

## Composition of grazed and cleared temperate grassy woodlands in eastern Australia: patterns in space and inferences in time

Clarke, Peter J.

*Botany, The University of New England, Armidale, NSW 2351, Australia;  
E-mail pclarke1@metz.une.edu.au*

**Abstract.** A regional vegetation survey of the temperate grassy woodlands (temperate savanna) in Australia was designed to assess the effects of clearing and grazing on the composition of vegetation remnants and the adjacent pasture matrix. Vegetation was sampled across a range of habitats using 77 0.1024-ha quadrats; the relative abundance of species was recorded. Classification analysis clustered the sites into three main groups that corresponded to intensity of grazing/clearing followed by groups based on underlying lithology (basalt, metasediment, granites). Using Canonical Correspondence Analysis, exogenous disturbance and environmental variables were related to the relative abundance of species; grazing intensity had the highest eigenvalue (0.27) followed by tree canopy cover (0.25), lithology (0.18), altitude (0.17) and slope (0.10). Based on two-dimensional ordination scores, six species response groups were defined relating to intensity of pastoralism and nutrient status of the landscape. Abundance and dominance of native shrubs, sub-shrubs, twiners and geophytes were strongly associated with areas of less-intense pastoralism on low-nutrient soils. The strongest effects on species richness were grazing followed by canopy cover. Continuously grazed sites had lower native species richness across all growth forms except native grasses. There was no indication that intermediate grazing intensities enhanced forb richness as a result of competitive release. Species richness for all native plants was lowest where trees were absent especially under grazed conditions. Canopy cover in ungrazed sites appeared to promote the co-existence of shrubs with the herbaceous layer. Predicted declines in forb richness in treeless, ungrazed, sites were not detected. The lack of a disturbance-mediated enhancement of the herbaceous layer was attributed to habitat heterogeneity at 0.1 ha sampling scale.

**Keywords:** CCA; Clearing; Competitive release; Exotic species; Grassland; Grazing; Savanna; Species richness.

**Nomenclature:** Harden 1990-1993.

### Introduction

Temperate grassy woodlands (temperate savanna) in Australia once covered about 1 million km<sup>2</sup>, about half of which has been cleared for cropping and grazing (Yates & Hobbs 2000). The effects of clearing and thinning trees on temperate woodlands for grazing include the following: replacement of native species by exotics (McIntyre & Lavorel 1994a; Pettit et al. 1995; Yates & Hobbs 1997), decreased species richness (McIntyre & Lavorel 1994a; Pettit et al. 1995), changes in the dominance of the herbaceous layer (Whalley et al. 1978; Trémont 1994; Wahren et al. 1994; McIntyre et al. 1995) and declines in the recruitment opportunities for tree and shrub species (Yates & Hobbs 1997; Clarke 2002; Henderson & Keith 2002). Evidence for these changes comes from historic records, comparative analysis of spatial patterns (natural 'experiments') and the results of experimental studies (Wilson 1990; Yates & Hobbs 1997; Clarke 2000). These effects appear to contrast with grassy communities with a long evolutionary history of grazing where changes in composition (species similarity), dominant species, growth-forms, and diversity are less pronounced (Milchunas & Laurenroth 1993).

In the tablelands of eastern Australia, agriculture is centred upon sheep and cattle grazing of native pastures after removal or thinning of eucalypt woodlands to promote native grasses and improved pasture. Anthropogenic native grasslands are now widespread on the tablelands and studies have mainly examined the impacts of stock grazing and other disturbances in natural 'experiments' in the pasture matrix (McIntyre et al. 1993; Trémont 1994; McIntyre & Lavorel 1994a, b; McIntyre et al. 1995). Conversely, regional vegetation surveys have mainly examined woodland or forest remnants assuming the cleared matrix is of little conservation value (e.g. Benson & Ashby 2000). However, landscape comparisons of floristic composition between open areas and those that retain eucalypts are lacking, nor has there been any attempt to partition the effects of tree removal from that of grazing. More broadly, the effects of understorey

grazing and tree canopy on vegetation composition have rarely been assessed in savanna ecosystems (Scholes & Archer 1997; Gibbs et al. 1999). Similarly, the effects of canopy and grazing interactions on competitive exclusion are poorly understood especially in temperate savanna (Scholes & Archer 1997).

The purpose of this paper is to examine the effects of anthropogenic disturbance on the composition of grassy communities. These effects were assessed by contrasting intrinsic environmental factors (altitude, slope and lithology) and anthropogenic modifications (grazing and tree cover) of the landscape to test whether; (1) anthropogenic disturbance or environmental factors more strongly influence species composition, (2) changes in abundance of species, growth forms and richness by disturbance interact with environmental factors and (3) competitive release by canopy shade or grazing increases understorey species richness.

## Methods

### Study system

The research was conducted on the New England Tablelands in eastern Australia covering an area of approximately 30 000 km<sup>2</sup>, about half of which was grassy eucalypt woodland or grassland. Mean annual rainfall ranges from about 750-900 mm, of which 60% falls in the summer months of November to March. Mean annual temperature is ca. 18 °C. The soils range from kurosols, over metasediments, to vertisols derived from basalt flows. The vegetation of the region is dominated by anthropogenic grasslands, grassy woodlands and forests (temperate savanna), shrubby woodlands (sclerophyll forests), with minor areas of heath and wetlands. Differences in the biophysical environment primarily influence natural vegetation patterns on the tablelands (800-1200 m) of eastern Australia (Benson & Ashby 2000). The most obvious of these patterns is segregation of the sclerophyll shrub-dominated communities on nutrient-poor lithosols (see Hunter & Clarke 1998) and the more widespread 'grassy' communities on deeper clay-rich soils. Natural treeless grasslands occur in cold air drainage basins on fertile soils and in grassy 'dells' within woodlands in minor drainage depressions. These tree-grass mixes appear to be stable over millennia with little evidence for grazing-browsing-fire interactions (Clarke unpubl.).

Whilst grasses dominate in the herbaceous layer, forbs are the richest species component in tableland grassy woodlands (McIntyre et al. 1993). The vegetation of the region forms a variegated landscape due to the intrinsic environmental variation within the region

and to the regimes of pastoral management (fire, fertilizer, stock, clearing, cultivation) (McIntyre & Barrett 1992). Fire frequency in the grassy landscapes over the last 50 yr is very low and fire extent is small due to fire suppression. Most woody plants resprout after fire in grassy woodlands (Clarke & Knox 2002). The main pre-European grazers/browsers in the landscape were grey kangaroos (*Macropus giganteus*) which were largely replaced after the 1860s by domestic sheep and cattle grazers.

### Sampling design

Vegetation was sampled with 77 0.1024-ha quadrats within relatively homogeneous patches of grasslands and grassy woodlands from a randomly selected population of predefined environmental classes (Table 1). These classes were identified by satellite images together with geological maps of the region and re-adjusted after site visitation. Polygons from satellite images (tree cover classes) were mapped onto the geology, elevation and topography using a GIS. Sets of polygons with the same class combinations were sequentially labelled and a random subset chosen for sampling. At each site a nested scoring approach was used to estimate density of each species using the frequency-score of Morrison et al. (1995). The presence/absence of vascular plant species was recorded in each of the ten concentric quadrats (2, 4, 8, 16, 32, 64, 128, 256, 512 and 1024 m<sup>2</sup>) to give a score out of ten for each species in the sample. This score reflects the density of each taxon rather than its cover or biomass as described and validated by Morrison et al. (1995).

**Table 1.** Environmental variables used to stratify sampling sites and analyses of species richness data.

Stratification / Level ( <i>n</i> )	Criteria
<b>Altitude (A)</b>	
Ah High (27)	> 1400 m
Ai Intermediate (33)	1100-1400 m
Al Low (17)	< 1100 m
<b>Lithology (L)</b>	
Ll Low nutrient (22)	Leucogranites and porphyry
Lm Medium nutrient (22)	Metamorphics and biotite granites
Lh High nutrient (33)	Basalt and alluvium
<b>Slope position (S)</b>	
Su Upper (10)	
Sm Mid (32)	
Sl Lower (35)	
<b>Grazing (G)</b>	
	Effects of sheep and cattle grazing.
	Knowledge of land use and physical condition of paddock swards used to assess level.
Gl Low/none (29)	Exlosures, National Parks, Nature Reserves
Gi Infrequent (19)	Stock routes, roadsides, 'back-paddocks'
Gc Frequent (29)	Paddocks intensively used
<b>Tree cover (T)</b>	
	Effects of land clearing rather than natural tree cover assessed. i.e. natural grassland excluded
Tc Open (19)	Paddocks cleared of trees with trees in adjacent areas of equivalent landscape position.
Tt Thinned (23)	Areas with stumps; scattered canopy cover.
Ti Canopy (35)	No recent evidence of clearing, mainly mature trees with canopies $\leq$ two canopy widths apart.

*Classification and ordination*

Cluster analysis was used to classify quadrat data collected to obtain a general account of the floristic variation across all sites sampled. This matrix consisted of 77 quadrats (objects) and 558 species (attributes). Species abundances were entered as frequency scores from 1 to 10. The Bray-Curtis coefficient was used to calculate an association matrix using unstandardized data. Sites were clustered using agglomerative classification (UPGMA,  $B = -0.1$ ) with the PATN package.

Canonical Correspondence Analysis (CCA) constrained on major environmental variables after comparison with correspondence analysis (ter Braak 1987). Five variables were used included: altitude, slope, lithology, tree canopy cover and grazing intensity (Table 1). Statistical tests of the significance of the relationship used Monte Carlo simulations with 999 permutations within CANOCO. Interpretations of the triplot ordination diagrams follow ter Braak & Verdonschot (1995).

*Species groups and growth form comparisons*

Each species was assigned to a group based on agglomerative classification of species (six group level) and position of individual species in the CCA two-dimensional ordination space. Within groups, comparisons of plant growth form abundances were made using summed abundance scores of all species in each of six growth forms plus exotic and native species richness; exotics, natives, native grasses, native forbs, native geophytes, native shrubs, native twiners, and native trees. Total species richness of each growth form was also calculated by summing growth form richness over all six groups. A *G*-test of association were used to test for significant differences ( $P < 0.05$ ) in ratios of abundance and richness among the six groups. Species with a summed abundance score across all sites  $\geq 10$  and occurring in  $\geq 10\%$  of sites were used to define group dominants (App. 1).

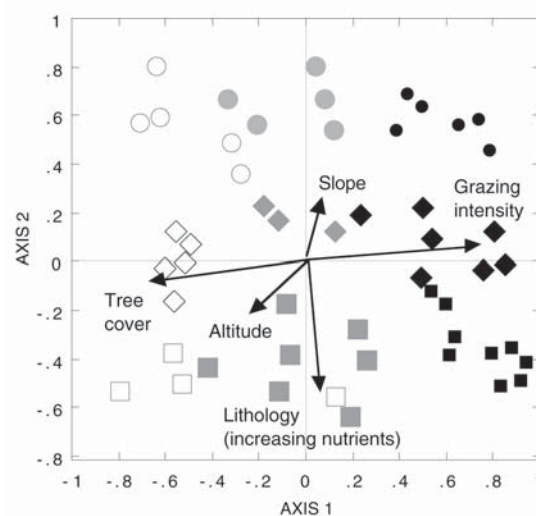
*Species richness*

Generalized linear models (GLIM) with a Poisson error structure with a log link function (Crawley 1993) were used for analysis of species richness response to altitude, lithology, grazing and tree cover classes (Table 1). Richness responses were evaluated by growth form and for all species. In these analyses the effects of grazing and canopy cover could be assessed independently because there were orthogonal combinations of both variables across lithology and to some extent altitude.

**Results**

*Classification and ordination of sites*

Classification analysis clustered the 77 quadrats/sites into three main groups that corresponded to high, intermediate, or low pastoral activity, but failed to discriminate according to grazing and clearing intensities independently. Sites were assigned to secondary groups related to lithology (basalt, metasediment, granites), providing a nine group analysis framework. These groups were superimposed on the distribution of sites in the ordination produced by using CCA (Fig. 1). Their position suggests that axis 1 corresponds with increasing pastoral activity and axis 2 with decreasing soil resource levels (Fig. 1). Constrained ordination showed that the first two axes accounted for 61% of the variance in weighted average abundances of species. The global model with all environmental variables produced a multivariate regression coefficient of 0.88 for axis 1 and 0.84 for axis 2. For axis 1, the highest canonical coefficient was grazing (0.58) followed by clearing (-0.50); for axis 2, lithology had a very high coefficient of -0.9. (Fig. 1). Overall, grazing intensity had the highest eigenvalue (0.27) followed by tree canopy cover (0.25), lithology (0.18), altitude (0.17) and slope (0.10).



**Fig. 1.** Constrained ordination of sites and major environmental factors of the first two axes of a Canonical Correspondence Analysis (CCA). These axes account for 61% of the variance. Quadrat groups, classified by UPGMA, are shown with different symbols and shading. Dark fill are those sites intensively grazed with little canopy cover, grey fill are those sites with intermediate grazing and no fill are those sites with low grazing intensities and a tree canopy. Basalt sites shown as squares, metasediments as diamonds, and granitoid as circles.

### *Species groups*

Six species groups were defined based on the position of the species in ordination space along the two environmental axes (intensity of pastoralism and lithology) and UPGMA classification of species. Six groups corresponded closely to three broad levels of pastoralism subdivided into two levels of lithology/edaphic contrasts. Assigning species into groups associated independently with canopy cover and grazing was not possible because of similar vectors in CCA. Hence the combined effects are termed 'intensity of pastoralism'. The species groups are (1) tolerant of intense pastoral activity on high soil resource levels (56 species); (2) tolerant of intense pastoralism on medium to low soil resource levels, (46 species); (3) tolerant of all levels of pastoralism on high soil resource levels (61 species); (4) tolerant of all levels of pastoral activity on low soil resource levels (146 species); (5) intolerant of pastoralism on high soil resource levels (72 species); and (6) intolerant of pastoralism on low soil resource levels (159 species).

### *Growth form abundance and richness of species response groups*

In all species groups, forbs had the highest summed abundances followed by grasses, shrubs, graminoids, trees, twiners, ferns and geophytes (Table 2). Between species response groups, growth form abundance and richness changed significantly (Table 2). In the pastoralism-tolerant groups native grasses were more abundant than forbs, but had lower richness than native forb and exotic species (mostly annuals) (Table 2, App. 1). Ferns, geophytes, sub-shrubs and twiners were either reduced in abundance or absent (Table 2, App. 1).

In the tolerant of all levels of pastoralism groups native grasses were also more abundant and less diverse than forbs (Table 2). These groups contained most of the widespread and commonly occurring perennial grasses, native forbs and the common introduced annuals that occur throughout temperate regions of Australia (Appendix). Common trees in the landscape were also represented in this group and a number of unpalatable shrub species (*Epacridaceae*) were present. Within the higher nutrient species group a major component of the flora was missing, with no twiners, ferns or geophytes represented (Table 2, App. 1).

In the pastoralism-intolerant groups native forbs were both more species-rich and abundant than native grasses and the prominence of exotics was lower (Table 2, App. 1). In contrast to the intolerant and intermediate response groups, ferns, geophytes, sub-shrubs, shrubs and twiner species were well represented both in terms of richness and abundance. Twiner species

were particularly abundant in the group associated with more fertile soils whilst native shrubs were the most represented growth form in the low nutrient response group.

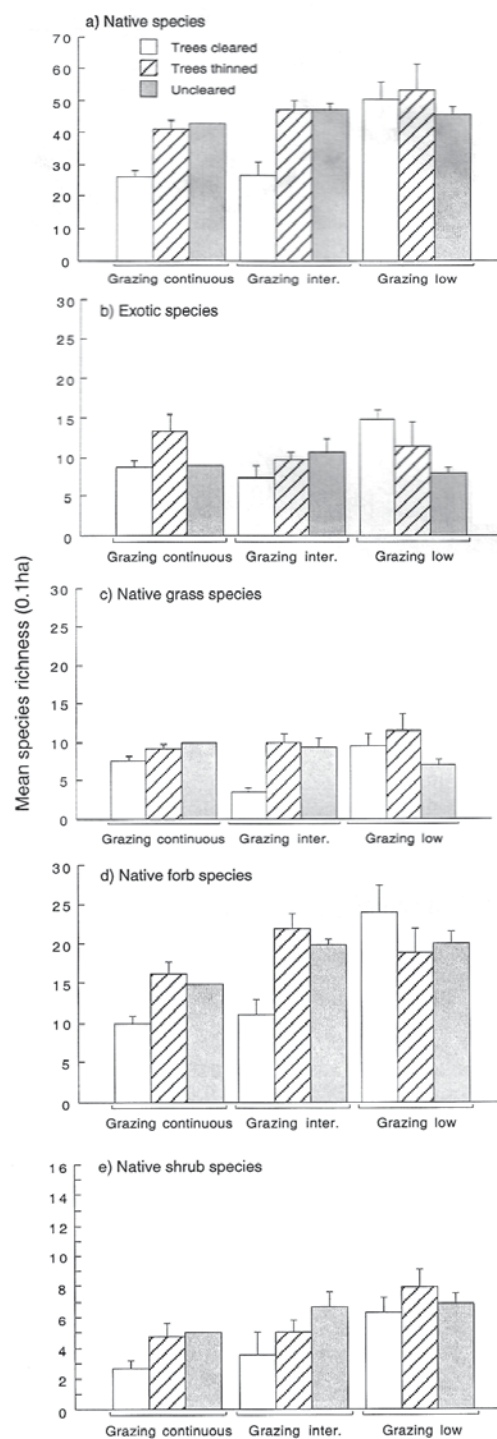
In summary, there was a large number of native herbaceous species in all pastoralism response groups, but particular species were strongly associated with anthropogenic disturbance and/or lithology. Rarer growth forms (ferns, geophytes, twiners) were more strongly associated with low levels of pastoralism. Shrub species presence was also associated with low levels of exogenous disturbance but this effect interacted with lithology whereby low nutrient sites had more shrub species (Table 2).

### *Species richness*

Total species richness ranged from 23 to 88 species with an average richness over all sites of 51.1 species per 0.1024 ha; about 20% of species were exotics (Table 3). The most species-rich growth form for native plants was forb, followed by grass, shrub, tree, graminoid, and twiner groups (Table 3). The strongest effects detected in species richness were those associated with grazing and canopy cover (Table 4). Continuously grazed sites had lower species richness for all native growth forms except grasses (Fig. 2). This pattern was consistent across all three classes of lithology, with no enhanced richness at either intermediate grazing or intermediate nutrient status (metasediments) (Fig. 3). Total, native and exotic species richness did not vary significantly with altitude or lithology, but exotic species showed some effects of lithology (Table 4, Fig. 3). For exotic species, richness was highest in infrequently grazed locations without tree cover but where tree cover was present it tended to suppress exotic species richness; hence the significant tree x grazing interaction (Table 4, Fig. 2b). Both native forb and shrub species had lower species richness in sites that were continuously grazed in open sites but the presence of a canopy increased species richness (Fig. 2d, e). Native forb species, however, had higher levels of species richness when there was no canopy and low grazing intensity (Fig. 2d). In contrast, the richness of native shrub species was enhanced where grazing intensity was low and tree cover was present (Fig. 2e).

**Table 2.** Comparison of growth form richness (R) and abundance (A) for species response groups. Proportional data for growth form groups shown as italics.

Species Group	Total		Native		Exotics		Native grass		Native forb		Native graminoid		Native twiner		Native shrub		Native tree		Ferns & geophytes	
	R	A	R	A	R	A	R	A	R	A	R	A	R	A	R	A	R	A	R	A
Tolerant of intense pastoralism/ Basalt	56	20.1	30	36.1	26	13.2	9	38.4	13	27.1	3	6.6	2	3.5	3	6.3	0	0	0	0
					<i>46.4</i>	<i>13.9</i>	<i>16.1</i>	<i>40.4</i>	<i>23.2</i>	<i>28.5</i>	<i>5.4</i>	<i>6.9</i>	<i>3.6</i>	<i>3.7</i>	<i>5.4</i>	<i>6.6</i>	0	0	0	0
Tolerant of intense pastoralism/ Metasediments and granites	46	22.0	34	23.4	12	18.2	9	50.7	9	13.0	8	24.7	0	0	8	3.1	0	0	0	0
					<i>26.1</i>	<i>16.6</i>	<i>19.6</i>	<i>46.2</i>	<i>19.6</i>	<i>11.9</i>	<i>17.4</i>	<i>22.5</i>	0	0	<i>17.4</i>	<i>2.8</i>	0	0	0	0
Tolerant of all pastoralism/ Basalt	61	34.9	45	38.5	16	25.8	8	62.3	18	45.7	4	16.0	0	0	11	23.8	3	16.0	0	0
					<i>26.2</i>	<i>13.5</i>	<i>13.1</i>	<i>33.2</i>	<i>29.6</i>	<i>24.0</i>	<i>6.6</i>	<i>8.4</i>	<i>1.6</i>	0	<i>18.0</i>	<i>12.5</i>	<i>4.9</i>	<i>8.4</i>	0	0
Tolerant of all pastoralism/ Metasediments and granites	146	30.9	115	32.0	31	26.9	23	63.9	43	31.7	8	30.2	4	9.0	24	13.8	9	22.4	4	7.7
					<i>21.6</i>	<i>13.1</i>	<i>15.8</i>	<i>31.1</i>	<i>29.5</i>	<i>15.4</i>	<i>5.5</i>	<i>14.7</i>	<i>2.7</i>	<i>4.4</i>	<i>16.4</i>	<i>6.7</i>	<i>6.2</i>	<i>10.9</i>	<i>2.7</i>	<i>3.7</i>
Intolerant of intense pastoralism/ Basalt	72	18.8	65	20.2	7	5.8	3	9.7	29	23.7	3	7.6	3	21.7	12	10.7	4	11.2	12	15.5
					<i>9.7</i>	<i>3.7</i>	<i>4.2</i>	<i>6.2</i>	<i>40.3</i>	<i>15.2</i>	<i>4.2</i>	<i>4.9</i>	<i>4.2</i>	<i>46.0</i>	<i>16.7</i>	<i>6.9</i>	<i>5.6</i>	<i>7.2</i>	<i>15.3</i>	<i>9.9</i>
Intolerant of intense pastoralism/ Metasediments and granites	159	16.5	146	16.5	13	15.7	18	21.5	46	23.3	3	25.0	4	17.2	52	12.1	14	16.1	13	4.1
					<i>8.0</i>	<i>11.6</i>	<i>11.0</i>	<i>15.9</i>	<i>28.2</i>	<i>17.2</i>	<i>1.8</i>	<i>18.5</i>	<i>2.5</i>	<i>13.1</i>	<i>31.9</i>	<i>8.9</i>	<i>8.6</i>	<i>11.9</i>	<i>8.0</i>	<i>3.0</i>



**Fig. 2.** Mean species richness (+ se) of (a) all native, (b) exotic, (c) native grass, (d) native forb, and (e) native sub-shrub and shrub for three levels of grazing frequency and three levels of canopy cover. For precise definitions see Table 1.

**Table 3.** Comparison of mean species richness per 0.1024 ha among native and exotic species and among main native plant growth forms. Note that other growth forms (geophytes, parasites, and ferns) also occur in small numbers and contribute to total species richness. The shrub growth form also includes sub-shrubs.

	Total	Native	Exotic	Native grass	Native forb	Native graminoid	Native Twiner	Native shrub	Native tree
Mean	51.4	41.3	10.1	8.4	21.3	2.6	2.4	5.3	2.7
SE	1.7	1.4	0.5	0.4	1.0	0.2	0.1	0.4	0.2
Range	23-88	11-73	3-27	1-17	4-48	0-7	0-6	0-14	0-6
Total	558	441	117	67	159	31	13	99	40

## Discussion

### *Do disturbance factors influence composition more than the environment?*

The floristic composition of the grassy woodlands and forests of the New England Tablelands was more strongly related to exogenous disturbance than to the environmental factors of lithology, altitude and slope. This result contrasts with a previous study of the herbaceous layer by McIntyre & Lavorel (1994a) in which anthropogenic and environmental factors were ranked equally. The differences between that study and the results presented here may be related to the larger sampling areas, the inclusion of rare species, and sampling of a broader range of environments in this study. The present findings are consistent with studies from a range of habitats of major floristic changes in response to pastoral management in the temperate regions of Australia (e.g. Leigh & Holgate 1979; Pettit et al. 1995; Henderson & Keith 2002; McIntyre & Martin 2002). In particular, a recent study of forest shrub species has shown that exogenous disturbance explained more variation in floristic composition than either environment or spatial factors (Henderson & Keith 2002).

### *Changes in growth form composition*

The differences in floristic composition along the disturbance gradient were reflected in the abundance of different growth form groups. Ferns and geophytes were virtually absent from sites of intense pastoralism, whilst shrubs, sub-shrubs and twiners were in very low abundance. These results are consistent with the predictions of McIntyre et al. (1995) and McIntyre & Lavorel (2001) that phanerophytes, chamaephytes and geophytes would be sensitive to exogenous disturbance.

These effects are modified by lithology: lower-resource soils support more shrub species. The cause of these patterns may be the lack of regeneration niches in grazed landscapes for native woody species which require seed burial and fire related germination cues to establish, and deep soil without competition to survive (Clarke et al. 2000; Clarke & Davison 2001; Clarke 2002). In grazed landscapes with low tree cover, fertile soils, fire suppression, and dense ground cover, the scope for shrub and twiner seedling recruitment is minimal.

Within the herbaceous layer, there was a shift in composition under increasing disturbance from dominance of native warm-season perennial grasses (e.g.

**Table 4.** Generalized linear models (log-linked model, Poisson error) for species richness in 0.1024 ha samples for different plant growth forms for models with lithology, altitude, tree cover and grazing as factors.

	df	All		Native		Exotic		Native grass		Native forb		Native geophyte		Native shrub		Native twiners		Native trees	
		Dev.	$\chi^2$	Dev.	$\chi^2$	Dev.	$\chi^2$	Dev.	$\chi^2$	Dev.	$\chi^2$	Dev.	$\chi^2$	Dev.	$\chi^2$	Dev.	$\chi^2$	Dev.	$\chi^2$
Altitude (A)	2	0.36	0.89 <sup>ns</sup>	1.03	2.56 <sup>ns</sup>	1.14	1.71 <sup>ns</sup>	9.90	14.85 <sup>**</sup>	3.89	5.84 <sup>ns</sup>	10.03	10.03 <sup>**</sup>	4.56	6.84 <sup>ns</sup>	4.34	4.34 <sup>ns</sup>	1.12	1.12 <sup>ns</sup>
Lithology (L)	2	1.51	3.77 <sup>ns</sup>	6.79	16.98 <sup>*</sup>	10.44	15.66 <sup>**</sup>	0.62	0.90 <sup>ns</sup>	2.24	3.36 <sup>ns</sup>	6.69	6.69 <sup>*</sup>	3.87	5.81 <sup>ns</sup>	4.39	4.39 <sup>ns</sup>	3.62	3.62 <sup>ns</sup>
Tree cover (T)	2	22.82	57.06 <sup>***</sup>	22.82	57.05 <sup>***</sup>	8.63	12.94 <sup>*</sup>	1.91	2.87 <sup>ns</sup>	17.40	26.09 <sup>**</sup>	0.96	0.96 <sup>ns</sup>	15.61	23.42 <sup>***</sup>	6.42	6.42 <sup>*</sup>	-	-
Grazing (G)	2	19.35	48.39 <sup>***</sup>	22.15	55.38 <sup>***</sup>	0.43	0.65 <sup>ns</sup>	2.26	3.39 <sup>ns</sup>	30.42	45.63 <sup>***</sup>	1.10	1.10 <sup>ns</sup>	8.89	13.35 <sup>*</sup>	1.51	1.51 <sup>ns</sup>	23.89	23.89 <sup>***</sup>
A x L	4	0.59	1.48 <sup>ns</sup>	1.47	3.67 <sup>ns</sup>	4.48	6.72 <sup>ns</sup>	1.24	1.86 <sup>ns</sup>	2.61	3.92 <sup>ns</sup>	12.10	12.10 <sup>*</sup>	1.07	1.60 <sup>ns</sup>	0.18	0.18 <sup>ns</sup>	2.96	2.96 <sup>ns</sup>
A x T	4	4.13	10.32 <sup>ns</sup>	5.98	14.97 <sup>ns</sup>	4.82	7.23 <sup>ns</sup>	2.27	3.40 <sup>ns</sup>	6.11	9.17 <sup>ns</sup>	4.11	4.11 <sup>ns</sup>	4.57	6.85 <sup>ns</sup>	1.09	1.09 <sup>ns</sup>	-	-
A x G	4	4.44	11.10 <sup>ns</sup>	2.41	6.03 <sup>ns</sup>	6.00	9.01 <sup>ns</sup>	7.32	0.12 <sup>ns</sup>	1.60	2.40 <sup>ns</sup>	3.29	3.29 <sup>ns</sup>	3.72	5.58 <sup>ns</sup>	3.86	3.86 <sup>ns</sup>	3.38	3.38 <sup>ns</sup>
L x T	4	9.43	23.59 <sup>*</sup>	7.95	19.9 <sup>ns</sup>	6.48	9.72 <sup>ns</sup>	1.09	1.64 <sup>ns</sup>	8.99	13.48 <sup>ns</sup>	6.82	6.82 <sup>ns</sup>	3.25	4.87 <sup>ns</sup>	3.27	3.27 <sup>ns</sup>	-	-
L x G	4	4.47	11.17 <sup>ns</sup>	5.68	14.21 <sup>ns</sup>	2.46	3.68 <sup>ns</sup>	0.91	1.37 <sup>ns</sup>	12.90	19.34 <sup>*</sup>	1.66	1.66 <sup>ns</sup>	5.00	7.51 <sup>ns</sup>	4.52	4.52 <sup>ns</sup>	1.73	1.73 <sup>ns</sup>
T x G	4	13.93	34.8 <sup>**</sup>	9.31	23.28 <sup>*</sup>	17.42	26.14 <sup>***</sup>	5.09	7.63 <sup>ns</sup>	7.87	11.80 <sup>ns</sup>	5.73	5.73 <sup>ns</sup>	10.08	15.12 <sup>*</sup>	4.18	4.18 <sup>ns</sup>	-	-
Residual	44	48.72	121.8 <sup>ns</sup>	39.05	97.62 <sup>ns</sup>	44.22	66.3 <sup>ns</sup>	31.98	47.98 <sup>ns</sup>	39.20	58.74 <sup>ns</sup>	30.55	30.55 <sup>ns</sup>	36.80	55.20 <sup>ns</sup>	17.73	17.73 <sup>ns</sup>	68.86	68.86 <sup>ns</sup>
Scale		2.5		2.5		1.5		1.5		1.5		1.0		1.5		1.0		1.0	

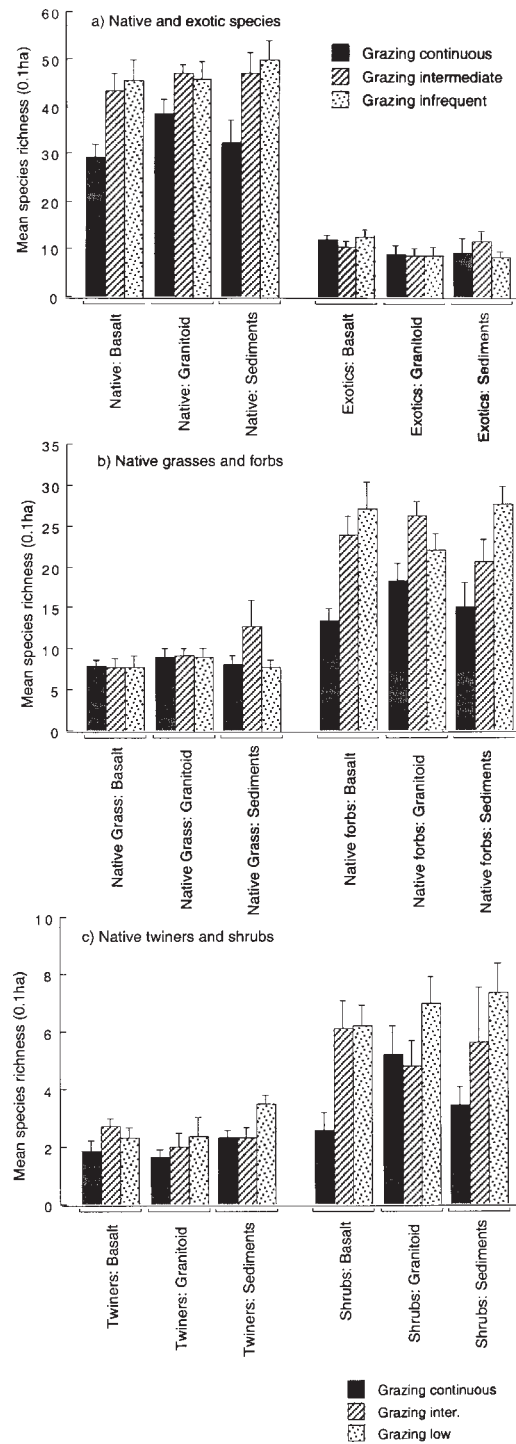
Dev. = deviance, <sup>ns</sup> = not significant; \* =  $P < 0.05$ ; \*\* =  $P < 0.01$ ; \*\*\* =  $P < 0.001$ .

*Themeda*) to short-lived exotic cool season grasses (e.g. *Bromus*). There was also replacement of native forbs by exotics under intense pastoral activity particularly on sites of higher fertility. Overall, native perennial grasses appear more persistent than native forbs because of the position of regenerating buds (McIntyre et al. 1995). Exotic herbaceous species also have smaller seed, longer dormancy and accumulate large seed banks, hence they are strongly associated with disturbance (McIntyre et al. 1995).

*Contrasting changes in different climate types*

The decreased shrub abundance under pastoralism in SE Australia contrasts with sub-humid and arid woodlands where woody plant encroachment into rangelands can occur when grazing is intense and competitive interactions with grasses are reduced (Wilson 1990; Milchunas & Laurenroth 1993; Scholes & Archer 1997). The reason may be that the discontinuity of the herbaceous layer in drier systems provides more scope for shrub seedling recruitment after periodic rainfall and/or fire events there than in more humid grassy communities (Scholes & Archer 1997) like the New England Tablelands.

The lack of exotic annual dominance of the intensively grazed herbaceous layer contrasts with grazed winter rainfall temperate woodlands in southern Australia (Hobbs & Huenneke 1992; Tremont & McIntyre 1993; Pettit et al. 1995) and Mediterranean grazed grasslands (Noy-Meir 1995). The dominance of exotic annuals in winter-rainfall woodlands may be a result of the inability of native perennial species to survive summer drought, defoliation and competition from exotic annuals, whereas native perennials do better in the New England region because of a longer growing season resulting from more summer rainfall. This comparison suggests that climate may modify the impacts of disturbance in grazed landscapes by changing opportunities for competitive displacement. This conclusion is consistent with that of Milchunas & Lauenroth (1993) whose global review of grazing showed that grazing effects were modified by productivity – moisture gradients.



**Fig. 3.** Mean species richness (+ se) of (a) native and exotic species, (b) native grasses and forbs, (c) Native twiners and shrubs on three lithologies; basalt (high nutrient soils), granitoid (intermediate nutrient soils) and metasediments (low nutrient soils) by three levels of grazing.

*Is there evidence for disturbance-mediated co-existence?*

It is well documented that lack of disturbance in grassy vegetation can result in competitive exclusion and decrease species richness (Grace 1999). Thus there was an expectation that in sites with low grazing and no canopy cover herbaceous species richness would be reduced, but it was not. Higher richness of forbs and grasses in low disturbance sites also contrasts with many studies that have shown that disturbance is required to reduce competition in tussock grasslands of Australia (Stuwe & Parsons 1977; Gibson & Kirkpatrick 1989; Lunt 1991, 1995; McIntyre & Lavorel 1994a, b; Prober & Thiele 1995). The reasons for these differences may lie with scales of sampling. At small spatial scales (1-100 m<sup>2</sup>) evidence for competitive exclusion is often stronger than at larger spatial scales (0.1 ha) (e.g. Stohlgren et al. 1999). At 0.1-ha scales local spatial habitat heterogeneity caused by ant and termite nests, fallen debris, rocks, mammal diggings, and cryptogamic soil crusts, may be sufficient to reduce competition in all but the most homogeneous grassy patches. The lack of a strong competitive exclusion effect on low disturbance sites at 0.1-ha scales is noteworthy because management of lowland Australian grasslands has focused on the use of frequent fire for reducing tussock grass competition to enhance interstitial forb richness (Tremont & McIntyre 1994; Lunt & Morgan 2002), perhaps unnecessarily.

Frequent grazing and the absence of a canopy reduced native species richness and in combination reduced richness in native forbs, shrubs and twiners. These results are consistent with studies on the effects of grazing in remnant temperate and subtropical woodlands of Australia (McDougall & Kirkpatrick 1994; Trémont & McIntyre 1994; Pettit et al. 1995; Prober & Thiele 1995; McIntyre & Martin 2002), but they differ from other studies around the world where total native species richness was not lowered by intermediate grazing intensity where the evolutionary history of grazing is long (Milchunas & Lauenroth 1993; Stohlgren et al. 1999; Grace 1999).

In contrast to the herbs, subshrubs and shrubs did show evidence for competitive exclusion in infrequently grazed sites with no canopy. Woody understorey species have decreased species richness and abundance in open sites with a grassy sward. This suggests that tree shade reduces the competitive ability of the herbaceous layer and allows shrub recruitment as most shrub species do not have bird-dispersed diaspores. Thus the open-canopied nature of eucalypts may provide a mechanism for coexistence of shrubs with the herbaceous layer.

*Are temperate Australian woodlands (savanna) different?*

The lack of replicated exclosure studies and manipulative experiments limits attempts to generalize about variation in the effects of exogenous disturbance relative to resource gradients and/or to evolutionary history of grazing. Nevertheless, some trends are clear. Firstly, compared with grassland biomes that have an evolutionary history of grazing (Milchunas et al. 1988; Milchunas & Lauenroth 1993), the effect of grazing on species composition is greater because the growth form composition of temperate Australian woodlands appears to be more diverse. Secondly, the effect of pastoralism on species composition (shrub composition and exotics) is modified locally by productivity gradients and regionally by seasonality of moisture availability. These resource gradients affect the competitive abilities of the perennial herbaceous layer as they do elsewhere (Milchunas & Lauenroth 1993). Thirdly, stock grazing does not appear to enhance herbaceous species richness through competitive release as occurs in other grassland biomes with long disturbance histories (Grace 1999).

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