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Abstract: Question: Does long-term grazing exclusion affect plant species diversity? And does this effect vary with long-term phytomass accumulation across a regional productivity gradient? Location: Lowland grassy ecosystems across the state of Victoria, southeast Australia. Methods: Floristic surveys and phytomass sampling were conducted across a broad-scale productivity gradient in grazing exclusion plots and adjacent grazed areas. Differences in species richness, evenness and life-form evenness between grazed and ungrazed areas were analysed. The environmental drivers of long-term phytomass accumulation were assessed using multiple linear regression analysis. Results: Species richness declined in the absence of grazing only at the high productivity sites (i.e. when phytomass accumulation was &gt;500 g m\(^{-2}\)). Species evenness and life-form evenness also showed a negative relationship with increasing phytomass accumulation. Phytomass accumulation was positively associated with both soil nitrogen and rainfall, and negatively associated with tree cover. Conclusions: Competitive dominance is a key factor regulating plant diversity in productive grassy ecosystems, but canopy disturbance is not likely to be necessary to maintain diversity in less productive systems. The results support the predictions of models of the effects of grazing on plant diversity, such as the dynamic equilibrium model, whereby the effects of herbivory are context-dependent and vary according to gradients of rainfall, soil fertility and tree cover.


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**Effects of grazing exclusion on plant species richness and phytomass accumulation vary across a regional productivity gradient**

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**Running title:** Grazing exclusion effects in grassy ecosystems
Abstract.

**Question:** Does long-term grazing exclusion affect plant species diversity? And does this effect vary with long-term phytomass accumulation across a regional productivity gradient?

**Location:** Lowland grassy ecosystems across the state of Victoria in south-eastern Australia.

**Methods:** Floristic surveys and phytomass sampling were conducted across a broad-scale productivity gradient in grazing exclusion plots and adjacent grazed areas. Differences in species richness, evenness and life-form evenness between grazed and ungrazed areas were analysed. The environmental drivers of long-term phytomass accumulation were assessed using multiple linear regression analysis.

**Results:** Species richness declined in the absence of grazing only at the high productivity sites (i.e. when phytomass accumulation was > 500 g.m$^{-2}$). Species evenness and life-form evenness also showed a negative relationship with increasing phytomass accumulation. Phytomass accumulation was positively associated with both soil nitrogen and rainfall, and negatively associated with tree cover.

**Conclusions:** Competitive dominance is a key factor regulating plant diversity in productive grassy ecosystems but canopy disturbance is not likely to be necessary to maintain diversity in less productive systems. The results support the predictions of models of the effects of grazing on plant diversity, such as the dynamic equilibrium model, whereby the effects of herbivory are context-dependent and vary according to gradients of rainfall, soil fertility and tree cover.

**Keywords:** Phytomass accumulation; Grazing effects; Productivity; Nitrogen; Rainfall; Tree cover.
Introduction

The Intermediate Disturbance Hypothesis (Connell 1978) predicts that species diversity is maximised at intermediate levels of disturbance. For grasslands, the dominance of superior competitors limits plant diversity at low disturbance, and the local extinction of disturbance-intolerant species limits diversity at high disturbance. However, this disturbance–diversity relationship varies with ecosystem productivity. A review by Proulx & Mazumder (1998) demonstrates that species richness increases under high levels of grazing in nutrient rich ecosystems, but decreases under high levels of grazing in nutrient-poor ecosystems. Such context-dependent effects of disturbance have been conceptualized in the Dynamic Equilibrium Model which posits that the disturbance–diversity relationship is unimodal, but the peak of maximum diversity moves to higher disturbance levels with increasing productivity (Huston 1979; Kondoh 2001).

At broad spatial scales, the primary variable used to explain grassland productivity is annual precipitation (Rosenzweig 1968; Lieth 1975; Lauenroth & Sala 1992). The precipitation–productivity relationship has been demonstrated at regional scales in grassy ecosystems in North America (Sala et al. 1988), South America (Jobbagy et al. 2002), Asia (Yu et al. 2004) and Africa (Deshmukh 1984). Globally, mean annual precipitation accounts for > 50% of variation in grassland productivity (Lauenroth 1979). Soil nitrogen (N) has been considered as secondary to rainfall as a driver of grassland productivity (Detling 1979; Stout & Jung 1992), though both correlative studies and N fertiliser experiments support the hypothesis of co-limitation of productivity by rainfall and N (Pastor et al. 1984; Tilman 1984; Hooper & Johnson 1999).

At small-scales, plant species richness is better correlated with above-ground phytomass than with productivity or habitat fertility, due to the more direct relationship between phytomass and light availability and plant competitive interactions (Grace 1999). Hence, the rate of above-ground phytomass accumulation in the absence of grazing is likely to be related to the frequency and intensity of disturbance required to maintain diversity in grasslands.

In addition to these factors, a key determinant of grassland disturbance–diversity relationships is a system’s evolutionary history of grazing (Milchunas et al. 1988). With increasing grazing pressure, grasslands with an evolutionary history of exposure to grazing by large herbivores are expected to experience less ecological change (and greater reversibility of these changes) than grasslands without such exposure (Cingolani et al. 2005).

In southern Australia, it is well established that native grasslands and grassy open woodlands (hereafter grassy ecosystems) dominated by the C4 perennial tussock grass Themeda triandra require frequent disturbance to promote species diversity (Stuwe & Parsons 1977; Lunt & Morgan 1999; Morgan & Lunt 1999). This is partly because these grasslands occur in high rainfall climates (i.e. > 550 mm.yr⁻¹) on fertile soils and hence phytomass recovers quickly after perturbation (Morgan & Lunt 1999); up to 457 g.m⁻² have been recorded within two years of burning (Lunt 1994). This phytomass accumulates with increasing time-since-fire as annual leaf production by the dominant grass essentially adds to the previous year’s litter which is slow to decompose (see Fig. 1...
in Morgan & Lunt 1999). No such consensus has been reached regarding the role of disturbance in southern Australia’s more xeric grassy ecosystems which are dominated by lower statured C3 perennial tussock grasses like *Austrodanthonia* spp. and *Austrostipa* spp. Disturbance has been considered crucial to maintaining plant diversity in xeric grasslands (Baker-Gabb 1993; Foreman 1999), although studies such as Williams (1969) and Conway (2000) observed no significant species richness response to grazing exclusion in these grasslands. Furthermore, there has been little research into the role of disturbance in the low-productivity grasslands of other regions, and no studies across broad productivity gradients in southern Australia. Hence, it remains unclear whether disturbance is necessary to maintain diversity in the less productive grassy ecosystems, nor whether these systems accumulate phytomass in the long-term absence of grazing. Regulators of phytomass accumulation and productivity in grassy ecosystems in southern Australia have also been little studied (Morgan 2007).

In this study we focus on native grassy ecosystems and ask: across rainfall and nutrient gradients, how does phytomass accumulate in the absence of disturbance? And how does grazing exclusion affect plant species richness across this gradient of phytomass accumulation? We also observe changes in species evenness and life-form composition, which are measures commonly used to conceptualise the response of plant communities to disturbances like grazing (e.g. McIntyre et al. 1995; Williams et al. 2005). We expect evenness and life-form composition measures to reflect the changes associated with competitive dominance when grazing is excluded, and for these changes to be more pronounced in the higher-productivity ecosystems.

We test the hypotheses that: (a) the effect of grazing exclusion on species richness, species evenness and life-form composition will be less negative in drier grassy ecosystems than in higher-rainfall regions, and (b) rainfall and soil N best explain variation in phytomass accumulation in the absence of grazing. Our results will be compared with studies in grassy ecosystems in other continents.

**Methods**

**Site selection**

Ten study sites, each containing one grazing-exclusion plot of known age and management, were sampled across the range of lowland grassy ecosystems in the state of Victoria, Australia. Sites encompassed a rainfall gradient from 270–960 mm yr\(^{-1}\) (Table 1, Fig. 1). All sites were grassy ecosystems (either tussock grassland or grassy woodland) dominated by native species. Large grazing herbivores (i.e. kangaroos, sheep or cattle) were excluded from each fenced plot for 5–15 years. Small grazers (notably rabbits) were not controlled at all sites, though fences did exclude rabbits at the four sites where substantial current grazing by rabbits was evident.

Exclusion plots varied in size from 0.01–7.5 ha. An area adjacent to each fenced plot was continuously grazed by large herbivores since establishment of the exclusion plot. The densities of herbivores outside the plots are unknown, but all sites showed physical evidence of high grazing pressure (i.e. cropped plants, trampling, high scat counts, and animals present). At each site, the
fenced plot represented an alternative management strategy imposed on a single patch within a landscape of homogenous management, and the adjacent control plots were similar in composition to the surrounding, grazed landscape. Hence, although no pre-treatment data exist, it was assumed that the grazed and ungrazed areas at each site did not significantly differ in species composition or phytomass prior to plot establishment, and that subsequent differences in composition were primarily due to the effect of the grazing exclusion treatment. The C3 grasses *Austrostipa* spp. and/or *Austrodanthonia* spp. were dominant in the more northern sites and the C4 grass *Themeda triandra* dominant in southern and western areas (Table 1). None of the sites had been burnt since exclosures were erected.

Soil sampling

To quantify the texture and nutrient status of soils at each site, soil samples were collected at the start of the growing season (August 2006) before the peak plant uptake of nutrients such as N and phosphorus (Tisdale *et al.* 1985). Three composite samples of ten soil cores (10 cm deep, 2 cm diameter) were collected from grazed areas surrounding each exclusion plot to give an average nutrient status of each site. Soils were analysed by CSBP Ltd. soil testing facility, Western Australia. Total soil N (nitrate and ammonia) was extracted with potassium chloride and measured colorimetrically on a Lachat Flow Injection Analyser. Soil organic matter (OM) was measured using the Walkley Black method (Walkley & Black 1934; Walkley 1947). Soil phosphorus was measured using the Colwell method (Colwell 1965). The soil proportions of sand, silt and clay were determined using the modified pipette procedure (particle-size analysis) of Indorante *et al.* (1990).

Vegetation surveys

At each site, two 15 m transects were established—one at 5 m each side of the exclusion plot fence and parallel to the fence. Careful examination showed no trampling effects along fence lines. Five 1 m² quadrats were sampled along each transect—one every 3 m. All species within each quadrat were identified and assigned a cover score. Species with < 5% cover (most species) were assigned a cover value to the nearest 1%. Species with > 5% cover were assigned a cover value to the nearest 5% increment. Within each quadrat, long-term phytomass accumulation (hereafter phytomass accumulation) was measured by harvesting above-ground phytomass (live + dead plant material) from a 0.25 m² nested quadrat and removing any soil, rock or tree litter from the sample. Floristic surveys and phytomass harvests were conducted in November–December 2006. The phytomass was dried at 80 °C for 48 hrs and weighed.

Each species in the survey was classified as either native or exotic to Australia (Walsh & Entwistle 1994; 1996; 1999), and assigned to one of five life-form classifications, according to a system modified from Raunkiaer (1934), based on the height of the perennating buds: (1) Therophytes – annual (monocarpic) plants, (2) Geophytes – persistent buds buried to a depth of 2–3 cm, (3) Chamaephytes – persistent buds ≥ 1 cm and < 20–30 cm above ground surface, (4) Phanerophytes – persistent buds > 20–30 cm above the ground, includes twiners and vines, and (5) Hemicryptophytes – persistent buds are in the immediate vicinity of the soil surface only.
Other site variables

We measured the diameter at breast height of all trees within a 50 m radius of the midpoint of the two transects to calculate the tree basal area of each site. Long-term rainfall data was found using HOWOFTEN? (Version 2.0.0.0, Agricultural Production Systems Research Unit, QLD).

Species data analysis

For all analyses, data from each transect were pooled so that values for phytomass accumulation, vegetation cover, richness and evenness were averages for each treatment at each site. Paired sample t-tests were used to test for significant differences (P < 0.05) between grazed and ungrazed plots in phytomass accumulation, vegetation cover, species richness, species evenness and life-form evenness. Linear regressions were used to test for significant relationships (P < 0.05) between phytomass accumulation and species richness, species evenness and life-form evenness. All t-tests and linear regressions were performed using SYSTAT version 9 (SPSS Ltd., Chicago).

The evenness index $J'$ (Pielou 1969) was used to calculate species evenness and life-form evenness (the equability of species abundance among the life-forms). $J'$ is based on Shannon’s diversity index ($\hat{H}'$):

$$\hat{H}' = -\sum_{i=1}^{S} \left[ \frac{n_i}{n} \ln \left( \frac{n_i}{n} \right) \right]$$

where $n_i$ is the cover of the $i$th species of $S$ species in the sample, and $n$ is the total cover of all the species in the sample. $J'$ is then calculated as:

$$J' = \frac{\hat{H}'}{\ln(S)}$$

When all species in a sample are equally abundant, species evenness is maximum ($J' = 1$), and this decreases towards zero as the relative abundances of species become less even. The difference in species evenness between grazed and ungrazed treatments ($\Delta J'_{sp}$) is calculated as:

$$\Delta J'_{sp} = J'_{spU} - J'_{spG}$$

where $J'_{spU}$ and $J'_{spG}$ are the species evenness of the ungrazed and grazed plots respectively. Similarly, the difference in life-form evenness between grazed and ungrazed treatments ($\Delta J'_{lf}$) is calculated as:

$$\Delta J'_{lf} = J'_{lfU} - J'_{lfG}$$
where $J'_{SPU}$ and $J'_{SPG}$ are the life-form evenness of the ungrazed and grazed plots respectively.

Linear regressions were also used to assess the differences in the cover of different life-forms between grazed and ungrazed plots across the phytomass accumulation gradient. The life-forms other than the hemicryptophytes and therophytes comprised very little of the total vegetation cover in all plots. Hence, the vegetation cover data for these life-forms were pooled and analysed as ‘other’ life forms.

**Analysis of phytomass accumulation with grazing exclusion**

Linear regressions were used to test for significant relationships ($P < 0.05$) between phytomass accumulation and the site environmental variables (soil and climate variables, tree cover, and time since grazing exclusion). An information-theoretic approach to multiple linear regression, *sensu* Burnham & Anderson (2002), was used to explain the variation in phytomass accumulation within exclosures across the study sites. A set of multiple competing hypotheses (models) to explain variation in the observed data were ranked using the Akaike Information Criteria (AIC). AIC favours model fit and simplicity, and is calculated using the residual sum of squares ($SS_{\text{resid}}$), the number of samples ($n$) and the number of predictor variables ($p$) of each model. Lower values of AIC indicate greater support for a model, relative to other models in the candidate set. The second-order AIC ($AIC_c$) was used as a small sample-bias adjustment, as recommended by Hurvich & Tsai (1989) for when the ratio of sample size to number of predictors $< 40:1$. The Akaike difference ($\Delta_i$) is the difference between the $AIC_c$ of any model and the lowest $AIC_c$ value in the candidate set. Any model with $\Delta_i < 2$ can be considered well supported (Burnham & Anderson 2002). $AIC_c$ was used to calculate Akaike weight ($w_i$), which represents the probability of that model being the best in the candidate set.

Six predictor variables were included in the models: (1) rainfall – average rainfall since 1990 (mm.yr$^{-1}$), (2) time since exclusion – time since large herbivores were excluded from plot (years), (3) tree cover – the basal area of tree cover at the site (m$^2$.ha$^{-1}$), (4) nitrogen – total soil N (%), (5) phosphorus – soil phosphorus content (mg.kg$^{-1}$) and (6) sand – soil sand component (%). Soil OM was removed from the model due to strong covariance with N (Barrett & Burke 2000). There was also strong covariance between the components of soil particle size (sand, silt and clay) and hence the sand component was included as the only representative variable of soil texture. All subsets of the six predictors provided 63 models. General Linear Modelling (GLM) was performed using SYSTAT version 9 (SPSS Ltd., Chicago) to calculate $SS_{\text{resid}}$ for each model.

**Results**

**Site-scale impacts of grazing exclusion**

When analysed at the site scale, grazing exclusion significantly increased phytomass accumulation at seven of the ten sites ($P < 0.05$), with a marginally significant ($P = 0.061$) effect at an eighth site (Table 2). Vegetation cover was significantly increased by grazing exclusion at five of these sites. Grazing exclusion led to a significant decrease in species richness at the two sites with
the highest phytomass accumulation (> 900 g.m⁻²), and to a significant increase in species richness at the least productive site (28 g.m⁻²). Grazing exclusion had no significant effect on species richness at the seven sites with intermediate levels of phytomass accumulation (i.e. 170–410 g.m⁻²). Species evenness significantly declined at all sites where grazing exclusion increased vegetation cover.

Grazing impacts across the phytomass accumulation gradient

The difference in species richness between grazed and ungrazed plots at the 1 m² scale (ΔSR) was negatively correlated with phytomass accumulation (P = 0.000, r² = 0.824, Fig. 2a). Thus, grazing exclusion decreased species richness at the high phytomass accumulation sites, and had neutral or small positive effects at low phytomass accumulation sites. The difference in vegetation cover between grazed and ungrazed plots (ΔVC) was positively correlated with phytomass accumulation (P = 0.004, r² = 0.665, Fig. 2b). Thus, the difference in cover between grazed and ungrazed treatments was substantially greater in the most productive sites, especially those where *Themeda triandra* was dominant. The difference in species evenness between grazed and ungrazed treatments (ΔJsp') was marginally significantly correlated to phytomass accumulation (P = 0.059, r² = 0.38, Fig. 2c), indicating that grazing exclusion also led to greater reductions in species evenness in the most productive sites. The difference in life-form evenness between grazed and ungrazed treatments (ΔJlf') was significantly negatively correlated with phytomass accumulation (P = 0.014, r² = 0.549, Fig. 2d). Thus, grazing exclusion led to greater reductions in life-form evenness in the most productive sites.

The different life forms responded differently to grazing exclusion. Hemicryptophyte cover (which includes perennial grasses) was substantially greater in ungrazed than grazed plots at high phytomass accumulation sites, but there was little difference in cover at low phytomass accumulation sites where *Austrodanthonia* spp. and *Austrostipa* spp. were dominant, creating a significant positive relationship between phytomass accumulation and hemicryptophyte cover (P = 0.007, r² = 0.625, Fig. 3a). The greater cover of vegetation in ungrazed compared to grazed plots at the high phytomass accumulation sites could be attributed solely to the hemicryptophytes, particularly perennial grasses (Fig. 3a). The change in therophyte cover between grazed and ungrazed plots was not significantly related to phytomass accumulation (P = 0.219, r² = 0.182, Fig 3b). However, the difference in cover of ‘other’ life-forms (geophytes, chamaephytes and phanerophytes) between grazed and ungrazed treatments was significantly negatively related to phytomass accumulation (P = 0.006, r² = 0.631, Fig. 3c). Thus, ‘other’ life forms had lower cover in exclosures than in grazed plots at the most productive sites but greater cover in exclosures at the least productive sites.

Regional trends in phytomass accumulation

Phytomass accumulation in ungrazed grassy ecosystems varied greatly (Table 2), from 28 g.m⁻² over 6 years at Grampians to 944 g m⁻² over 12 years at Warrambeen. Phytomass accumulation showed significant, positive linear relationships with three of the predictor variables (Fig. 3): annual rainfall (P = 0.047, r² = 0.407), nitrogen (P = 0.021, r² = 0.507) and soil OM (P =
There was no significant relationship between phytomass accumulation and soil phosphorus, sand content, tree basal area or time-since-exclosure ($P > 0.05$).

‘Rainfall + tree basal area’ provided the best AIC model for explaining phytomass accumulation (Table 3). Phytomass accumulation increased with increasing rainfall, and decreased with increasing tree basal area (Fig. 4), despite the relationship between phytomass accumulation and tree basal area alone being not significant. The models for ‘nitrogen’ and ‘nitrogen + phosphorus’ were also well supported. All other 60 models were not well supported ($\Delta_i < 2$). Sand content and time-since-exclosure were not important predictors of phytomass accumulation.

**Discussion**

**Impacts of grazing exclusion**

In lowland grassy ecosystems across southern Australia, species richness, species evenness and life-form evenness were all reduced by grazing exclusion only at sites with high phytomass accumulation (> 500 g.m$^{-2}$). Species richness was not significantly affected by grazing exclusion at all the lower phytomass accumulation sites except one, where it increased.

The productive sites that had sharp declines in species richness with grazing exclusion were both dominated by *Themeda triandra*, a vigorous and deep-rooted perennial (McDougall 1989). Many studies have documented reduced diversity in *Themeda*-dominated grasslands in southeastern Australia in the absence of disturbance (Stuwe & Parsons 1977; Lunt & Morgan 1999; Morgan & Lunt 1999) as many native forbs are sensitive to competition for light from matrix-forming grasses (Morgan 1997; 1998). This indicates an important role for disturbance in maintaining richness in grasslands where productivity is high. As such, *Themeda*-dominated grasslands demonstrate ecological convergence with grassy ecosystems elsewhere that have similar rainfall regimes, e.g. flooding Pampa (Sala *et al.* 1986, 924 mm.yr$^{-1}$), South African lowveld savanna (Jacobs & Naiman 2008, 500-600 mm.yr$^{-1}$) and North American tallgrass prairie (Hartnett *et al.* 1996, 838 mm.yr$^{-1}$), all of which depend on disturbance to maintain species richness.

In contrast to the *Themeda*-dominated grasslands, species richness was not reduced significantly by grazing exclusion at sites of low phytomass accumulation (< 407 g.m$^{-2}$, and < 410 mm.yr$^{-1}$ average rainfall), suggesting that disturbance is not necessary to maintain species richness at these sites. While this has been observed before in a number of single-site studies from the Riverine Plain of northern Victoria (Williams 1969; Foreman 1996; Conway 2000), our results suggest that a similar lack of decline in richness in response to grazing exclusion can be expected across the suite of more xeric grassy ecosystems that occur across Victoria. The results also highlight the distinction between the low- and high-productivity grassy ecosystems. These drier grasslands show greater affinities with North American rocky mountain grasslands (Stohlgren *et al.* 1999), Patagonian grass-shrub steppes (Perelman *et al.* 1997) and low-productivity arctic and alpine grasslands (Moen & Oksanen 1998; Olofsson *et al.* 2002), where the absence of disturbance rarely results in significant phytomass accumulation or species richness declines.
In the drier grasslands, it may be that periodic droughts cause sufficient phytomass removal to negate competitive exclusion and the requirement for disturbances such as grazing (Lewis et al. 2008). Dry summers and late arrival of autumn rains on the Riverine Plain can lead to substantial mortality of dominant perennial grasses (Williams 1969), reducing the likelihood of long-term phytomass accumulation. Conway (2000) observed that litter cover declined from over 50% to <10% in a single year during drought in northern Victoria and hence, phytomass accumulation is less likely there. We expect that similar phytomass removal has occurred at our study sites over the period of grazing exclusion.

The negative correlation of ∆SR to phytomass accumulation provides support for the Dynamic Equilibrium Model (DEM), in which the disturbance level that achieves maximum diversity increases with increasing productivity. One consequence of the DEM that has been demonstrated by Proulx & Mazumder (1998) and Bakker et al. (2006) is the reversal of grazing effects on species richness between productive and unproductive ecosystems. Our results suggest that the productivity gradient across grassy ecosystems in southern Australia straddles the threshold of this reversal of grazing effects. Furthermore, Gibson & Kirkpatrick (1989) examined the effects of grazing exclusion in Tasmanian grassy ecosystems across a higher rainfall gradient (800–1800 mm yr\(^{-1}\) c.f. 270–960 mm yr\(^{-1}\) for the present study). They also observed that species richness response to grazing exclusion was negatively correlated with productivity, though species richness decreased at all sites, so the correlation was driven by the magnitude of the decrease. This suggests that the rainfall gradient that they sampled did not cross the threshold for the reversal of grazing effects, and that the predictions of the DEM are robust across southern Australia.

Despite our study region’s short evolutionary history of grazing, we do not expect the ecosystem responses to grazing to be greater than in regions with long evolutionary history of grazing, as predicted by Milchunas & Lauenroth (1993) and Adler et al. (2004). Though the current grazing pressure in Australia’s grassy ecosystems is higher than historic levels, soil and vegetation are a result of transformations caused by past livestock grazing (rare, small grazing refugia are an exception), and cannot be viewed as having little evolutionary exposure to heavy grazing (see Lunt et al. (2007) for a review). Hence, we expect grazing effects across productivity gradients to be similar to those observed in continents with long evolutionary histories of grazing, such as Africa and North America.

Where significant effects were observed, grazing exclusion always reduced species evenness. Many global grazing experiments have found higher evenness in grazed than ungrazed treatments (Noy-Meir 1995; Bai et al. 2001; Cingolani et al. 2003; Hillebrand 2003; Altesor et al. 2005), which is attributed to the suppression of dominant species. Hillebrand (2003) demonstrated the opposing effects of grazing and productivity on evenness, which declined with increasing productivity due to the increased dominance of a few species. This was reflected in our results, with the greatest reductions in species evenness occurring in the high-productivity Themeda-dominated sites, which had very low evenness (J’ < 0.3) in the exclusion plots due to the almost-complete canopy dominance of *Themeda triandra*. These evenness changes with grazing exclusion again highlight the contrasting ecology of Victoria’s low- and high-productivity grassy ecosystems.
The reduction in life-form evenness under grazing exclusion can be attributed to the enhanced cover of hemicryptophytes (primarily perennial grasses). This effect was most substantial at the highest phytomass accumulation sites, due to the competitive dominance of *Themeda triandra* and the suppression of herbaceous species. The cover of the ‘other’ life forms (geophytes, chamaephytes and phanerophytes) decreased with grazing exclusion at the high productivity sites, but increased in the least productive sites. These results suggest that for the low-productivity sites, grazing exclusion may increase the abundance and cover of a range of species, not only the perennial grasses, and that competition from perennial grasses does not influence species composition like it does in the high-productivity grasslands.

**Regulating factors**

As hypothesised, rainfall contributed to the strongest GLM model for phytomass accumulation, but it accounted for only 42% of the observed variation in phytomass accumulation across our study sites—much less than in studies such as Lane *et al.* (1998), Sala *et al.* (1988) and Deshmukh (1984) who found that rainfall explained 92%, 90% and 67% respectively of the observed variation in productivity over a similar rainfall gradients to this study (see Table 4). This discrepancy may be due to factors such as the variation in tree cover across study sites.

Tree cover did not show a significant correlation to phytomass accumulation, but influenced the best-supported AIC model, with phytomass accumulation generally decreasing with increasing tree cover. While woody species have been shown to both suppress (Aguiar *et al.* 1992; Riegel *et al.* 1992) and enhance (Weltzin & Coughenour 1990; Belsky 1994; Callaway 1995) grass productivity, our results are consistent with studies in eucalypt woodlands of eastern Australia which demonstrate that trees suppress grass-layer productivity (Walker *et al.* 1972; Harrington & Johns 1990; Scanlan & Burrows 1990; Jackson & Ash 1998).

Though ‘rainfall + tree cover’ provided the best AIC model, the ‘nitrogen’ model was also well supported, and N provided the strongest single-predictor linear regression for explaining variation in phytomass accumulation across the study region. Our analyses suggest close similarities in the controls on productivity between the study region and the Central Grassland region in the USA, where Burke *et al.* (1997) showed that net primary production and N availability both increase with annual rainfall, making it impossible to separate the extent to which productivity is controlled by water or N.

**Conclusion**

We demonstrate that the impact of disturbance by grazing has contrasting effects on species diversity across a regional productivity gradient regulated by rainfall, soil resources and tree cover, as hypothesised by Huston (1979) and Milchunas *et al.* (1988). While there is some uncertainty in our model fit, reflecting our low sample size, we believe that the Dynamic Equilibrium Model has support for explaining the impacts of herbivory on plant diversity in southern Australia. Negative, neutral and positive effects of grazing on small-scale species richness appear possible, reflecting how grazing differentially affects competitive interactions across a gradient of decreasing
environmental stress. Such recognition represents a shift in the traditional conceptual understanding of lowland grassy ecosystem function in southern Australia where disturbance has generally been thought to be crucial to maintaining small-scale diversity (e.g. Baker-Gabb 1993; Tremont & McIntyre 1994; Foreman 1999). We illustrate the importance of undertaking regional-scale comparisons to place local responses within a broader spatial and geographic context (see also Glenn et al. (1992) for an example), and to allow the development of robust, site-specific strategies for the conservation of biodiversity across an ecosystem’s range.

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**References**


Table 1. Description of the study sites (Location, time-since-exclosure, exclosure size, average annual rainfall, dominant species and current grazers), and mean values (± SEM) for total soil nitrogen (N), soil phosphorus content (P), soil organic carbon (OC), soil sand content (Sand), and tree basal area at each site.

<table>
<thead>
<tr>
<th>Region and site name</th>
<th>Location</th>
<th>Time-since-exclosure (yrs)</th>
<th>Size (ha)</th>
<th>Average rainfall (mm.yr⁻¹)</th>
<th>Dominant perennial grasses</th>
<th>Current grazers</th>
<th>N (%)</th>
<th>P (mg.kg⁻¹)</th>
<th>OC (%)</th>
<th>Sand (%)</th>
<th>Tree basal area (m².ha⁻¹)</th>
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<td><strong>Mallee</strong></td>
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<tr>
<td>Murray-Sunset</td>
<td>34°16' S 141°49' E</td>
<td>15</td>
<td>6.25</td>
<td>272</td>
<td>Austrodanthonia spp.</td>
<td>kangaroos, rabbits, goats</td>
<td>0.08 (0.006)</td>
<td>9.67 (0.68)</td>
<td>0.81 (0.06)</td>
<td>81.5 (3.40)</td>
<td>4.0</td>
</tr>
<tr>
<td>Hattah-Kulkyne</td>
<td>34°42' S 142°18' E</td>
<td>9</td>
<td>6.25</td>
<td>293</td>
<td>Austrostipa spp.</td>
<td>kangaroos, rabbits</td>
<td>0.05 (0.007)</td>
<td>6.00 (0.45)</td>
<td>0.61 (0.04)</td>
<td>92.9 (0.48)</td>
<td>13.9</td>
</tr>
<tr>
<td><strong>Northern Riverine Plain</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
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<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pine Grove</td>
<td>36°13' S 144°25' E</td>
<td>10</td>
<td>0.04</td>
<td>381</td>
<td>Austrodanthonia spp. Austrostipa spp.</td>
<td>sheep</td>
<td>0.12 (0.012)</td>
<td>12.00 (1.18)</td>
<td>1.54 (0.13)</td>
<td>58.0 (0.72)</td>
<td>20.6</td>
</tr>
<tr>
<td>Mitiamo</td>
<td>36°13' S 144°25' E</td>
<td>5</td>
<td>0.03</td>
<td>381</td>
<td>Austrodanthonia spp. Austrostipa spp.</td>
<td>sheep</td>
<td>0.12 (0.003)</td>
<td>7.33 (0.68)</td>
<td>1.46 (0.01)</td>
<td>73.8 (0.70)</td>
<td>12.8</td>
</tr>
<tr>
<td>Kinypanial</td>
<td>36°19' S 143°48' E</td>
<td>12</td>
<td>0.04</td>
<td>409</td>
<td>Austrodanthonia spp. Austrostipa spp.</td>
<td>sheep, rabbits</td>
<td>0.09 (0.007)</td>
<td>3.67 (0.26)</td>
<td>0.93 (0.04)</td>
<td>53.9 (1.69)</td>
<td>0.0</td>
</tr>
<tr>
<td><strong>Western Plains</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
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<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Grampians</td>
<td>37°03' S 142°22' E</td>
<td>6</td>
<td>1.0</td>
<td>629</td>
<td>Austrodanthonia spp. Neurachne alopecuroides</td>
<td>kangaroos, wallabies</td>
<td>0.05 (0.003)</td>
<td>2.00 (0.00)</td>
<td>0.70 (0.07)</td>
<td>88.0 (2.11)</td>
<td>48.9</td>
</tr>
<tr>
<td>Warrambeen</td>
<td>37°55' S 143°52' E</td>
<td>12</td>
<td>0.04</td>
<td>587</td>
<td>Themeda triandra</td>
<td>sheep, rabbits</td>
<td>0.20 (0.028)</td>
<td>5.67 (0.68)</td>
<td>3.03 (0.14)</td>
<td>40.8 (2.64)</td>
<td>0.0</td>
</tr>
<tr>
<td>Inverleigh</td>
<td>38°05' S 144°03' E</td>
<td>11</td>
<td>0.01</td>
<td>523</td>
<td>Themeda triandra</td>
<td>kangaroos, rabbits</td>
<td>0.10 (0.035)</td>
<td>3.67 (0.93)</td>
<td>1.40 (0.37)</td>
<td>87.8 (1.98)</td>
<td>27.6</td>
</tr>
<tr>
<td>Craigieburn</td>
<td>37°35' S 144°56' E</td>
<td>8</td>
<td>7.5</td>
<td>665</td>
<td>Austrostipa spp. Austrodanthonia spp.</td>
<td>sheep</td>
<td>0.30 (0.025)</td>
<td>11.00 (1.18)</td>
<td>4.13 (0.29)</td>
<td>43.6 (0.78)</td>
<td>0.0</td>
</tr>
<tr>
<td><strong>Wilson’s Promontory</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Wilson’s Promontory</td>
<td>38°53’ S 146°14'E</td>
<td>16</td>
<td>0.01</td>
<td>960</td>
<td>Themeda triandra</td>
<td>kangaroos, wombats, deer</td>
<td>0.28 (0.020)</td>
<td>7.33 (1.13)</td>
<td>2.90 (0.15)</td>
<td>88.5 (1.10)</td>
<td>2.5</td>
</tr>
</tbody>
</table>
Table 2. Mean phytomass, vegetation cover, species richness, and species evenness in grazed and ungrazed areas.
The differences between grazed and ungrazed areas for each measure are shown. Significant differences (paired sample t-tests) are marked with an asterisk (*).

<table>
<thead>
<tr>
<th>Site</th>
<th>Phytomass (PM)</th>
<th>Vegetation cover (VC)</th>
<th>Species richness (SR)</th>
<th>Species evenness ($J'$)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Grazed (g.m$^{-2}$)</td>
<td>Ungrazed (g.m$^{-2}$)</td>
<td>∆PM (g.m$^{-2}$)</td>
<td>Grazed (%)</td>
</tr>
<tr>
<td>Murray Sunset</td>
<td>146 (67)</td>
<td>172 (58)</td>
<td>26</td>
<td>54.5 (10.9)</td>
</tr>
<tr>
<td>Hattah Kulkyne</td>
<td>33 (7)</td>
<td>171 (74)</td>
<td>139*</td>
<td>6.0 (0.2)</td>
</tr>
<tr>
<td>Pine Grove</td>
<td>46 (42)</td>
<td>162 (32)</td>
<td>115*</td>
<td>10.6 (3.5)</td>
</tr>
<tr>
<td>Mitiamo</td>
<td>115 (28)</td>
<td>407 (184)</td>
<td>291*</td>
<td>10.3 (0.4)</td>
</tr>
<tr>
<td>Kinypanial</td>
<td>98 (52)</td>
<td>208 (69)</td>
<td>110*</td>
<td>10.2 (1.3)</td>
</tr>
<tr>
<td>Grampians</td>
<td>1.0 (0.9)</td>
<td>28 (24)</td>
<td>27</td>
<td>5.4 (0.3)</td>
</tr>
<tr>
<td>Warrambeen</td>
<td>38 (33)</td>
<td>944 (162)</td>
<td>906*</td>
<td>11.7 (1.0)</td>
</tr>
<tr>
<td>Inverleigh</td>
<td>39 (30)</td>
<td>306 (83)</td>
<td>267*</td>
<td>8.2 (2.2)</td>
</tr>
<tr>
<td>Craigieburn</td>
<td>186 (215)</td>
<td>350 (239)</td>
<td>164</td>
<td>26.5 (8.1)</td>
</tr>
<tr>
<td>Wilson's Promontory</td>
<td>168 (94)</td>
<td>941 (298)</td>
<td>772*</td>
<td>14.5 (0.7)</td>
</tr>
</tbody>
</table>
Table 3. Outcomes of model selection to explain variation in phytomass accumulation data.

Models are shown in ascending order of the second-order Akaike Information Criteria (AICc). AICc differences ($\Delta$) and Akaike weights ($w_i$) are shown. The 60 models that were not well supported ($\Delta > 2$) are not shown.

<table>
<thead>
<tr>
<th>Model</th>
<th>AICc</th>
<th>$\Delta$</th>
<th>$w_i$</th>
</tr>
</thead>
<tbody>
<tr>
<td>rainfall + tree basal area</td>
<td>109.09</td>
<td>0.00</td>
<td>0.20</td>
</tr>
<tr>
<td>nitrogen</td>
<td>109.80</td>
<td>0.71</td>
<td>0.14</td>
</tr>
<tr>
<td>nitrogen + phosphorus</td>
<td>111.07</td>
<td>1.98</td>
<td>0.08</td>
</tr>
</tbody>
</table>
Fig. 1. Location of study sites in south-eastern Australia.
Fig. 2. Relationship between phytomass accumulation and the effect of grazing exclusion on (a) species richness ($\Delta SR$), (b) vegetation cover ($\Delta VC$), (c) species evenness ($\Delta J'_SP$) and (d) life-form evenness ($\Delta J'_LF$). Non-significant relationships are shown by a dashed trendline.
Fig. 3. Relationship between phytomass accumulation and the effect of grazing exclusion (a) hemicryptophyte cover, (b) therophyte cover, and (c) the cover of other life-forms. Non-significant relationships are shown by a dashed trendline.
Fig. 4. The relationships of phytomass accumulation to (a) annual rainfall, (b) total soil nitrogen and (c) soil organic carbon.