

Annual mowing maintains plant diversity in threatened temperate grasslands

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Abstract

Questions: Disturbance regimes shaped the evolution of grasslands but grazing exclusion and fire suppression have caused unprecedented increases in grassland biomass and biodiversity declines. Mowing reduces biomass but is not widely practiced in conservation reserves because of concerns about facilitating exotic plant invasion and altering ecosystem function. We asked whether regular mowing affected (1) the diversity of native and exotic functional groups, (2) spatial turnover in vegetation composition (β -diversity), (3) vegetation attributes relating to biomass and structural heterogeneity, (4) community composition and (5) the distribution and abundance of individual native and exotic species.

Location: Five temperate grassland reserves, south-eastern Australia, encompassing C_3 and C_4 dominated communities.

Methods: Vegetation within reserves had been cut to 10 cm, once per year, for 10 years in late spring/early summer to maintain access tracks. We surveyed plant communities in mowed areas and nearby (<5 m) unmowed control areas (40 subplots per reserve, 200 total) and used linear mixed-effects models to examine the effects of mowing.

Results: Of 24 functional groups, the richness of 16 native and exotic groups significantly increased with mowing. In 14 of these cases, effects were consistent across C_3 - and C_4 -dominated grassland. Mowing reduced spatial turnover, but this did not reduce species richness at any spatial scale. When accounting for species abundance and evenness (Shannon diversity), effects of mowing were generally positive for native species and neutral for exotic species. Mowing increased native perennial grass cover and bare earth, decreased exotic perennial grass cover and litter, and changed community composition. Mowing reduced vegetation height but not structural heterogeneity. Mowing positively affected six individual native species and no exotic species. One native (*Asperula conferta*) and two exotic (*Avena* spp. and *Nassella neesiana*) species were found in lower abundance on mowed plots.

Conclusions: Annual mowing can be a useful conservation tool for threatened temperate grasslands but should be heterogeneous to ensure the persistence of mowing-sensitive native species. Good vehicle hygiene is essential and localized complementary management (e.g., herbicide) might be required to reduce exotic forbs and grasses.

KEYWORDS

community ecology, disturbance regime, functional ecology, invasive species, meadow, prairie, savanna, slashing

1 | INTRODUCTION

Disturbance regimes, including temporal and spatial variation in fire and grazing by native herbivores, have played a central role in shaping the evolution of grassland ecosystems (Forrestel, Donoghue, & Smith, 2014; Koerner & Collins, 2014). Homogenization of grazing regimes (e.g., set stocking rates) and alteration of traditional burning regimes have facilitated exotic plant invasion and caused declines in grazing-sensitive plant species (e.g., palatable or tall) or species relying on regular biomass removal for persistence (Díaz et al., 2007; Fuhlendorf & Engle, 2004). This problem is particularly apparent in protected areas where livestock grazing has been excluded and fire has been suppressed (Lunt, Eldridge, Morgan, & Witt, 2007). Active management of disturbance regimes in grasslands is therefore essential to conserve biodiversity and ecosystem function.

A major management problem associated with modified disturbance regimes and plant invasion is an increase in above-ground biomass, which can be several times greater in invaded compared with un-invaded grasslands (four- to 13-fold increases in biomass are frequently reported; e.g., Blumenthal et al., 2013; Going, HilleRisLambers, & Levine, 2009; Stoner, Adams, & Simmons, 2004). This negatively affects native plant communities through direct competition for moisture and light (Skálová, Jarošík, Dvořáčková, & Pyšek, 2013), reduction in pollinator visitation (McKinney & Goodell, 2010) and altered rates of decomposition and nutrient cycling (Ashton, Hyatt, Howe, Gurevitch, & Lerdau, 2005). In some cases, increased biomass leads to local extinction of native species (Gilbert & Levine, 2013; Morgan, 2015). High biomass levels also increase fire fuel loads, threatening biodiversity and human communities by changing fire regimes (Coates et al., 2016; Rossiter, Setterfield, Douglas, & Hutley, 2003). Biomass control is therefore a high priority for management agencies.

At the landscape scale, grassland biomass is typically managed with grazing, burning and/or mowing. Grazing is integral to maintaining grassland function and diversity (Liu et al., 2016) but in regions with strong climatic variability native herbivore grazing does not sufficiently control biomass in highly productive years (Driscoll, 2017; McIntyre, Cunningham, Donnelly, & Manning, 2015). Stock grazing can supplement native herbivore grazing but can negatively impact biodiversity (Eldridge, Poore, Ruiz-Colmenero, Letnic, & Soliveres, 2016; Lunt et al., 2007) and is often difficult due to conflicts between production and conservation (Dorrough et al., 2004). Burning can control biomass while maintaining ecosystem function and diversity (Prober, Thiele, Lunt, & Koen, 2005) but is expensive (Setterfield et al., 2013) and often inappropriate in urban areas where there is concern for public safety (McDougall, Milner, Driscoll, & Smith, 2016; Radeloff et al., 2005). Mowing potentially circumvents some of these problems and could be a useful addition to the biomass management toolbox.

Regular mowing can maintain grassland biodiversity (Collins, Knapp, Briggs, Blair, & Steinauer, 1998; Prober, Thiele, & Lunt, 2007) and has been integral to the management of semi-natural grasslands in Europe for thousands of years (Hansson & Fogelfors, 2000). In many regions, however, mowing is not used or supported by agencies who manage land primarily for conservation for at least three reasons.

First, mowing can decrease biodiversity if done at high frequency or early in the growing season (Socher et al., 2012) or if excessive litter is produced which suppresses seedling establishment (Morgan, 2015). Second, it is often assumed that mowing reduces structural vegetation heterogeneity when compared with grazing (Tälle et al., 2016; Valkó, Török, Matus, & Tóthmérész, 2012). Third, mowing can increase the reproduction and density of invasive plant species (Firn, Ladouceur, & Dorrough, 2017). This is particularly the case for species with increased seedling establishment following disturbance (e.g., *Lespedeza cuneata* in USA; Brandon, Gibson, & Middleton, 2004), which spread vegetatively when cut (e.g., Japanese knotweed, *Fallopia japonica* in Europe; Beerling, Bailey, & Conolly, 1994), or which have seeds readily dispersed by attaching to mowing equipment (e.g., Chilean needle grass, *Nassella neesiana* in Australia and New Zealand; Bourdôt, Lamoureaux, Watt, Manning, & Kriticos, 2012). The presence of such species has led to policies to exclude mowing where follow-up or supplementary control cannot occur (CRC for Australian Weed Management 2003; National Roads Authority 2010). However, if mowing increases both exotic and native species diversity, it could provide a better alternative to the exotic monoculture that can develop with a complete lack of disturbance (Driscoll, 2017). Thus, there could be a net benefit for mowing, especially if supplementary control (e.g., localised burning or herbicide) can be applied to invasive species that benefit from mowing. Research is needed to evaluate the effect of mowing on biodiversity while also examining the effects on individual species. This would allow managers to control biomass with mowing and pinpoint invasive species that require additional control, or native species that require special protection.

We quantified the effects of annual mowing over the past decade on grassland biodiversity in threatened temperate grasslands of south-eastern Australia to develop guidelines on implementing mowing regimes. Specifically, we tested whether mowing affected (1) the diversity of native and exotic functional species groups, (2) spatial turnover in vegetation composition (β -diversity), (3) the cover of vegetation attributes that relate to biomass and structural heterogeneity, (4) community composition and (5) the distribution and abundance of individual native and exotic species. We focussed on biodiversity metrics used by government agencies to monitor grassland quality (e.g., 'indicator' species richness) and on functional groups that provide insight into the mechanism underlying observed responses (e.g., legumes involved in N cycling). Our analysis accounted for grass type (C_3/C_4 -dominated) to determine whether mowing was broadly applicable across different grassland communities. Ultimately, we aimed to provide an evidence base for land managers under urgent pressure to conserve grassland biodiversity through practical and affordable biomass management techniques.

2 | METHODS

2.1 | Study design and vegetation survey

The study was undertaken in five reserves in the Australian Capital Territory, around the city of Canberra (Figure 1a). The region has

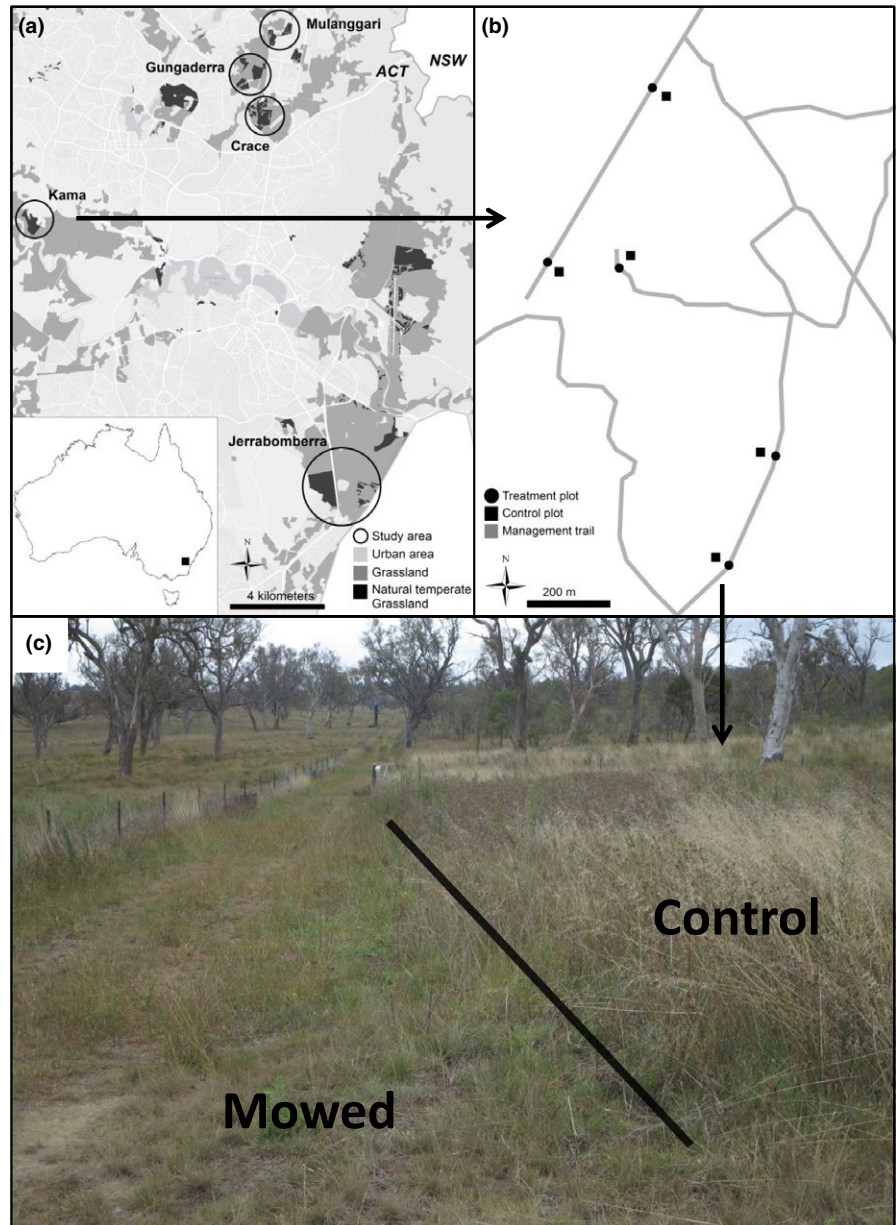


FIGURE 1 (a) Plant biodiversity was surveyed in five natural temperate grassland reserves (circled) around the city of Canberra, south-eastern Australia. (b) At each reserve there were five sites, each consisting of a mowed treatment plot and a control plot. (c) Plots were located along trail edges, outside the area of vehicle compaction, where mowing to maintain trail access has taken place annually for the past 10 years [Colour figure can be viewed at wileyonlinelibrary.com]

a cool temperate climate, with mean temperatures ranging from 13–28°C in summer to 0–11°C in winter (Australian Government Bureau of Meteorology). Mean annual precipitation is 629 mm but is highly variable and rainfall is generally distributed throughout the year. The ecological community is classified as Natural Temperate Grassland and is listed as threatened at the regional level (Australian Capital Territory Government *Nature Conservation Act* 2014) and as critically endangered at the national level (Australian Government *Environment Protection and Biodiversity Conservation Act* 1999). Approximately 95% of Natural Temperate Grassland in Australia has been cleared or degraded since European colonization (Keith, 2004). Only small fragments (25–140 ha) remain in an urban and agricultural matrix (ACT Government 2005). Native grasses include *Themeda*, *Austrostipa*, *Rytidosperma*, *Poa* and *Bothriochloa* species and common exotic grasses include *Avena*, *Phalaris*, *Bromus*, *Aira* and *Vulpia* species.

Trails in the reserves have been mowed annually in November or December for at least 10 years to maintain access for management vehicles. Vegetation was mowed to 10-cm high and the cut biomass was retained on site. The total mowed area was ca. 5-m wide, leaving a buffer at the edge of the trail where vehicles rarely passed. In each reserve, we established five sites in the trail buffers (Figure 1b). Sites were selected using random points generated in ArcMap 10 (ESRI) and were separated by at least 150 m (range: 150–830 m) within reserves. We restricted site selection to low-use management trails where no rutting was evident. Each site comprised one treatment plot (mowed) and one control plot (not mowed; Figure 1c). Mowed plots were ca. 1.5 m from the main trail, avoiding areas of vehicle compaction. Control plots were 5 m from the edge of the mowed area where the matched treatment plot was located. Each plot consisted of four 1-m² subplots in a 1 m × 4 m configuration (200 subplots in total: 100 mowed, 100 control). All sites were in naturally treeless areas where

native perennial grasses and native herbaceous plants occurred (ACT Government 2005).

Two experienced botanists (RNCM and RLB) surveyed vegetation between Sept and Nov 2015 (spring). All plant taxa observed within each subplot were counted. Most taxa (85%) were identified to species following NSW Flora Online (<http://plantnet.rbgsyd.nsw.gov.au>). Nineteen taxa were difficult to identify depending on life stage and were assigned to a genus (e.g., *Avena*, *Aira*, *Conyza*, *Vulpia*; see Table S1) or to three different morphospecies (*Rytidosperma*). There are two dominant native perennial grass types within our study region: *Themeda triandra* (C_4) dominated and *Austrostipa/Rytidosperma* spp. (C_3) dominated, which differ in community composition (Armstrong, Turner, McDougall, Rehwinkel, & Crooks, 2013) and might therefore have different responses to mowing. Thus, to quantify dominant grass type, we also recorded the percentage cover of these grass taxa to the nearest 10% within each subplot. Each plot was assigned to one of two dominant grass types based on the summed cover over the four subplots.

We recorded point-based measures of vegetation cover and vegetation height as proxies for biomass and structural heterogeneity (Godínez-Alvarez, Herrick, Mattocks, Toledo, & Van Zee, 2009; Ónodi et al., 2017). At every 20 cm, along three 4-m transects (60 points per plot), we recorded: litter (organic material unattached to a plant or the ground), bare earth, native grass (all perennial), perennial exotic grass, annual exotic grass, native forbs, perennial exotic forbs, annual exotic forbs and vegetation height. The three transects were 50 cm from, and parallel to, the vegetation survey plots and each was spaced 50 cm apart.

2.2 | Definition of response variables

2.2.1 | Richness and diversity of functional groups

We classified each taxon into categories based on origin (native/exotic), life span (annual/perennial), growth form (forb, grass, shrub, sedge, rush), photosynthetic pathway for grasses (C_3/C_4) and ability to fix N (legume/non-legume, Díaz et al., 2007; Table S1). We also used three binomial categories that are used by the local government to monitor grassland quality (Australian Government 2017; Rehwinkel, 2015): (1) indicator species (sensitive native taxa that are indicative of high value Natural Temperate Grassland), (2) important species (taxa used to classify vegetation as Box-Gum Grassy Woodland and Derived Native Grassland under the Australian *Environment Protection and Biodiversity Conservation Act 1999*) and (3) increaser species (common native taxa that tolerate or respond positively to disturbance). Taxa were assigned to 24 functional groups based on these categories in a hierarchical way. For example, we analysed the diversity of all taxa, native taxa and exotic taxa separately, while native and exotic grasses were further divided into C_3 and C_4 categories (Table S1). This allowed us to examine broad functional responses while also examining which functional traits drove broader patterns. For each functional group in each subplot, we calculated species richness (number of species) and, to account for variation in abundance and evenness among

species, the Shannon diversity index (H'). These data were analysed at the subplot level (200 observations).

2.2.2 | Beta diversity and effects of spatial scale

Our species richness data were collected and analysed at the 1-m² subplot scale, but mowing could potentially take place across a whole reserve. Since the response of species richness to disturbance is scale-dependent (Dorrough, Ash, Bruce, & McIntyre, 2007; McIntyre, Heard, & Martin, 2003), we conducted two analyses to determine whether effects of mowing on total species richness would be influenced by the spatial scale of sampling. First, we analysed β -diversity to assess whether spatial turnover in species composition differed among treatments at the reserve scale. We used Whittaker's (1960) β -diversity $\beta = \gamma/\alpha$, where γ was the total number species within a reserve (including both treatments so that the values would reflect species losses and gains under different management regimes) and α was total species richness at the 1-m² scale. Second, we generated spatial accumulation curves for each treatment separately and then for native and exotic species within treatments separately (Gotelli & Colwell, 2010). To do this, we calculated geographic distances between all pairs of subplots and divided the data into distance classes, d , based on the distribution of pair-wise distances across the entire study region ($d = 0, 1, 2, 3, 200, 400, 600, 800, 1,000, 2,000, 3,000, 4,000, 5,000, 10,000, 15,000, 20,000, 30,000$ m). For each d , we calculated the species richness in each subplot + all subplots falling within d . For example, in d_0 , species richness was equal to α . In d_{200} , species richness was the number of species in subplot i + all subplots within 200 m of subplot i . We examined the change in species richness with increasing distance to assess the influence of spatial scale on responses to mowing.

2.2.3 | Vegetation cover and structural heterogeneity

Point-based measures of litter, bare earth, native and exotic vegetation cover and vegetation height represented vegetation cover and biomass, while variability in vegetation height represented structural heterogeneity. For all response variables except height, the number of points were summed to represent cover at the transect level (150 observations). We analysed height data at the point level for absolute height (3000 observations) and at the plot level (three transects combined) for variation in height (50 observations) using the coefficient of variation (SD/mean ; Myers, Mason, Hokschi, Cambardella, & Pfrimmer, 2015).

2.2.4 | Community composition

To quantify community composition, we used a Bray-Curtis dissimilarity matrix, based on the abundance data of all species with three or more occurrences, and ordinated the matrix using Principal Coordinates Analysis (Legendre & Anderson, 1999) in the 'vegan' package for R (R Foundation for Statistical Computing, Vienna, Austria). We then extracted the first five multivariate axes (explaining

52% of variation in community composition) for use as separate response variables. This allowed us to analyse community composition as a function of mowing and dominant grass using the same mixed-effects model structure as for our other response variables (similar to Magnago et al., 2015, see modelling details below).

2.2.5 | Individual species occurrence and abundance

We were interested in analysing the distribution and abundance of dominant native grass species, important native species (classified as 'indicator' or 'important' as described above) and exotics that have high invasive potential and/or contribution to biomass. Some species were sparsely distributed within and/or across reserves so we only included species that were recorded on >5% of subplots. To further reduce the complexity of the individual species data, we removed data from a reserve if a species was recorded on fewer than three subplots within that reserve. We also removed all subplots for a dominant grass type when <10% of records were recorded on that grass type. Our individual species analysis ultimately included 14 natives (*Asperula conferta*, *Austrostipa bigeniculata*, *Austrostipa scabra*, *Chrysocephalum apiculatum*, *Eryngium ovinum*, *Glycine tabacina*, *Goodenia pinnatifida*, *Hypericum gramineum*, *Lomandra coriacea* subsp. *filiformis*, *Plantago varia*, *Rytidosperma carphoides*, *Rytidosperma* sp. 1, *Themeda triandra* and *Triptilodiscus pygmaeus*) and five exotics (*Avena* spp., *Carthamus lanatus*, *Hypericum perforatum*, *Nassella neesiana* and *Phalaris aquatica*).

2.3 | Modelling the effects of mowing

All data were analysed using mixed-effects models in lme4 (Bates, Mächler, Bolker, & Walker, 2015) and glmmADMB in R. We used Gaussian linear models for Shannon's diversity, β -diversity, height, variation in height and the five community composition axes. For species richness and vegetation cover (count data) we used a Poisson error distribution with a log link function. We modelled the response of individual species to mowing and dominant grass in two steps. First, we analysed species occurrence using binomial GLM with logit link function. Second, we analysed only the positive values in the data using a truncated Poisson error distribution and a log link function. Thus, we analysed abundance conditional on presence, appropriate for the high proportion of zeros in our data (30%–95%; Catford, Vesk, White, & Wintle, 2011; Smith et al., 2016).

We used a similar model structure and model selection procedure for each response variable. First, we fit a full model with an interaction between mowing treatment and dominant grass. We removed the interaction term when it was not significant ($p < .05$) and subsequently removed the dominant grass term if it was not significant. To account for spatial clustering, plot nested within reserve was fitted as a random effect in all models except for variation in height, which was analysed at the plot level and included only reserve as a random effect. *Themeda triandra*, *Rytidosperma* spp. and *Austrostipa* spp. were used to classify plots by dominant grass, so we did not fit the dominant grass term in these models. Instead, we analysed the effect of mowing only in their

respective community. For individual species that only occurred in one of the two dominant grass communities following the filters described above, we did not fit the dominant grass term. We considered mowing effects to be significant when $p < .05$ and near-significant when $p < .1$. For Poisson models, we considered the data to be overdispersed when sum of squared residuals/residual degrees of freedom did not approximate a χ^2 distribution ($p < .05$). In these cases, we fitted an individual-level random effect to account for overdispersion (Maironid & Braun, 2010).

3 | RESULTS

We recorded 122 species, of which 60% were native (Table S1). Mowing had largely positive or neutral effects on species diversity, vegetation structure and individual species, with few negative effects (Table 1; Appendix S1).

Of 24 functional groups analysed, the richness of 16 native and exotic groups significantly increased with mowing (Table 1; Appendix S1). In 14 of these 16 cases, effects were independent of dominant grass type, indicating a consistent effect of mowing on species richness across the two grassland communities (Figure 2). When accounting for species abundance and evenness (H'), native species showed generally positive responses (in line with richness), while H' in exotic species was mostly neutral (Table 1). In exotic perennial forbs, mowing decreased H' , but had no effect on richness (Figure 2f). The richness of all native grasses increased with mowing in *Austrostipa/Rytidosperma* grasslands but not *Themeda* grasslands (Appendix S1) and this interaction was likely driven the response of native C_4 grasses (Figure 2h). Four functional groups had more species in *Themeda* than *Austrostipa/Rytidosperma* grasslands (main effects of dominant grass; Figure S1: Appendix S2). There were near-significant increases in the richness of important ($p = .066$) and indicator ($p = .094$) species (Appendix S2: Figure S1). There were insufficient data to analyse the effect of mowing on the richness of native leguminous forbs and exotic C_4 grasses.

Gamma diversity ranged from 46 to 72 species per reserve. At the reserve scale, in all reserves, there were more species in mowed than unmowed grassland (Figure 3a). Beta diversity was lower in mowed grassland than control areas (Figure 3b; $p = .011$). Species richness was higher in mowed grassland than control areas at all spatial scales (Appendix S2: Figure S2a). At the reserve scale (<2,083 m), exotic species in mowed and control areas accumulated more quickly than native species in control areas, but native species in mowed grassland had the highest richness at all spatial scales (Appendix S2: Figure S2b).

Mowing increased native perennial grass cover (Figure 4a) and decreased exotic perennial grass cover (Figure 4b). Mowed subplots had less litter (Figure 4c) and more bare earth (Figure 4e) than control subplots. There was more litter in *Themeda* grassland (main effect of dominant grass; Figure 4d). Mowing reduced vegetation height (Figure 4f) but had no effect on variability in height (Appendix S1), indicating that mowing did not reduce structural heterogeneity. Of the ordination axes representing community



Functional group	Native		Exotic	
	Richness	H'	Richness	H'
All species	+	+	+	Neutral
Increase species	+	+	NA	NA
Important & indicator species	+	+	NA	NA
All forbs	+	+	Neutral	Neutral
Annual forbs	Neutral	Neutral	+	Neutral
Perennial forbs	+	Neutral	Neutral	-
Leguminous forbs	NA	NA	+	+
Non-leguminous forbs	+	+	Neutral	Neutral
All grasses	See perennial	See perennial	+	Neutral
Annual grasses	NA	NA	+	Neutral
Perennial grasses	+(interaction)	+(interaction)	Neutral	Neutral
C ₃ grasses	+	+	+	Neutral
C ₄ grasses	+(interaction)	+	NA	NA
Sedges & rushes	Neutral	Neutral	NA	NA
Vegetation cover	Native cover		Exotic cover	
Perennial grass	+		-	
Annual grass	NA		Neutral	
Forb	Neutral		Neutral	
Individual species	Occurrence	Abundance	Occurrence	Abundance
Increased	+4 species	+2 species	0 species	0 species
Decreased	0 species	-1 species	0 species	-2 species
No effect	10 species	7 species	5 species	3 species

TABLE 1 A summary of the influence of mowing of native and exotic components of species richness and diversity (H'), vegetation cover and the occurrence and abundance of individual species

All responses were significant ($p < .05$) except for important and indicator groups which had near-significant ($p < .1$) increases on mowed subplots. An interaction indicates the effect only occurred in *Austrostipa/Rytidosperma*-dominated plots and not *Themeda*-dominated plots. NA indicates the category was not relevant (e.g., there are no annual native grasses) or that there were not enough data for analysis (e.g., there was only one exotic C₄ grass). In addition to the effects shown here, mowing significantly increased the combined (native and exotic) richness and H' of all species and all C₃ grass species. Coefficients for all models are in Appendix S1. Green = positive, red = negative and grey = neutral responses (colour version online).

composition, mowing had a significant effect on the first two axes (Appendix S2: Figure S3) but no effect on the third, fourth and fifth axes (Appendix S1). There were no effects of dominant grass on community composition.

Mowing increased the occurrence of *Rytidosperma* sp. 1 (native; Figure 5a) and the abundance of *Austrostipa scabra* and *Goodenia pinnatifida* (both native; Figure 5c,e). The abundance of one native (*Asperula conferta*; Figure 5b) and two exotic (*Avena* spp. and *Nassella neesiana*; Figure 5d,f) species decreased with mowing. The occurrence of *Chrysocephalum apiculatum* (native) had a near-significant increase on mowed subplots ($p = .062$). *Hypericum perforatum* (exotic) was more common in *Themeda* grassland ($p = .020$; Appendix S1). The occurrence of two native species could not be modelled due to limited data but all nine records (*Rytidosperma carphoides*, 'increase' species) and ten of 11 records (*Triptilodiscus pygmaeus*, 'indicator' species) occurred on mowed subplots.

4 | DISCUSSION

Our study showed that annual mowing for the past 10 years has maintained plant diversity in threatened temperate grasslands, consistently across C₃- and C₄-dominated communities. Both native and exotic species richness increased with mowing but most of the positive effects on exotic species were not evident when accounting for species abundance and evenness (Shannon diversity H'). Furthermore, while the richness of exotic species increased with mowing, their cover did not. Thus, the responses were generally positive for native species diversity and neutral for exotic species diversity. Mowing decreased spatial turnover in community composition but this did not reduce plant biodiversity at the reserve scale; mowed grassland had more species than unmowed grassland at all spatial scales.

Mowing positively influenced six native species but no exotic species. One native (*Asperula conferta*) and two exotic (*Avena* spp. and *Nassella neesiana*) species were less abundant in mowed areas. The

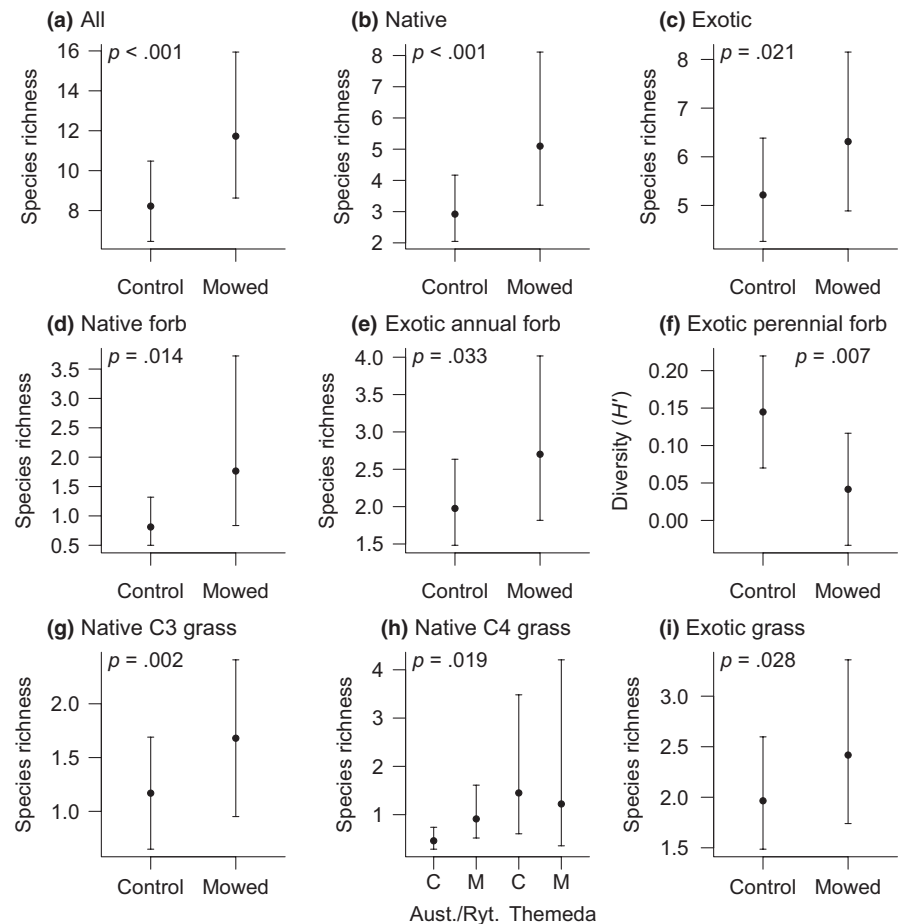


FIGURE 2 A representative set of responses to mowing and dominant grass on species richness and diversity (Shannon index, H') in functional species groups (model estimates $\pm 95\%$ CI). (a–e, g, i) Effects of mowing were largely positive for native and exotic groups, with some exceptions. (f) The diversity of exotic perennial forbs decreased with mowing but the richness of this group did not (see Appendix S1). (h) Mowing increased native C_4 grass richness in *Austrostipa/Rytidosperma* (Aust./Ryt.) grassland but not *Themeda* grassland (C = control; M = mowed). All responses are summarized in Table 1 and coefficients for all models are in Appendix S1

exotics are two of the most problematic weeds for managers of conservation land as they out-compete native species and reduce biodiversity (Driscoll, 2017; Morgan & Lunt, 1999). *Avena* increases fire risk (McDougall et al., 2016) and produces excessive litter containing allelopathic chemicals that inhibit forb germination (Tinnin & Muller, 1972). There is an extremely high risk of *N. neesiana* seed being spread by mowing equipment (Taylor, Conolly, & Gruber, 2016) but our data showed this species was less abundant in mowed areas. *Nassella neesiana* produces self-fertilized seed in stem nodes and can reproduce even under frequent mowing (CRC for Australian Weed Management 2003). Thus, the negative effects of mowing on *N. neesiana* are likely the result of improved grassland resilience to weed invasion, rather than a direct effect of mowing (Going et al., 2009; Lunt & Morgan, 2000; Tilman, 1997). In our study, mowing equipment was cleaned before entering reserves and we stress that good vehicle hygiene is critical to prevent the spread of invasive species. Research is needed to quantify the risk of mowing on seed spread and to develop evidence-based procedures for using mowing equipment inside and outside nature reserves (Taylor et al., 2016).

In line with increased species richness in mowed subplots (α -diversity), there were also more species in mowed grassland at the reserve level. Meanwhile, β -diversity was lower on mowed grassland, indicating that unmowed control areas had higher spatial turnover in species composition. Mowing therefore created more spatially homogeneous plant communities across reserves, but this did not result in

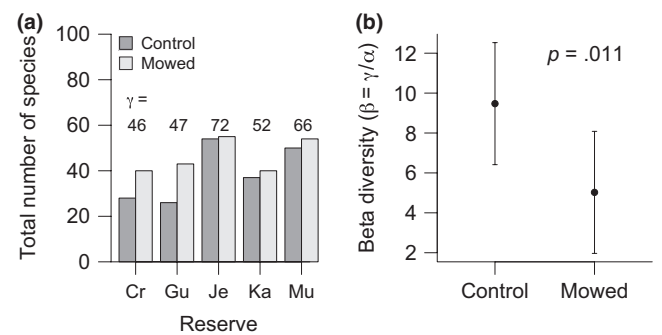


FIGURE 3 Variation in species richness and species turnover between treatments at the reserve scale. (a) Within all reserves, mowed grassland had higher total species richness than unmowed control areas. Gamma diversity (γ) was calculated as the total number of species within reserves in both treatments, thus incorporating gains and losses under different management regimes. (b) Beta diversity was calculated as $\beta = \gamma/\alpha$, where α is the species richness at the 1-m² subplot scale. A linear mixed-effects model showed that unmowed control areas had higher β than mowed areas (error bars are 95% CI)

lower diversity at the reserve level (Figure 3a), or across the entire study region (Appendix S2: Figure S2a). Unmowed 1-m² subplots were often dominated by one or few species, resulting in high outlier values for β -diversity. However, when we analysed β -diversity without these outliers, or when we calculated α -diversity at the 1 × 4 m plot level

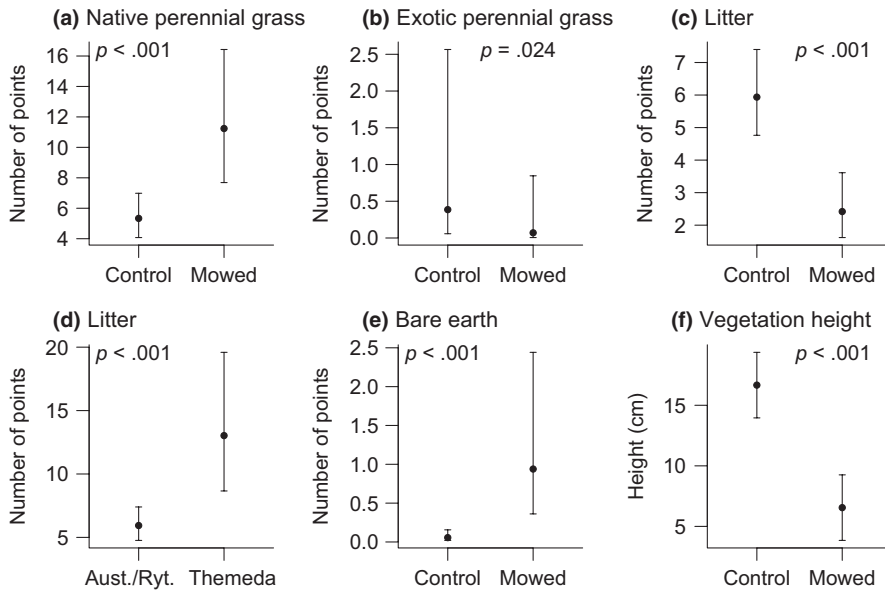


FIGURE 4 (a–f) The estimated effect of mowing ($\pm 95\%$ CI) on vegetation cover (number of points along transect) and vegetation height (cm). The cover of litter was affected by (c) mowing (estimates shown for *Austrostipa/Rytidosperma* [Aust./Ryt.] grassland) and (d) dominant grass type (estimates shown for control subplots)

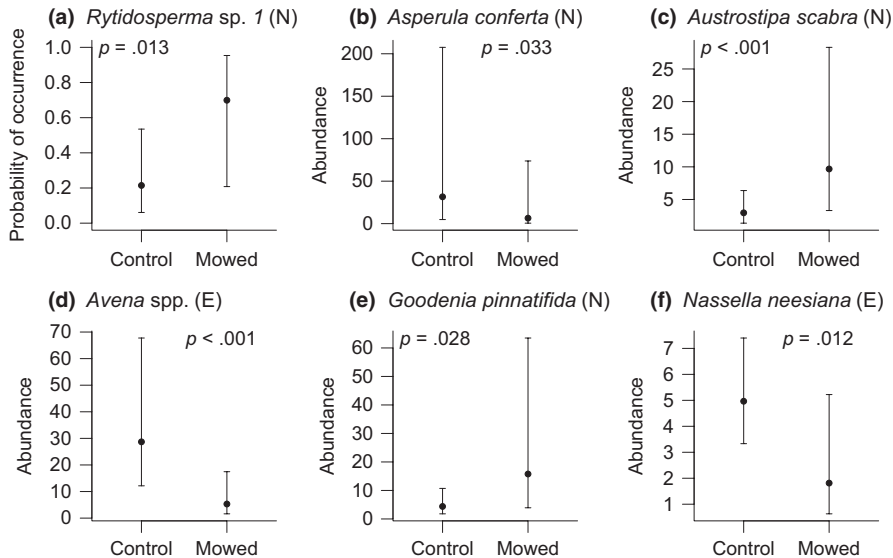


FIGURE 5 The estimated effect of mowing on individual native (N) and exotic (E) species ($\pm 95\%$ CI). Mowing significantly increased (a) the probability of occurrence of *Rytidosperma* sp. 1 and (b–f) the abundance of five species, conditional on presence

(incorporating a larger spatial scale), the pattern of higher turnover in control plots remained (data not shown). Exotic plant species can accumulate faster than native species with distance, increasing spatial turnover (Hulme, 2008; Martin & Wilsey, 2015). In our study however, mowed subplots had the highest rates of spatial accumulation for both native and exotic species (Appendix S2: Figure S2b).

The increased space and light that mowing creates might promote co-existence of mowing-tolerant species at the 1-m² scale, reducing β -diversity. The shorter, more open vegetation that we observed on mowed subplots (Figure 4) might have also increased seed dispersal (Soons, Heil, Nathan, & Katul, 2004), reducing spatial turnover by allowing species to mix among mowed subplots (Cadotte & Fukami, 2005; Kneitel & Miller, 2003). Unmowed grassland might readily lose species that are sensitive to excessive biomass and readily gain species from the reserve-level pool that are mowing sensitive (Beauvais, Pellerin, & Lavoie, 2016; Koleff & Gaston, 2002; Schultz, Reid, Lodge,

& Hunter, 2016), increasing β -diversity. It would thus be unwise to homogeneously mow an entire reserve because high turnover in unmowed areas suggests there might be a suite of mowing-sensitive species. We only detected one of these in our individual species analysis (*Asperula conferta*) but were restricted to analysing species with substantial data. When mowing regimes are implemented, monitoring and adaptive management are essential to ensure the persistence of native species. For example, mowing could be reduced in patches that contain mowing-sensitive native species, such as *A. conferta*, and alternative biomass control implemented.

It is often assumed that mowing homogenizes vegetation structure (Tälle et al., 2016) but we found no decline in structural vegetation heterogeneity on mowed subplots (mowing reduced vegetation height, but not variation in height). Increased light availability from reduced vegetation height and biomass likely contributed to the positive effects of mowing on species diversity (Baoyin, Li, Minggagud, Bao, &

Zhong, 2015; Skálová et al., 2013). Removing cut biomass after mowing reduces soil nutrient levels (Venterink, Kardel, Kotowski, Peeters, & Wassen, 2009) and can have positive effects on Australian grasslands that are threatened by nutrient enrichment (Verrier & Kirkpatrick, 2005). However, we recorded positive effects of mowing on biodiversity even though cut biomass was retained on site. This is probably because mowing was repeated annually. Positive outcomes are unlikely from a single mowing event (Lewis, Reid, Clarke, & Whalley, 2010) or when biomass has accumulated past a threshold (i.e., extensive dead material).

Mowing increased the richness and diversity of the leguminous component of exotic forbs (predominantly *Trifolium* species). This potentially increased rates of N mineralization and might have contributed to increased diversity of exotic annual grasses on mowed subplots (Groves, Austin, & Kaye, 2003; Spehn et al., 2002). However, the total cover of forbs did not increase with mowing in this study, so the mechanism underlying the changes in exotic species richness requires more investigation. Nevertheless, supplementary control of exotic forbs might be warranted.

The effects of mowing in our study were broadly consistent across two different grassland communities (*Themeda triandra* (C_4) dominated and *Austrostipa/Rytidosperma* spp. (C_3) dominated) and the richness of native C_3 and C_4 grasses increased with mowing. These results are surprising considering that mowing occurred when native grass species are flowering (late spring/early summer). Even larger biodiversity outcomes might be gained from mowing in late summer, after native grass species have seeded. Mowing can benefit C_4 species more than C_3 species because the light, moisture and temperature microclimate favours C_4 growth (Collins et al., 1998; Shao, Chen, Li, & Zhang, 2012) but we found no evidence for this in terms of species richness and diversity (we did not separate C_3 and C_4 grasses when examining total cover). Nutrient enrichment in Australian grasslands has been associated with a transition from C_4 to C_3 dominance and a decline in biodiversity (Groves et al., 2003), so it is worth investigating whether mowing could be used to restore C_3/C_4 ratios (Prober et al., 2007).

Declines in mowing and haymaking over the past century have reduced biodiversity in regions where mowing has been integral to the historical management of semi-natural grasslands (e.g., several hundred years in Asia and over a thousand years in Europe; Baoyin et al., 2015; Feurdean et al., 2015; Koyama, Koyanagi, Akasaka, Takada, & Okabe, 2017; Pärtel, Helm, Reitalu, Liira, & Zobel, 2007). Few studies have quantified the effect of mowing on biodiversity in Australian grasslands (Fensham et al., 2017; Lewis et al., 2010; Morgan, 2015; Verrier & Kirkpatrick, 2005). The distribution of temperate grasslands in Australia is controlled predominantly by soil and climate (Lunt, Prober, & Morgan, 2012) but, prior to European colonization, their composition was maintained by native herbivore grazing and burning (ignited by lightning or Aboriginal people; Lunt & Morgan, 2002). Introduced herbivores (mainly rabbits and domestic stock) and prescribed burning by public management agencies became additional factors in the disturbance regime after European colonization. Our results are important because they support a general positive effect of mowing on biodiversity in grasslands (when following a strict vehicle

hygiene protocol). They align with results from North America showing that mowing can benefit biodiversity (Maron & Jefferies, 2001; Middleton, Bettina, & van Diggelen, 2006) even when it has not been part of the traditional (i.e., pre-European) disturbance regime (Foster et al., 2003).

One caveat concerning our results is that detectability might have been higher in mowed than unmowed grassland since mowing can stimulate flowering (Endels, Jacquemyn, Brys, & Hermy, 2007), grasses in vegetative states or at low abundances can be hard to detect (Milberg, Bergstedt, Fridman, Odell, & Westerberg, 2008) and excessive biomass could obscure individual plants (Ng & Driscoll, 2015). Thus, while our surveys were thorough and conducted with extreme care, there is a chance that low detectability in unmowed areas might have contributed to the lower diversity that we recorded. This risk should be quantified in future.

4.1 | Management synthesis

We found that mowing once per year can maintain plant biodiversity in threatened temperate grasslands. The reduced abundance of internationally problematic invasive species in mowed areas (*Avena* spp. and *Nassella neesiana*) indicates that mowing might assist community resistance to invasion. While too frequent mowing can negatively affect biodiversity (Morgan & Lunt, 1999; Socher et al., 2012), mowing once per year, to 10 cm, in late spring/early summer positively affected plant diversity in our study. Good vehicle hygiene (e.g., cleaning seeds from equipment before entering reserves) is imperative to ensure that invasive species are not spread. Localized complementary management (e.g., herbicide) might be required to control exotic forbs and grasses. Mowing might have negative impacts on biodiversity in low productivity years or regions (Lunt et al., 2007) so mowing patterns should be modified to account for variation in productivity. The disturbance regime appropriate for plants is not always optimal for other groups (e.g., invertebrates; Fiedler, Wrbka, & Dullinger, 2017). Thus, when managing habitat for threatened species with conflicting habitat requirements, mowing should be applied in a mosaic pattern, creating areas with contrasting vegetation structure. If these caveats are accounted for, mowing could be integrated into conservation programmes and biomass management in threatened temperate grasslands.

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AUTHOR CONTRIBUTION

RNCM designed the study and collected the data with RLB. ALS analysed the data and wrote the paper with extensive input from RNCM and contributions from RLB.

DATA ACCESSIBILITY

Data supporting this article have been uploaded as part of the Supplementary Material.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

Table S1 Species list from vegetation surveys and functional groups used in analysis

APPENDIX S1 Model results, including coefficients and SE from all response variables analysed in the study

APPENDIX S2 Three supplementary figures referred to in the text

Figure S1 Response of species richness to dominant grass type and responses of important and indicator species richness to mowing

Figure S2 Spatial accumulation of species richness

Figure S3 Multi-dimensional scaling showing the effect of mowing treatment and reserve on plant community composition

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