living grasses	Calculated based on visual cover estimations of each species in a circular plot with 30 cm radius
<i>%Exotic forb cover</i>	Percentage of area covered by exotic forb species	Calculated based on visual cover estimations of each species in the plot
<i>Tussock distance</i>	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
<i>Tussock height</i>	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
<i>Tussock diameter</i>	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
<i>%Cryptogams</i>	Percentage of area covered by cryptogams	Calculated based on visual estimations within a circular plot with 30 cm radius



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

207

### 208 Data analysis

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

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

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

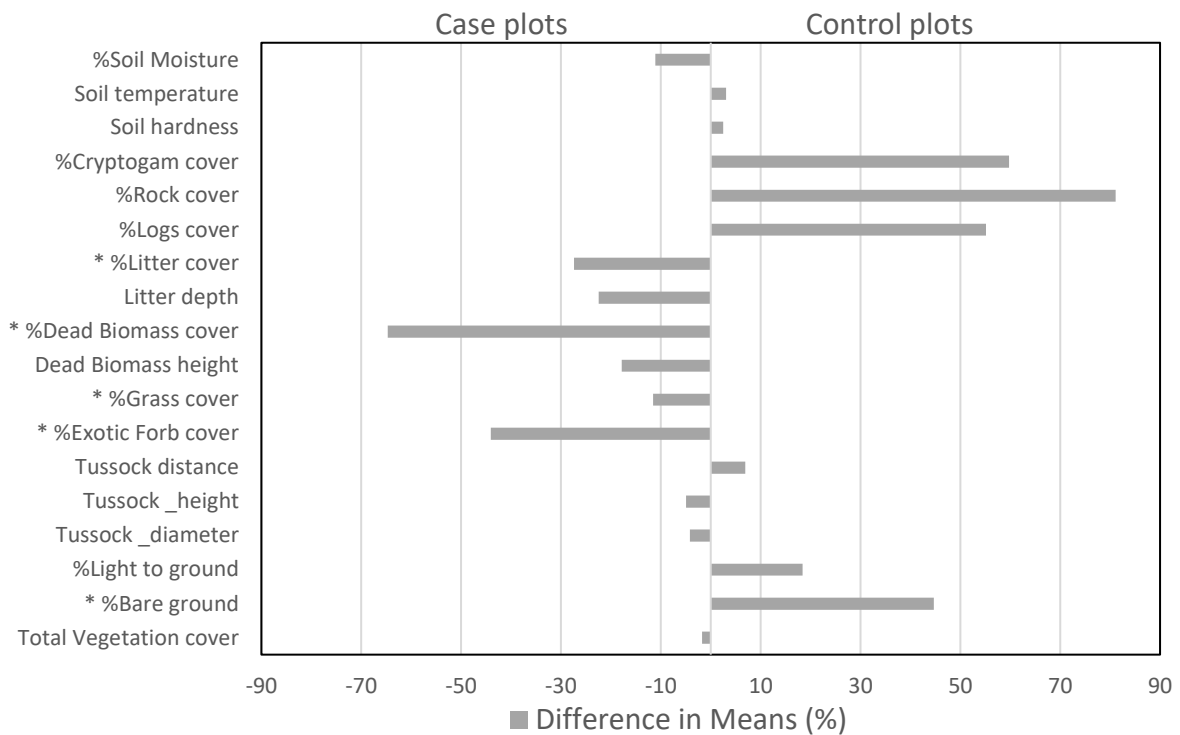
## 231 Results

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

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

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

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



244

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

248

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

254

255 **Table 3.** Terms in the best conditional logistic regression model used to predict the odds that a native  
 256 forb is present. Estimates for each variable, standard errors, statistical significance, odds ratio with  
 257 95% confidence interval and model BIC. Delta-BICs (relative to best-model, including all these  
 258 variables, with BIC = 217.7) indicates the change in BIC that would occur if a single variable is omitted  
 259 from the model.

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

%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

260

## 261 Discussion

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

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

276 Ground litter and standing dead biomass were negatively associated with native forb  
 277 occupancy, and had the greatest influence on the accuracy of the model (Delta-BIC = 92 and 70,  
 278 respectfully) most likely due to their effects on the regeneration niche (recruitment conditions)  
 279 (Kelemen *et al.* 2013; O'Halloran *et al.* 2013). Ground litter affects the regeneration niche by  
 280 obstructing the arrival of seed (Ruprecht and Szabó 2012) and seedling emergence (Johnson *et al.*  
 281 2018; Letts *et al.* 2015). Negative correlations between light reaching the ground, and litter depth and  
 282 percentage dead biomass cover ( $r = -0.68$  and  $-0.61$  respectively) suggests that the reduction of light  
 283 may be one mechanism for the negative effects of litter and dead biomass on native forbs. Light  
 284 affects germination of some native forb species (Morgan 1998a), and early survival (Borer *et al.* 2014;  
 285 Hautier *et al.* 2009) of forbs. Litter and standing dead biomass can also have a positive effect on  
 286 seedling survival through the retention of soil moisture (Loydi *et al.* 2013), but available soil moisture  
 287 can also increase the likelihood that native forbs are replaced by species in other functional groups

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

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

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

312 The negative influence that (total) area of bare ground had on native forb occupancy is  
313 counter-intuitive, as gaps between tussocks can provide habitat for subordinate species (Hellström *et al.*  
314 *et al.* 2009; Morgan 1998b), and implies that habitat quality within some gaps may not be suitable for  
315 forbs. We propose two reasons why forbs may not have found suitable habitat conditions in gaps:  
316 average gaps sizes were too small, or the soil surface was unsuitable for establishment. Total bare  
317 ground area could potentially increase if gaps become greater in number while remaining small  
318 enough to affect adult forb survival or too small to isolate seedlings from competition (Fibich *et al.*  
319 2013; Morgan 1998b). Even though the average gap radius between larger tussocks (28.72 cm) was  
320 much greater than 18 cm (the threshold below which Morgan (1998b) suggests native forb seedling  
321 survival may be affected), the gaps between smaller grasses (not measured in our study) generally  
322 appeared much smaller than 18 cm. It is also possible that years of compaction from grazing have

323 degraded soil surface condition and led to lower rates of infiltration and nutrient cycling (McIntyre and  
324 Tongway 2005), affecting seed germination in some bare ground patches. However, soil hardness was  
325 not a significant influence and the mean total vegetation cover of 90.9% (Table 2) suggests generally  
326 non-hostile soil conditions.

327 The relative importance of competitive biotic interactions identified in our results are  
328 consistent with predictions for productive grassland (Scherrer *et al.* 2019). We would expect fewer  
329 negative effects of litter and dead biomass in unproductive areas (Morgan 1998b; Williams *et al.* 2007)  
330 where there is less biomass produced, less competition from dominant species (Price and Morgan  
331 2010), and greater filtering by abiotic conditions relative to biotic interactions (the stress gradient  
332 hypothesis) (Spotswood *et al.* 2017). We acknowledge that forb occurrence in the study site may have  
333 been slightly affected by grazing by kangaroos and rabbits, even though populations of both are  
334 managed, indirectly because these wild grazers consume grass biomass, and directly because forbs are  
335 a part of the normal diet of rabbits (Travers *et al.* 2018).

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

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## 352 Supporting Information

353 Appendix S1: Explanatory variables

354 Appendix S2: Plant species

## 355 References

- 356 ACT Govt. Environment and Planning Directorate, TL2432#01 - Department of the Interior - Property  
357 and Survey Branch. Block 21 Belconnen - O.H. Dixon
- 358 King, G. (1996). "Property survey – 'Kama', Formally Block 167 Belconnen", ACT Govt. Parks and  
359 Conservation.
- 360 Antos M. & Williams N. S. G. (2015) The wildlife of our grassy landscapes. In: *Land of sweeping plains:  
361 managing and restoring the native grasslands of south-eastern Australia* (eds N. S. G. Williams, A. J.  
362 Marshall and J. W. Morgan). CSIRO Publishing.
- 363 Borer E. T., Seabloom E. W., Gruner D. S., Harpole W. S., Hillebrand H., Lind E. M., Adler P. B., Alberti J.,  
364 Anderson T. M., Bakker J. D., Biederman L., Blumenthal D., Brown C. S., Brudvig L. A., Buckley Y. M.,  
365 Cadotte M., Chu C., Cleland E. E., Crawley M. J., Daleo P., Damschen E. I., Davies K. F., DeCrappeo N. M.,  
366 Du G., Firn J., Hautier Y., Heckman R. W., Hector A., HilleRisLambers J., Iribarne O., Klein J. A., Knops J.  
367 M. H., La Pierre K. J., Leakey A. D. B., Li W., MacDougall A. S., McCulley R. L., Melbourne B. A., Mitchell  
368 C. E., Moore J. L., Mortensen B., O'Halloran L. R., Orrock J. L., Pascual J., Prober S. M., Pyke D. A., Risch  
369 A. C., Schuetz M., Smith M. D., Stevens C. J., Sullivan L. L., Williams R. J., Wragg P. D., Wright J. P. & Yang  
370 L. H. (2014) Herbivores and nutrients control grassland plant diversity via light limitation. *Nature* **508**,  
371 517-20.
- 372 Brandt A. J. & Seabloom E. W. (2011) Regional and decadal patterns of native and exotic plant  
373 coexistence in California grasslands. *Ecological Applications* **21**, 704-14.
- 374 Brandt A. J. & Seabloom E. W. (2012) Seed and establishment limitation contribute to long-term native  
375 forb declines in California grasslands. *Ecology* **93**, 1451-62.
- 376 Bullock J. M., Hill B. C., Silvertown J. & Sutton M. (1995) Gap Colonization as a Source of Grassland  
377 Community Change: Effects of Gap Size and Grazing on the Rate and Mode of Colonization by Different  
378 Species. *Oikos* **72**, 273-82.
- 379 Ceulemans T., Merckx R., Hens M. & Honnay O. (2013) Plant species loss from European semi-natural  
380 grasslands following nutrient enrichment – is it nitrogen or is it phosphorus? *Global Ecology and  
381 Biogeography* **22**, 73-82.
- 382 Chesson P. (2000) Mechanisms of Maintenance of Species Diversity. *Annual Review of Ecology and  
383 Systematics* **31**, 343-66.
- 384 Daehler C. C. (2003) Performance Comparisons of Co-Occurring Native and Alien Invasive Plants:  
385 Implications for Conservation and Restoration. *Annual Review of Ecology, Evolution, and Systematics* **34**,  
386 183-211.
- 387 Dawson W., Rohr R. P., van Kleunen M. & Fischer M. (2012) Alien plant species with a wider global  
388 distribution are better able to capitalize on increased resource availability. *New Phytologist* **194**, 859-  
389 67.
- 390 Diaz S., Lavorel S., McIntyre S. U. E., Falczuk V., Casanoves F., Milchunas D. G., Skarpe C., Rusch G.,  
391 Sternberg M., Noy-Meir I., Landsberg J., Zhang W. E. I., Clark H. & Campbell B. D. (2007) Plant trait  
392 responses to grazing – a global synthesis. *Global Change Biology* **13**, 313-41.
- 393 Dix R. L. (1961) An Application of the Point-Centered Quarter Method to the Sampling of Grassland  
394 Vegetation. *Journal of Range Management* **14**, 63-9.
- 395 Dorrrough J. & Scroggie M. P. (2008) Plant responses to agricultural intensification. *Journal of Applied  
396 Ecology* **45**, 1274-83.
- 397 Driscoll D. A. (2017) Disturbance maintains native and exotic plant species richness in invaded grassy  
398 woodlands. *Journal of Vegetation Science* **28**, 573-84.
- 399 Fibich P., Vítová A., Macek P. & Lepš J. (2013) Establishment and spatial associations of recruits in  
400 meadow gaps. *Journal of Vegetation Science* **24**, 496-505.
- 401 Flores-Moreno H., Reich P. B., Lind E. M., Sullivan L. L., Seabloom E. W., Yahdjian L., MacDougall A. S.,  
402 Reichmann L. G., Alberti J., Báez S., Bakker J. D., Cadotte M. W., Caldeira M. C., Chaneton E. J., D'Antonio  
403 C. M., Fay P. A., Firn J., Hagenah N., Harpole W. S., Iribarne O., Kirkman K. P., Knops J. M. H., La Pierre K.  
404 J., Laungani R., Leakey A. D. B., McCulley R. L., Moore J. L., Pascual J. & Borer E. T. (2016) Climate modifies  
405 response of non-native and native species richness to nutrient enrichment. *Philosophical Transactions  
406 of the Royal Society B: Biological Sciences* **371**.

- 407 Foley J. A., DeFries R., Asner G. P., Barford C., Bonan G., Carpenter S. R., Chapin F. S., Coe M. T., Daily G.  
 408 C., Gibbs H. K., Helkowski J. H., Holloway T., Howard E. A., Kucharik C. J., Monfreda C., Patz J. A., Prentice  
 409 I. C., Ramankutty N. & Snyder P. K. (2005) Global Consequences of Land Use. *Science* **309**, 570-4.
- 410 Fox J. W. (2013) The intermediate disturbance hypothesis should be abandoned. *Trends in Ecology &*  
 411 *Evolution* **28**, 86-92.
- 412 Goldberg D. E. & Barton A. M. (1992) Patterns and Consequences of Interspecific Competition in Natural  
 413 Communities: A Review of Field Experiments with Plants. *The American Naturalist* **139**, 771-801.
- 414 Harper J. L., Williams J. T. & Sagar G. R. (1965) The Behaviour of Seeds in Soil: I. The Heterogeneity of  
 415 Soil surfaces and its Role in Determining the Establishment of Plants from Seed. *Journal of Ecology* **53**,  
 416 273-86.
- 417 Hautier Y., Niklaus P. A. & Hector A. (2009) Competition for Light Causes Plant Biodiversity Loss After  
 418 Eutrophication. *Science* **324**, 636-8.
- 419 Hellström K., Huhta A.-P., Rautio P. & Tuomi J. (2009) Seed introduction and gap creation facilitate  
 420 restoration of meadow species richness. *Journal for Nature Conservation* **17**, 236-44.
- 421 Hobbs R. J. & Huenneke L. F. (1992) Disturbance, Diversity, and Invasion: Implications for Conservation.  
 422 *Conservation Biology* **6**, 324-37.
- 423 Hobbs R. J., Suding K. N., International P. S. E. R., Cale P. & Allen-Diaz B. H. (2013) *New Models for*  
 424 *Ecosystem Dynamics and Restoration*. Island Press.
- 425 Howe H. F. (1994) Managing Species Diversity in Tallgrass Prairie: Assumptions and Implications.  
 426 *Conservation Biology* **8**, 691-704.
- 427 Isaacs R., Tuell J., Fiedler A., Gardiner M. & Landis D. (2009) Maximizing arthropod-mediated ecosystem  
 428 services in agricultural landscapes: the role of native plants. *Frontiers in Ecology and the Environment* **7**,  
 429 196-203.
- 430 Isselstein J., Tallowin J. R. B. & Smith R. E. N. (2002) Factors Affecting Seed Germination and Seedling  
 431 Establishment of Fen-Meadow Species. *Restoration Ecology* **10**, 173-84.
- 432 Jiménez-Alfaro B., Silveira F. A. O., Fidelis A., Poschod P. & Commander L. E. (2016) Seed germination  
 433 traits can contribute better to plant community ecology. *Journal of Vegetation Science* **27**, 637-45.
- 434 Johnson D. P., Catford J. A., Driscoll D. A. & Gibbons P. (2018) Seed addition and biomass removal key to  
 435 restoring native forbs in degraded temperate grassland. *Applied Vegetation Science* **21**, 219-28.
- 436 Keating K. A., Cherry S. & Lubow. (2004) Use and interpretation of logistic regression in habitat-selection  
 437 studies. *Journal of Wildlife Management* **68**, 774-89.
- 438 Kelemen A., Török P., Valkó O., Migléc T. & Tóthmérész B. (2013) Mechanisms shaping plant biomass  
 439 and species richness: plant strategies and litter effect in alkali and loess grasslands. *Journal of Vegetation*  
 440 *Science* **24**, 1195-203.
- 441 Kiehl K., Thormann A. & Pfadenhauer J. (2006) Evaluation of Initial Restoration Measures during the  
 442 Restoration of Calcareous Grasslands on Former Arable Fields. *Restoration Ecology* **14**, 148-56.
- 443 Lavorel S., Grigulis K., Lamarque P., Colace M.-P., Garden D., Girel J., Pellet G. & Douzet R. (2011) Using  
 444 plant functional traits to understand the landscape distribution of multiple ecosystem services. *Journal*  
 445 *of Ecology* **99**, 135-47.
- 446 Letts B., Lamb E., Mischkolz J. & Romo J. (2015) Litter accumulation drives grassland plant community  
 447 composition and functional diversity via leaf traits. *Plant Ecology* **216**, 357-70.
- 448 Levine J. M. & HilleRisLambers J. (2009) The importance of niches for the maintenance of species  
 449 diversity. *Nature* **461**, 254.
- 450 Liao J., De Boeck H. J., Li Z. & Nijs I. (2015) Gap formation following climatic events in spatially structured  
 451 plant communities. *Scientific Reports* **5**, 11721.
- 452 Liberman A. M. (2005) How Much More Likely? The Implications of Odds Ratios for Probabilities.  
 453 *American Journal of Evaluation* **26**, 253-66.
- 454 Lindsay E. & Cunningham S. (2012) Effects of exotic grass invasion on spatial heterogeneity in the  
 455 ground-layer of grassy woodlands. *Biological Invasions* **14**, 203-13.
- 456 Loydi A., Eckstein R. L., Otte A. & Donath T. W. (2013) Effects of litter on seedling establishment in natural  
 457 and semi-natural grasslands: a meta-analysis. *Journal of Ecology* **101**, 454-64.
- 458 Lunt I. D. & Morgan J. W. (1999) Vegetation Changes after 10 Years of Grazing Exclusion and Intermittent  
 459 Burning in a *Themeda triandra* (Poaceae) Grassland Reserve in South-eastern Australia.  
 460 *Australian Journal of Botany* **47**, 537-52.



- 461 Mann C. J. (2003) Observational research methods. Research design II: cohort, cross sectional, and case-  
 462 control studies. *Emergency Medicine Journal* **20**, 54-60.
- 463 McCain K. N. S., Baer S. G., Blair J. M. & Wilson G. W. T. (2010) Dominant Grasses Suppress Local Diversity  
 464 in Restored Tallgrass Prairie. *Restoration Ecology* **18**, 40-9.
- 465 McDougall K. L. & Morgan J. W. (2005) Establishment of native grassland vegetation at Organ Pipes  
 466 National Park near Melbourne, Victoria: Vegetation changes from 1989 to 2003. *Ecological Management  
 467 & Restoration* **6**, 34-42.
- 468 McIntyre B. S. & Tongway D. (2005) Grassland structure in native pastures: links to soil surface condition.  
 469 *Ecological Management & Restoration* **6**, 43-50.
- 470 McIntyre S. (2005) Biodiversity attributes of different sward structures in grazed grassland. *Ecological  
 471 Management & Restoration* **6**, 71-3.
- 472 McIntyre S. (2011) Ecological and anthropomorphic factors permitting low-risk assisted colonization in  
 473 temperate grassy woodlands. *Biological Conservation* **144**, 1781-9.
- 474 McIntyre S. & Lavorel S. (2007) A conceptual model of land use effects on the structure and function of  
 475 herbaceous vegetation. *Agriculture, Ecosystems & Environment* **119**, 11-21.
- 476 McIntyre S., Lavorel S. & Tremont R. M. (1995) Plant Life-History Attributes: Their Relationship to  
 477 Disturbance Response in Herbaceous Vegetation. *Journal of Ecology* **83**, 31-44.
- 478 McIntyre S., Nicholls A. O. & Manning A. D. (2017) Trajectories of floristic change in grassland: landscape,  
 479 land use legacy and seasonal conditions overshadow restoration actions. *Applied Vegetation Science* **20**,  
 480 582-93.
- 481 Miller A., Chesson P., Associate Editor: Claire de M. & Editor: Donald L. D. (2009) Coexistence in  
 482 Disturbance-Prone Communities: How a Resistance-Resilience Trade-Off Generates Coexistence via the  
 483 Storage Effect. *The American Naturalist* **173**, E30-E43.
- 484 Monahan P. O., McHorney C. A., Stump T. E. & Perkins A. J. (2007) Odds Ratio, Delta, ETS Classification,  
 485 and Standardization Measures of DIF Magnitude for Binary Logistic Regression. *Journal of Educational  
 486 and Behavioral Statistics* **32**, 92-109.
- 487 Morgan J. W. (1998a) Comparative Germination Responses of 28 Temperate Grassland Species.  
 488 *Australian Journal of Botany* **46**, 209-19.
- 489 Morgan J. W. (1998b) Importance of Canopy Gaps for Recruitment of some Forbs in *Themeda triandra*-  
 490 dominated Grasslands in South-eastern Australia. *Australian Journal of Botany* **46**, 609-27.
- 491 Morgan J. W. (2015) Biomass management in native grasslands. In: *Land of sweeping plains: managing  
 492 and restoring the native grasslands of south-eastern Australia* (eds N. S. G. Williams, A. J. Marshall and  
 493 J. W. Morgan). CSIRO Publishing.
- 494 Morgan J. W. & Williams N. S. G. (2015) The ecology and dynamics of temperate native grasslands in  
 495 south-eastern Australia. In: *Land of sweeping plains: managing and restoring the native grasslands of  
 496 south-eastern Australia* (eds N. S. G. Williams, A. J. Marshall and J. W. Morgan) pp. 61-85. CSIRO  
 497 Publishing.
- 498 O'Halloran L. R., Borer E. T., Seabloom E. W., MacDougall A. S., Cleland E. E., McCulley R. L., Hobbie S.,  
 499 Harpole W. S., DeCrappeo N. M., Chu C., Bakker J. D., Davies K. F., Du G., Firn J., Hagenah N., Hofmockel  
 500 K. S., Knops J. M. H., Li W., Melbourne B. A., Morgan J. W., Orrock J. L., Prober S. M. & Stevens C. J. (2013)  
 501 Regional Contingencies in the Relationship between Aboveground Biomass and Litter in the World's  
 502 Grasslands. *PLoS ONE* **8**, e54988.
- 503 Öster M., Ask K., Römermann C., Tackenberg O. & Eriksson O. (2009) Plant colonization of ex-arable  
 504 fields from adjacent species-rich grasslands: The importance of dispersal vs. recruitment ability.  
 505 *Agriculture, Ecosystems & Environment* **130**, 93-9.
- 506 Pallett D. W., Pescott O. L. & Schäfer S. M. (2016) Changes in plant species richness and productivity in  
 507 response to decreased nitrogen inputs in grassland in southern England. *Ecological Indicators* **68**, 73-81.
- 508 Price J., Tamme R., Gazol A., de Bello F., Takkis K., Uria-Diez J., Kasari L. & Pärtel M. (2017) Within-  
 509 community environmental variability drives trait variability in species-rich grasslands. *Journal of  
 510 Vegetation Science* **28**, 303-12.
- 511 Price J. N., Gazol A., Tamme R., Hiiesalu I. & Pärtel M. (2013) The functional assembly of experimental  
 512 grasslands in relation to fertility and resource heterogeneity. *Functional Ecology*, n/a-n/a.
- 513 Price J. N. & Morgan J. W. (2010) Small-scale patterns of species richness and floristic composition in  
 514 relation to microsite variation in herb-rich woodlands. *Australian Journal of Botany* **58**, 271-9.

- 515 Price J. N. & Pärtel M. (2013) Can limiting similarity increase invasion resistance? A meta-analysis of  
 516 experimental studies. *Oikos* **122**, 649-56.
- 517 Prober S. M. & Thiele K. R. (2005) Restoring Australia's temperate grasslands and grassy woodlands:  
 518 integrating function and diversity. *Ecological Management & Restoration* **6**, 16-27.
- 519 Prober S. M., Thiele K. R. & Lunt I. D. (2007) Fire frequency regulates tussock grass composition, structure  
 520 and resilience in endangered temperate woodlands. *Austral Ecology* **32**, 808-24.
- 521 Prober S. M., Thiele K. R. & Speijers J. (2013) Management legacies shape decadal-scale responses of  
 522 plant diversity to experimental disturbance regimes in fragmented grassy woodlands. *Journal of Applied*  
 523 *Ecology* **50**, 376-86.
- 524 R Core Team. (2016) R: A language and environment for statistical computing. R Foundation for  
 525 Statistical Computing, Vienna, Austria.
- 526 Roxburgh S. H., Shea K. & Wilson J. B. (2004) THE INTERMEDIATE DISTURBANCE HYPOTHESIS: PATCH  
 527 DYNAMICS AND MECHANISMS OF SPECIES COEXISTENCE. *Ecology* **85**, 359-71.
- 528 Ruprecht E. & Szabó A. (2012) Grass litter is a natural seed trap in long-term undisturbed grassland.  
 529 *Journal of Vegetation Science* **23**, 495-504.
- 530 Saiz H., Bittebiere A.-K., Benot M.-L., Jung V. & Mony C. (2016) Understanding clonal plant competition  
 531 for space over time: a fine-scale spatial approach based on experimental communities. *Journal of*  
 532 *Vegetation Science* **27**, 759-70.
- 533 Scharfy D., Funk A., Olde Venterink H. & Güsewell S. (2011) Invasive forbs differ functionally from native  
 534 graminoids, but are similar to native forbs. *New Phytologist* **189**, 818-28.
- 535 Scherrer D., Mod H. K., Pottier J., Litsios-Dubuis A., Pellissier L., Vittoz P., Götzenberger L., Zobel M. &  
 536 Guisan A. (2019) Disentangling the processes driving plant assemblages in mountain grasslands across  
 537 spatial scales and environmental gradients. *Journal of Ecology* **107**, 265-78.
- 538 Schmidt-Entling M. H. & Döbeli J. (2009) Sown wildflower areas to enhance spiders in arable fields.  
 539 *Agriculture, Ecosystems & Environment* **133**, 19-22.
- 540 Seabloom E. W., Borer E. T., Buckley Y. M., Cleland E. E., Davies K. F., Firn J., Harpole W. S., Hautier Y.,  
 541 Lind E. M., MacDougall A. S., Orrock J. L., Prober S. M., Adler P. B., Anderson T. M., Bakker J. D.,  
 542 Biederman L. A., Blumenthal D. M., Brown C. S., Brudvig L. A., Cadotte M., Chu C., Cottingham K. L.,  
 543 Crawley M. J., Damschen E. I., Dantonio C. M., DeCrappeo N. M., Du G., Fay P. A., Frater P., Gruner D. S.,  
 544 Hagenah N., Hector A., Hillebrand H., Hofmockel K. S., Humphries H. C., Jin V. L., Kay A., Kirkman K. P.,  
 545 Klein J. A., Knops J. M. H., La Pierre K. J., Ladwig L., Lambrinos J. G., Li Q., Li W., Marushia R., McCulley R.  
 546 L., Melbourne B. A., Mitchell C. E., Moore J. L., Morgan J., Mortensen B., O'Halloran L. R., Pyke D. A.,  
 547 Risch A. C., Sankaran M., Schuetz M., Simonsen A., Smith M. D., Stevens C. J., Sullivan L., Wolkovich E.,  
 548 Wragg P. D., Wright J. & Yang L. (2015) Plant species' origin predicts dominance and response to  
 549 nutrient enrichment and herbivores in global grasslands. *Nat Commun* **6**.
- 550 Sears A. L. W. & Chesson P. (2007) New Methods for Quantifying the Spatial Storage Effect: an Illustration  
 551 with Desert Annuals. *Ecology* **88**, 2240-7.
- 552 Spotswood E. N., Mariotte P., Farrer E. C., Nichols L. & Suding K. N. (2017) Separating sources of density-  
 553 dependent and density-independent establishment limitation in invading species. *Journal of Ecology*  
 554 **105**, 436-44.
- 555 Staples T. L., Dwyer J. M., Loy X. & Mayfield M. M. (2016) Potential mechanisms of coexistence in closely  
 556 related forbs. *Oikos* **125**, 1812-23.
- 557 Stevens C. J., Duprè C., Dorland E., Gaudnik C., Gowing D. J. G., Bleeker A., Diekmann M., Alard D.,  
 558 Bobbink R., Fowler D., Corcket E., Mountford J. O., Vandvik V., Aarrestad P. A., Muller S. & Dise N. B.  
 559 (2010) Nitrogen deposition threatens species richness of grasslands across Europe. *Environmental*  
 560 *Pollution* **158**, 2940-5.
- 561 Suding K. N. (2011) Toward an Era of Restoration in Ecology: Successes, Failures, and Opportunities  
 562 Ahead. *Annual Review of Ecology, Evolution, and Systematics* **42**, 465-87.
- 563 Tilman D., Reich P. B. & Knops J. M. H. (2006) Biodiversity and ecosystem stability in a decade-long  
 564 grassland experiment. *Nature* **441**, 629-32.
- 565 Travers S. K., Eldridge D. J., Dorrough J., Val J. & Oliver I. (2018) Introduced and native herbivores have  
 566 different effects on plant composition in low productivity ecosystems. *Applied Vegetation Science* **21**,  
 567 45-54.

- 568 Tremont R. & McIntyre S. (1994) Natural Grassy Vegetation and Native Forbs in Temperate Australia:  
569 Structure, Dynamics and Life-Histories. *Australian Journal of Botany* **42**, 641-58.
- 570 Tschardt T., Klein A. M., Kruess A., Steffan-Dewenter I. & Thies C. (2005) Landscape perspectives on  
571 agricultural intensification and biodiversity – ecosystem service management. *Ecology Letters* **8**, 857-74.
- 572 Tzialla C. E., Veresoglou D. S., Papakosta D. & Mamolos A. P. (2006) Changes in soil characteristics and  
573 plant species composition along a moisture gradient in a Mediterranean pasture. *Journal of*  
574 *Environmental Management* **80**, 90-8.
- 575 Whittaker R. J., Willis K. J. & Field R. (2001) Scale and Species Richness: Towards a General, Hierarchical  
576 Theory of Species Diversity. *Journal of Biogeography* **28**, 453-70.
- 577 Williams D. W., Jackson L. L. & Smith D. D. (2007) Effects of Frequent Mowing on Survival and Persistence  
578 of Forbs Seeded into a Species-Poor Grassland. *Restoration Ecology* **15**, 24-33.
- 579 Williams N. M., Ward K. L., Pope N., Isaacs R., Wilson J., May E. A., Ellis J., Daniels J., Pence A., Ullmann  
580 K. & Peters J. (2015) Native wildflower plantings support wild bee abundance and diversity in agricultural  
581 landscapes across the United States. *Ecological Applications* **25**, 2119-31.
- 582 Wragg P. D., Mielke T. & Tilman D. (2018) Forbs, grasses, and grassland fire behaviour. *Journal of Ecology*  
583 **0**.
- 584 Wratten S. D., Gillespie M., Decourtye A., Mader E. & Desneux N. (2012) Pollinator habitat enhancement:  
585 Benefits to other ecosystem services. *Agriculture, Ecosystems & Environment* **159**, 112-22.
- 586 Zhao Y., Peth S., Krümmelbein J., Horn R., Wang Z., Steffens M., Hoffmann C. & Peng X. (2007) Spatial  
587 variability of soil properties affected by grazing intensity in Inner Mongolia grassland. *Ecological*  
588 *Modelling* **205**, 241-54.

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## Appendix S1: Explanatory variables

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

Explanatory variable	Selection reason/comments
<i>%Soil moisture</i>	Soil conditions influence forb germination and seedling survival (Fay and Schultz 2009; Harper <i>et al.</i> 1965; Morgan 1998a; Pennington <i>et al.</i> 2017; Prober <i>et al.</i> 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.
<i>Soil temperature</i>	
<i>Soil hardness</i>	
<i>%Light to ground</i>	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).
<i>%Bare ground</i>	
<i>%Rocks</i>	Rock and log cover preclude forbs from occupying that space.
<i>%Logs</i>	
<i>%Litter cover</i>	Litter influences the regeneration niche, through interference during seed dispersal (Ruprecht and Szabó 2012), and seedling emergence (Loydi <i>et al.</i> 2013). Cover and depth may influence forbs in different ways.
<i>Litter depth</i>	
<i>%Dead biomass cover</i>	Standing dead biomass affects seedling survival primarily through light restriction (Carson and Peterson 1990). Cover and height may influence forbs in different ways.
<i>Dead biomass height</i>	
<i>%Grass cover</i>	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 <i>et al.</i> 2016). Potential for additional biotic interactions between native and functionally similarity exotic forbs.
<i>%Exotic forb cover</i>	
<i>Tussock distance</i>	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).
<i>Tussock height</i>	
<i>Tussock diameter</i>	
<i>%Cryptogams</i>	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 <i>et al.</i> 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
<u>Grasses - Exotic</u>				<u>Grasses - Native</u>			
<i>Aira spp</i>	Annual	31	7	<i>Austrostipa bigeniculata</i>	Perennial	44	15
<i>Avena sativa</i>	Annual	46	17	<i>Austrostipa scabra</i>	Perennial	44	12
<i>Briza minor</i>	Annual	13	5	<i>Bothriochloa macra</i>	Perennial	18	14
<i>Bromus diandrus</i>	Annual	30	14	<i>Dichelachne spp</i>	Perennial	1	25
<i>Bromus hordaceus</i>	Annual	108	4	<i>Elymus scaber</i>	Perennial	25	3
<i>Cynosurus echinatus</i>	Annual	2	1	<i>Eragrostis brownii</i>	Perennial	4	5
<i>Holcus lanatus</i>	Annual	5	3	<i>Microleana stipoides</i>	Perennial	107	18
<i>Vulpia spp</i>	Annual	59	7	<i>Panicum effusum</i>	Perennial	4	4
<i>Lolium perenne</i>	Perennial	8	2	<i>Poa labillardieri</i>	Perennial	1	5
<i>Phalaris aquatica</i>	Perennial	6	21	<i>Poa sieberiana</i>	Perennial	22	13
				<i>Rytidosperma spp</i>	Perennial	59	8
				<i>Themeda australis</i>	Perennial	311	30
<u>Forbs - Exotic</u>				<u>Forbs - Native (Case plots)</u>			
<i>Centaureum erythraea</i>	Annual	1	1	<i>Euchiton sphaericus</i>	Annual	1	40
<i>Conyza bonariensis</i>	Annual	18	3	<i>Triptilodiscus pygmaeus</i>	Annual	5	3
<i>Echium plantagineum</i>	Annual	2	3	<i>Hypericum gramineum</i>	Either	5	4
<i>Hypochaeris glabra</i>	Annual	38	4	<i>Vittadinia cuneata</i>	Either	6	29
<i>Lactuca serriola</i>	Annual	14	5	<i>Acaena ovina</i>	Perennial	7	20
<i>Petrorhagia nanteuillii</i>	Annual	28	5	<i>Asperula conferta</i>	Perennial	3	8
<i>Plantago lanceolata</i>	Annual	30	6	<i>Bulbine bulbosa</i>	Perennial	11	8
<i>Sonchus oleraceus</i>	Annual	2	1	<i>Cheilanthes spp</i>	Perennial	6	15
<i>Tolpis barbata</i>	Annual	8	2	<i>Chrysocephalum apiculatum</i>	Perennial	14	29
<i>Tragopogon dubias</i>	Annual	6	3	<i>Convolvulus erubescens</i>	Perennial	3	5
<i>Trifolium angustifolium</i>	Annual	1	1	<i>Cymbonotus preissianus</i>	Perennial	9	9
<i>Trifolium arvense</i>	Annual	9	7	<i>Desmodium varians</i>	Perennial	1	3
<i>Trifolium glomeratum</i>	Annual	2	1	<i>Dichondra repens</i>	Perennial	4	25
<i>Trifolium subterranean</i>	Annual	10	11	<i>Dichopogon fimbriatus</i>	Perennial	3	10
<i>Carthamus lanatus</i>	Annual	4	3	<i>Eryngium ovinum</i>	Perennial	6	12
<i>Cirsium vulgare</i>	Annual	24	8	<i>Euchiton gymnocephalus</i>	Perennial	1	20
<i>Acetosella vulgaris</i>	Perennial	33	11	<i>Gonocarpus tetragynus</i>	Perennial	1	4
<i>Chondrilla juncea</i>	Perennial	5	6	<i>Haloragis heterophylla</i>	Perennial	5	44
<i>Hypericum perforatum</i>	Perennial	75	10	<i>Hydrocotyle laxiflora</i>	Perennial	6	23
<i>Hypochaeris radicata</i>	Perennial	28	9	<i>Leptorhynchus squamatus</i>	Perennial	11	7
<i>Paronychia brasiliiana</i>	Perennial	7	9	<i>Oxalis perennans</i>	Perennial	2	23
<i>Sanguisorba minor</i>	Perennial	1	20	<i>Plantago varia</i>	Perennial	11	20
				<i>Senecio quadridentatus</i>	Perennial	2	9
				<i>Solenogyne dominii</i>	Perennial	2	20
<u>Rushes &amp; Sedges</u>							
<i>Lomandra filiformis</i>	Perennial	24	8	<i>Tricoryne elatior</i>	Perennial	6	6
<i>Lomandra longifolia</i>	Perennial	1	15	<i>Vittadinia meulleri</i>	Perennial	2	6
<i>Carex inversa</i>	Perennial	11	8	<i>Wahlenbergia stricta</i>	Perennial	12	6

<i>Juncus filicaulis</i>	Perennial	2	2
Other sedge		14	4
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<u>Other</u>			
<i>Rubus spp</i>	Perennial	1	8
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Forbs - Native (Control plots only)

<i>Erodium cicutarium</i>	Annual	1	5
<i>Euchiton involucratis</i>	Perennial	1	5
<i>Geranium solanderi</i>	Perennial	2	3
<i>Rumex brownii</i>	Perennial	2	16
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