

Perennial grassland dynamics on fertile plains: Is coexistence mediated by disturbance?

TOM LEWIS,^{1,2} PETER J. CLARKE,^{2*} NICK REID² AND RALPH D. B. WHALLEY²

¹*Department of Primary Industries and Fisheries, Gympie, Queensland, and* ²*School of Environmental Sciences and Natural Resources Management, University of New England, Armidale, NSW 2351, Australia (Email: pclarke1@une.edu.au)*

Abstract The response of grasslands to disturbance varies with the nature of the disturbance and the productivity of the landscape. In highly productive grasslands, competitive exclusion often results in decreased species richness and grazing may allow more species to coexist. Once widespread, grasslands dominated by *Dichanthium sericeum* (Queensland bluegrass) and *Astrebla* spp. (Mitchell grass) occur on fertile plains but have been reduced in extent by cultivation. We tested the effects of exclusion of livestock grazing on these grasslands by comparing the floristic composition of sites in a nature reserve with an adjacent stock reserve. In addition, sites that had been cultivated within the nature reserve were compared with those where grazing but no cultivation had occurred. To partition the effects of temporal variation from spatial variation we sampled sites in three different years (1998, 2002 and 2004). Some 194 taxa were recorded at the nature reserve and surrounding stock routes. Sampling time, the occurrence of past cultivation and livestock grazing all influenced species composition. Species richness varied greatly between sampling periods relating to highly variable rainfall and water availability on heavy clay soils. Native species richness was significantly lower at previously cultivated sites (13–22 years after cultivation), but was not significantly influenced by grazing exclusion. After 8 years it appears that reintroducing disturbance in the form of livestock grazing is not necessary to maintain plant species richness in the reserve. The highly variable climate (e.g. droughts) probably plays an important role in the coexistence of species by negating competitive exclusion and allowing interstitial species to persist.

Key words: cultivation, grazing, Mitchell grass, old field, species richness.

INTRODUCTION

Species richness in herbaceous communities often decreases as biomass increases or as stress or disturbance increase, giving rise to a unimodal response (Grime 1973; Mittlebach *et al.* 2001) especially at small spatial scales (Gross *et al.* 2000). Hence, the removal of grassland biomass through grazing and other disturbances is thought to promote competitive release and maintain species richness in grassland communities (Grime 1973; Huston 1979). There is evidence that long-term removal of grazing and other disturbances in productive grasslands leads to reductions in plant richness at small spatial scales both in the northern (Grime 1973; Collins & Barber 1985; Milchunas *et al.* 1988; Noy-Meir *et al.* 1989; Collins *et al.* 1998; Frank 2005), and southern hemispheres (Stuwe & Parsons 1977; Belsky 1986, 1992; Trémont & McIntyre 1994; Trémont 1994; Morgan & Lunt 1999; Fynn *et al.* 2004). Nevertheless, some reviews report neutral or even positive effects of reduced

grazing on plant diversity (Brady *et al.* 1989; Stohlgren *et al.* 1999; Spooner *et al.* 2002; Clarke 2003). This is because grasslands respond in different ways to grazing exclusion depending on rainfall, soil fertility and the height and competitiveness of dominant grasses (see review by Olf & Ritchie 1998).

Competitive release through disturbances such as grazing may be an overly simplistic model of grassland richness because disturbance can increase resource levels available to plants, increase productivity and increase competition intensity (e.g. Collins *et al.* 1998). Conversely, disturbances may induce stress through the removal of the regeneration niche (e.g. Jutila & Grace 2002) as occurs with cultivation (Austrheim & Olsson 1999; McIntyre *et al.* 2002; Römermann *et al.* 2005). Fundamentally, however, disturbance mediates richness by affecting rates of species colonization, from seed banks and dispersal, and extinction of standing populations. Hence, short-term experiments may mask longer-term responses to disturbance because of biomass fluctuations in response to seasonal conditions.

An important step in understanding the species richness dynamics of grasslands is to describe the

*Corresponding author.

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spatial and temporal variability in species richness in relation to disturbance regimes. In the southern hemisphere, species richness and dominance studies have mainly focused on *Themeda* grasslands and grassy woodlands of the higher rainfall climate across a variety of soil fertility levels (e.g. Stuwe & Parsons 1977; Belsky 1986, 1992; Trémont & McIntyre 1994; Trémont 1994; Morgan & Lunt 1999; Clarke 2003). In contrast, there is a dearth of knowledge about semi-arid floodplain grasslands growing on the fertile black soil plains, which have been extensively grazed by livestock and are often cultivated. Many of the southern hemisphere studies report differences in richness between grazed and ungrazed sites at small spatial scales, but there is doubt as to whether these studies really provide evidence of disturbance-mediated coexistence because changes in richness are more likely to be detected at small scales (Stohlgren *et al.* 1999; Morgan 2003).

In drier environments, the general model of Milchunas *et al.* (1988) predicts that herbivore exclusion will have little effect on species richness especially at larger spatial scales. In part, this might be due to the reduced species pool size in resource poor regions, but also to the temporal variability inducing adult mortality and recruitment failure, which in turn prevents competitive dominance. Conversely, it is predicted that repeated cultivation will change dominance and species richness because both seed banks and standing plants are disturbed and because the pool of species for recolonization can be reduced at paddock scales.

This study focused on semi-arid grasslands on fertile heavy clay soils in and adjacent to a nature reserve in north-west New South Wales (NSW), Australia. We aimed to determine how floristic composition is affected by grazing and cultivation, and tested whether: (i) the exclusion of grazing from the nature reserve has reduced species richness at both small (2 m²) and large (1024 m²) scales; (ii) past cultivation has reduced the species richness; and (iii) variation through time has a larger effect than past management on species richness and composition.

METHODS

Study site

Kirramingly Nature Reserve is located on the Moree Plains in north-west NSW. The reserve is situated 10 km west of Gurley, which is approximately 30 km south of Moree on the Newell Highway. The reserve covers an area of 1296 ha and is the largest area of remnant grassland not grazed by livestock on the Moree Plains. It was purchased by the NSW National Parks and Wildlife Service (now Department of Envi-

ronment and Conservation) in 1996. The reserve was formerly a pastoral property and some paddocks were sown with cereal crops until 1991 (P. Wall, pers. comm., 2002). A survey of the vegetation of the reserve was carried out by Clarke *et al.* (1998), who established vegetation monitoring points in paddocks (referred to as management units) with different management histories. By revisiting monitoring sites, it was possible to compare the recovery of previously cultivated management units with never-cultivated grasslands over time, in the absence of livestock grazing since 1996.

Kirramingly Nature Reserve is located on fine-grained, cracking, grey clay soil, free of sand or gravel, and typical of the floodplain soils in the region. The cracking clay soils have high fertility compared with most Australian soils, and this is the main reason for their agricultural development in this region.

Kirramingly was grazed only by sheep until 1977, and was grazed only by a small number of cattle (40) as well as by sheep until it was destocked in 1996. Although stocking rates for the reserve are unavailable, anecdotal evidence suggests it was stocked heavily (probably greater than three dry sheep equivalents per hectare) from approximately 1929–1945 (P. Wall, pers. comm., 2002). After 1945, Kirramingly was not heavily stocked (one to two dry sheep equivalents per hectare), and was destocked during dry periods. *Astrelba* spp. seed was spread by Sid Nicholson (former manager) in the 1920s. Seed from three introduced grasses, Rhodes grass (*Chloris gayana*), purple pigeon grass (*Setaria incrassata*) and giant panic (*Panicum antidotale*) was also spread through part of the reserve, but did not establish (P. Wall, pers. comm., 2002). During this study, the travelling stock routes surrounding the reserve were subject to intermittent, intense grazing by cattle. This recent grazing regime for the stock routes differs to that reported for Kirramingly before livestock removal. Given that the nature of herbivory by sheep and cattle differs some caution is required in determining the effects of grazing when comparing sites within the reserve to those on the neighbouring stock routes. Nevertheless, both the reserve and the stock routes have been grazed by sheep and cattle over time.

Cultivated areas sampled in this study were first sown in 1967 and cropping ceased in 1982. Paddocks were sown with mainly oats and wheat and no fertilizer was used in paddocks in which sites are located (P. Wall, pers. comm., 2003).

The average annual rainfall for Kirramingly Nature Reserve is 552 mm (unpubl. data, collected from 1927 to 1994). Rainfall is summer-dominant (60%) but might occur at any time during the year. A total of 257 mm fell at Moree (35 km from Kirramingly) in the 4 months before sampling in February 1998, 196 mm fell over the same period, before the March

Table 1. Variables used in multivariate and univariate analyses, site numbers (referred to in Fig. 1) and sample sizes

Variable	Variable categories	Total <i>n</i> multivariate	Site numbers	Total <i>n</i> univariate
Sampling period	1) February–May 1998	14	1, 5, 7, 8, 10, 13, 14, 15, 16, 17, 18, 19, 20, 22	22
	2) February–March 2002	14	as for 1998	25
	3) March 2004	14	as for 1998	15
Cultivation	1) Yes	3	1, 18, 22	4 (1998), 6 (2002), 3 (2004)
	2) No	8	7, 8, 13, 15, 16, 17, 19, 20	12 (1998), 13 (2002), 9 (2004)
Grazing	1) Yes	3	5, 10, 14	4 (1998), 5 (2002), 3 (2004)
	2) No	8	7, 8, 13, 15, 16, 17, 19, 20	11 (1998), 11 (2002), 8 (2004)

2002 sampling and 300 mm fell before the March 2004 sampling. Above average rainfall was recorded in 1998 and 2001 (748 mm and 805 mm, respectively) but rainfall was particularly low in 2002 (277 mm for the year) in a drought (Commonwealth Bureau of Meteorology 2004).

Background and sampling methods

A vegetation survey of Kirramingly Nature Reserve and surrounding stock routes was conducted between February and May 1998 by Clarke *et al.* (1998). They established 22 monitoring sites representing the different vegetation types of the reserve. All sites were marked with a labelled steel post in the centre of the quadrat and their GPS locations recorded. At each site a series of 10 nested concentric subquadrats, each doubling in sample area, was sampled (i.e. 2, 4, 8, 16, 32, 64, 128, 256, 512 and 1024 m²). The theoretical basis for this method is provided by Morrison *et al.* (1995). The incidence of all vascular plant species was recorded in each of the concentric subquadrats, and a score out of 10 assigned to each species in the 1024 m² quadrat, based on the number of subquadrats in which it occurred. In addition, each species was given a Braun-Blanquet cover abundance score. The sites established by Clarke *et al.* (1998) were resurveyed in March 2002 and in March 2004, to determine how vegetation composition and abundance varied over time at the reserve.

Taxonomy

Nomenclature for vascular plants follows 'Flora of NSW' (Harden 1992, 1993, 2000, 2002) and Wheeler *et al.* (2002). An exception to this was for the genus *Ixiolaena* (Asteraceae), which was recently revised to *Leiocarpa* (Wilson 2001). Each species identification was checked by at least one specialist, to ensure taxonomic accuracy. Voucher specimens have been retained by the University of New England's NCW Beadle Herbarium.

Multivariate statistical analysis

We tested whether the effects of grazing removal and past cultivation had changed floristic composition of the grassland and whether over time, previously cultivated sites converged towards the uncultivated sites whilst grazed sites remained distinct. We used CANOCO, version 4.5 (ter Braak & Šmilauer 2002) to test these hypotheses. Time, grazing and cultivation were defined as nominal variables (Table 1). There were three survey periods: 1998, 2002 and 2004. To limit the effect of potentially confounding variables (tree canopy and proximity to dams) and focus on the variables of most interest (i.e. cultivation and grazing), a subset of the sites sampled in each of the survey periods was selected for multivariate analysis (Table 1). Species cover data were analysed for species occurring within each quadrat (1024 m²).

Ordination involved two steps: indirect gradient analysis (unconstrained ordination) and direct gradient analysis (constrained ordination) (Lepš & Šmilauer 2003). Indirect gradient analysis (detrended correspondence analysis) suggested species were responding roughly linearly to the measured variables and no major unmeasured gradients were detected. Accordingly, direct gradient analysis was used to explain the vegetation data in terms of specific explanatory variables of interest (i.e. cultivation and grazing). Redundancy analysis (RDA) was chosen as the most appropriate constrained ordination technique. Infrequent species (with two occurrences or less) were removed from the dataset before analysis. Species data were transformed because the data contained many zeros, by taking logarithms, using the transformation $\ln(10 \times X + 1)$, where X = species cover score. Transformation was suggested by ter Braak and Šmilauer (2002) as species abundance values often have a highly skewed distribution. To determine the influence of variables without sampling time, a partial RDA was carried out with sampling time as a covariable (Palmer 2001). This was performed by partitioning the variance to determine the relative influence of sampling time and the other

variables on species composition. It involved 'factoring out' variables in separate analyses with each of the variables set as a covariate in the different analyses, and one analysis with no covariates (see Palmer 2001).

To determine which species were correlated with different explanatory variables, *t*-value biplots were constructed, where biplot projections were used to approximate the *t*-values of the regression coefficients that would be obtained from simple regression with one predictor (explanatory variable or variable category) and one response (species) (ter Braak & Šmilauer 2002).

Univariate statistical analysis

We tested the hypothesis that species richness was reduced in ungrazed sites using repeated measures analysis of variance. Response variables included total, native, introduced, forb, grass, graminoid and shrub species richness. Square root transformations were applied to satisfy the assumptions of ANOVA for total, native, introduced, forb, grass and shrub species richness. The response variable, graminoid richness, could not be transformed to meet the assumptions of ANOVA and was analysed using a non-parametric Kruskal–Wallis ANOVA. All results significant at the 5% level are reported. The occurrence of tree canopy and proximity to dams were covariates in the analysis. Proximity to dams was only relevant in comparing cultivated and uncultivated sites because two cultivated sites were within 100 m of dams, but no grazed sites occurred near dams. Occurrence of tree canopy was only relevant in comparing grazed and ungrazed sites because two grazed sites, but no ungrazed sites were influenced by tree canopy. It was not possible to investigate interactions between cultivation and grazing because none of the grazed sites had a history of cultivation. Post-hoc contrasts were used to identify the effects of grazing and cultivation in 1998, 2002 and 2004. Contrasts were also used to identify differences between sampling times. The numbers of grazed, ungrazed, cultivated and uncultivated sites in analyses are provided in Table 1.

RESULTS

Changes in composition and richness over time

A total of 194 taxa and 49 plant families were recorded in quadrats at Kirramingly Nature Reserve and the surrounding stock routes over all sites and times (Appendix I; <http://www.ecolsoc.org.au/>

<http://www.ecolsoc.org.au/Publications/Austral%20Ecology/AE.html>). Approximately 80% of all taxa were native.

Ordination of sites constrained by time, grazing history and past cultivation showed distinct clusters of sites associated with each of the variables (Fig. 1). Approximately 12% of the variance was explained by sampling time, 8% by cultivation and 7% by grazing, all of which were significant using Monte Carlo testing. No convergence or divergence of sites was detected through time and the grazed and cultivated sites were more similar than the ungrazed sites in the nature reserve.

Species richness varied greatly between sampling times at the reserve (Fig. 2). Total richness ranged from 27 to 72 species per 0.1024-ha quadrat with the lowest richness occurring in 1998 and the highest in 2004. Total species richness significantly increased between sampling in 1998 and 2002 (Fig. 2a; $F_{1,14} = 59.02$, $P < 0.001$), but not between 2002 and 2004 (Fig. 2a; $F_{1,14} = 2.86$, $P = 0.113$). Native richness did, however, increase between 2002 and 2004 (Fig. 2b; $F_{1,14} = 8.79$, $P = 0.010$). The increase in native species richness appeared to be due to a gradual trend of increasing grass, forb and shrub/subshrub richness over time (Fig. 2). Graminoid species richness did not vary significantly over time (Fig. 2f).

The effects of livestock grazing exclusion (large scales)

Partial RDA of species cover data identified 22 species that were significantly correlated with reserve sites (Appendix I). Fourteen species were negatively correlated with reserve sites and 15 species were recorded only at the grazed sites (Fig. 3; Appendix I).

Ungrazed sites within the nature reserve were consistently separated in ordination space over time (Fig. 1). Hence, no significant interactions between grazing and sampling time were detected in the univariate analyses (Table 2). Livestock grazing had no significant impact on total, native, introduced, forb, grass or shrub species richness (Table 2). Graminoid richness also did not vary significantly between grazed and ungrazed sites ($H = 0.629$, d.f. = 1, $P = 0.380$) in 2002 (this variable could not be analysed at other sample times because Kruskal–Wallis ANOVA requires sample sizes of ≥ 5). Forb richness was higher in ungrazed sites in 2002 and 2004 ($F_{1,14} = 5.87$, $P = 0.030$ and $F_{1,9} = 5.49$, $P = 0.044$, respectively), although the presence of tree canopy appeared to have a stronger influence on forb richness than the occurrence of grazing (Table 2): forb species richness was lower at sites with canopy ($P = 0.058$; Table 2).

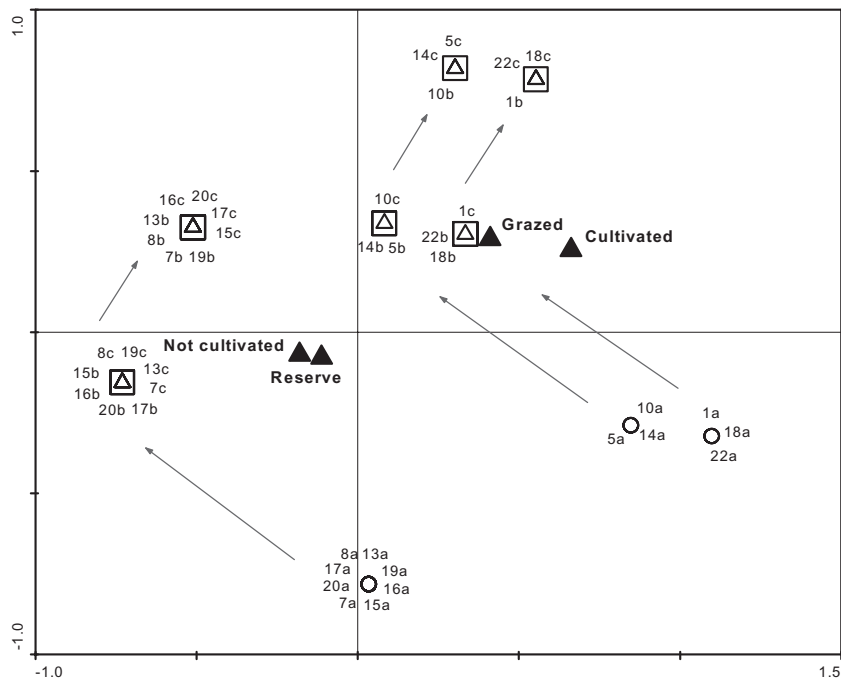


Fig. 1. Ordination (redundancy analysis) showing that species composition varied through time and that sites were grouped according to their grazing and cultivation history. Grey arrows (added to the diagram post-hoc) show a trend in the movement of sites (site numbers provided in Table 2) through time. There was no convergence of cultivated sites with uncultivated sites, nor divergence of grazed sites with the reserve sites through time. The grazed and cultivated sites were more similar in species composition than the ungrazed sites in the reserve. Filled triangles represent the grazing and cultivation variables in the analysis. Non-filled circles represent 1998 sites; non-filled triangles represent 2002 sites; and non-filled squares represent 2004 sites (non-filled triangles within non-filled squares indicates the presence of both 2002 and 2004 sites). Site numbers followed with 'a' are 1998 sites; 'b' are 2002 sites; and 'c' are 2004 sites.

The effects of livestock grazing exclusion (small scales)

To determine whether richness responded to grazing at smaller sampling scales, total species richness per 2 m² (in the first of 10 concentric quadrats) was compared among treatments. No significant grazing effect was detected at the 2-m² scale for total, native or introduced species richness (Table 3).

The effects of past cultivation

Sites that had been previously cultivated were consistently separated from adjacent sites that had not been cultivated and where grazing had been excluded (Fig. 1). The influence of cultivation on composition was obvious. Previously cultivated sites were usually dominated by native grasses such as *Enteropogon acicularis*, *Dichanthium sericeum*, *Chloris truncata*, *Aristida leptopoda* and *Panicum decompositum* and the native subshrub *Sclerolaena muricata* var. *muricata*. Despite reduced species richness, the abundance of 12 species was significantly correlated with cultivated sites

(Appendix I) and eight species were recorded only at cultivated sites (Fig. 3; Appendix I).

Twenty-seven species were recorded only at uncultivated sites in the reserve (Fig. 3) and 19 species were negatively correlated with cultivated sites (Appendix I). All of these were native, and included forbs (eight species), grasses (seven species) and subshrubs (two species). Both Mitchell grasses (*Astrelba elymoides* and *Astrelba lappacea*) and *Desmodium campylocaulon* (listed as endangered in the NSW *Threatened Species Conservation Act 1995*) were more abundant at uncultivated sites in the reserve.

There were significant interactions between cultivation and sampling time for introduced and grass species richness (Table 2). These interactions were due to a greater increase in introduced and grass species richness at cultivated sites relative to uncultivated sites in autumn 2002 (Fig. 2a,c,e). Introduced species richness was significantly higher at cultivated sites in 2002 (Fig. 2c; $F_{1,17} = 6.17$, $P = 0.024$) and across all times at the 2-m² quadrat scale (Table 3). Despite this increase in 2002, total species richness was significantly higher at uncultivated sites when averaged across all three times

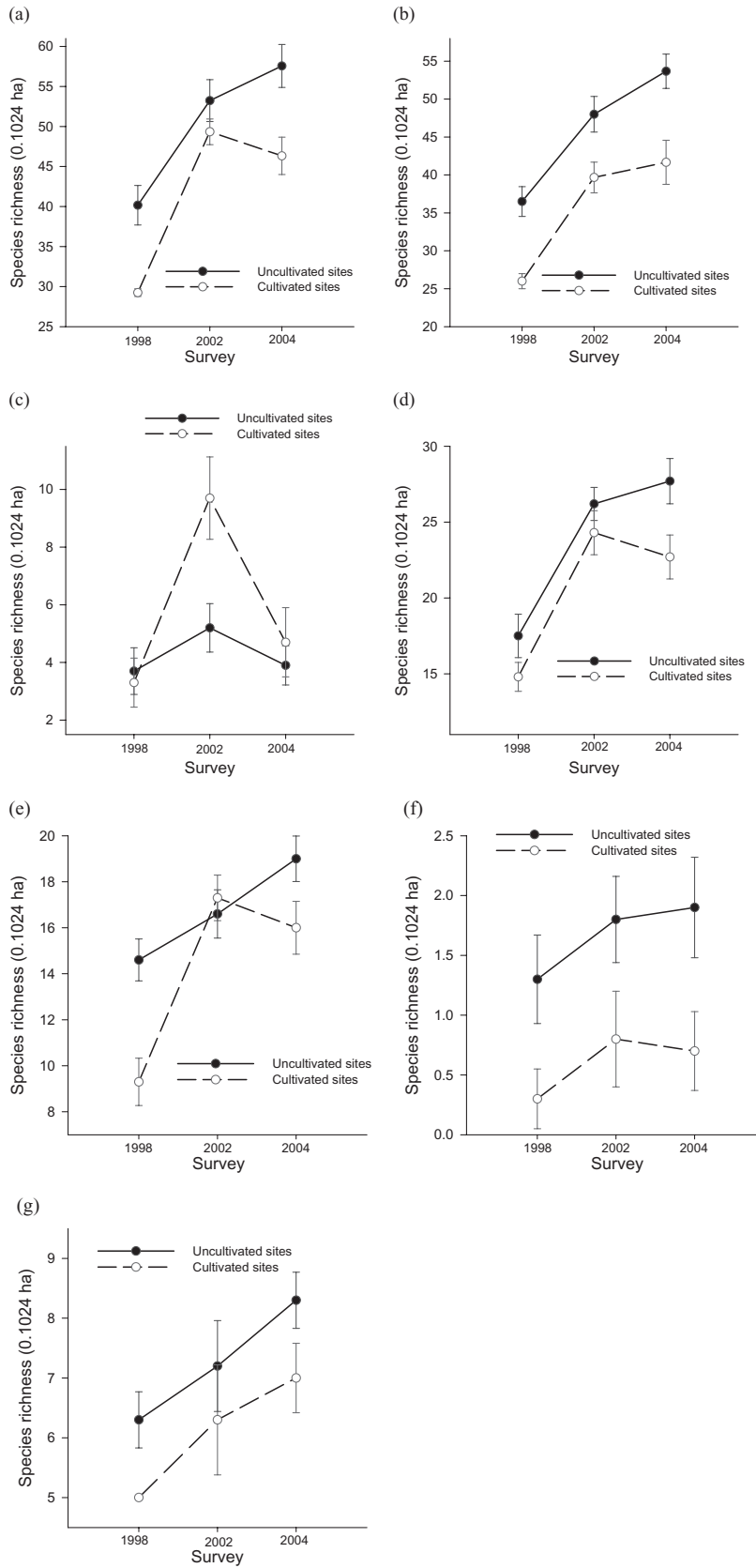


Fig. 2. Changes in richness (mean \pm SE) through time at uncultivated sites and cultivated sites for (a) total, (b) native, (c) introduced, (d) forb, (e) grass, (f) graminoid, and (g) shrub species richness. Refer to Table 1 for sample sizes at each time.

(Table 2, Fig. 2a). Native and forb species richness was significantly higher at uncultivated sites (Table 2, Fig. 2b,d). Grass species richness was higher at uncultivated sites in 1998 only (Fig. 2e; $F_{1,14} = 12.68$, $P = 0.003$). Proximity to dams (covariate) had a significant influence on total, introduced and forb species richness (Table 2). The three sites close to dams had higher total species richness, due to higher richness of introduced forbs.

DISCUSSION

Variations in composition and richness through time

Marked temporal changes in species richness and composition were characteristic of these grasslands irrespective of grazing or cultivation history. Total species richness increased significantly between 1998 and 2004 and sampling time had a greater influence on species composition than livestock grazing and cultivation. Another survey found annual and introduced species richness were lower at the reserve during late summer–autumn, than in sampling carried out in November 1999 and December 2001 (Lewis 2006). This is not surprising given the presence of winter-growing species in this region (Clarke *et al.* 1998; Hunter & Earl 1999). The variation in composition and species richness between seasons and between years suggests that caution must be applied to studies where space is substituted for time in these grasslands.

Grazing, species richness and dominance

Despite large fluctuations in species richness through time, the differences between sites where grazing had

been removed and those where grazing had been continued remained constant. The lack of a grazing by time interaction indicated that removal of grazing did not reduce species richness. In particular, the expected decrease in forb species richness was not detected in the ungrazed sites compared with those in the adjacent stock route. This suggests that exclusion of livestock grazing for approximately 8 years has not inhibited the

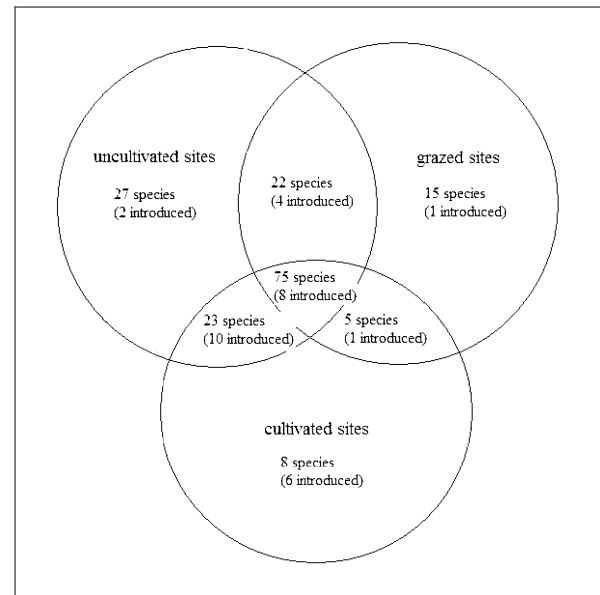


Fig. 3. Number of unique species occurring within different habitats (uncultivated, cultivated and grazed sites) and their intersection. Number of introduced species unique to each habitat is provided in parentheses. Cultivated and uncultivated sites were located within the nature reserve (i.e. were ungrazed) and grazed sites were located on surrounding stock routes. Refer to Appendix I for the species occurring within each habitat.

Table 2. Repeated measures ANOVA table (three February to March sampling periods) showing differences between cultivated and uncultivated sites, grazed and ungrazed sites and the influences of covariates (proximity to dams and tree canopy) at the 1024-m² sampling scale for different species richness variables

Variable	d.f.	Total		Native		Introduced		Forb		Grass		Shrub	
		<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Between-subjects													
Cultivation	1	7.70	0.012	9.56	0.006	1.17	0.292	4.51	0.046	1.81	0.193	2.02	0.170
Grazing	1	0.08	0.786	0.00	0.977	0.60	0.446	1.19	0.289	0.89	0.358	0.03	0.862
Covariates	2	3.00	0.072	1.10	0.353	6.21	0.008	5.08	0.016	1.24	0.310	0.64	0.536
Dam	1	5.95	0.024	1.86	0.188	11.25	0.003	6.12	0.022	1.75	0.201	0.00	0.983
Tree canopy	1	0.06	0.811	0.33	0.570	1.18	0.290	4.05	0.058	0.74	0.400	1.29	0.270
Residual	20												
Within-subjects													
Time	2	64.32	<0.001	53.58	<0.001	33.02	<0.001	61.33	<0.001	18.02	<0.001	8.59	0.001
Time × cultivation	2	3.05	0.063	0.92	0.408	8.68	0.004	0.59	0.506	7.06	0.004	1.03	0.369
Time × grazing	2	0.44	0.648	0.16	0.853	1.16	0.317	0.08	0.864	0.87	0.421	0.60	0.554
Residual	30												

Table 3. Repeated measures ANOVA table (three February to March sampling periods) showing effects of cultivation and grazing and the influences of covariates (proximity to dams and tree canopy) at the 2-m² sampling scale for total, native and introduced species richness

Variable	d.f.	Total		Native		Introduced	
		F	P	F	P	F	P
Between-subjects							
Cultivation	1	1.53	0.230	2.20	0.154	5.49	0.030
Grazing	1	2.11	0.162	1.36	0.257	0.10	0.761
Covariates	2	2.05	0.154	1.51	0.245	2.33	0.123
Dam	1	0.36	0.556	0.99	0.333	3.57	0.074
Tree canopy	1	3.75	0.067	2.04	0.169	1.10	0.306
Residual	20						
Within-subjects							
Time	2	29.60	<0.001	36.54	<0.001	4.82	0.021
Time × cultivation	2	0.91	0.395	1.71	0.201	1.46	0.250
Time × grazing	2	0.69	0.480	0.65	0.514	0.62	0.519
Residual	31						

persistence of interstitial forb species through competition with perennial grasses. Williams and Mackey (1983) similarly reported that excluding sheep from *Astrebla* grassland in south-western Queensland for 29 years produced slightly more diverse grassland than under station management. This contrasts with studies in temperate Australia (Stuwe & Parsons 1977; Gibson & Kirkpatrick 1989; Lunt 1991; Trémont 1994; Trémont & McIntyre 1994; Morgan & Lunt 1999) and in temperate grasslands in South Africa and America (Fynn *et al.* 2004; Frank 2005) where richness decreases when biomass increases. Nevertheless, in our study there were marked floristic differences among grazed and ungrazed sites as in temperate grasslands.

Habitat heterogeneity at the 0.1-ha sampling scale was proposed as the reason for the lack of disturbance-related response in forb richness in temperate grassy woodlands on the New England Tablelands (Clarke 2003). However, scale of sampling had no effect on the influence of livestock grazing in the current study. The lack of grazing effects at the small scale was surprising given that small scales are generally more responsive to disturbance and competitive effects (Tilman 1994; Stohlgren *et al.* 1999).

Periodic water stress, combined with kangaroo grazing, may provide enough disturbance in these floodplain grasslands, to prevent grass densities from becoming too high to limit growth of intertussock species. The occurrence of drought and its effect on grass densities may be exacerbated in these semiarid grasslands by the increased difficulty for plants to extract water from the heavy clay soils (Williams 1956, 1968; Meinke *et al.* 1993).

It is possible that a longer period of time will be required before perennial grasses exclude smaller interstitial species. The cover of tall perennial grass

species may increase following protection from grazing (e.g. Stuwe 1986; McDougall 1989; Noy-Meir *et al.* 1989; Belsky 1992) and it is possible that livestock grazing exclusion at the nature reserve will encourage tall species, such as *Themeda avenacea*, or other dominant grasses, like *A. leptopoda*, over a longer period of time. Nevertheless, 8 years after the removal of livestock grazing some bare ground (approximately 10–20%) has remained in these grasslands and there is evidence from other *Astrebla* grasslands to suggest that they typically retain an open nature with some bare ground between tussocks (Williams & Mackey 1983).

Species pool and phylogenetic diversity

Another explanation for the lack of evidence of competitive exclusion in our study is the size of the available herbaceous species pool (Grace 2001) and the consequent diversity of alternative traits that potentially allow species to coexist in space and time. Such traits include the ability to reproduce vegetatively, by transferring stored resources from an established parent plant to offspring (Grime 1979; Belsky 1992). Many species on floodplain grasslands have the ability to resprout vegetatively (e.g. *Astrebla* spp., *A. leptopoda* and many other perennial grasses). A second trait is the spreading, climbing or twining habits that allow plants to either reach light by spreading over large areas to find spaces in the canopy (e.g. *Desmodium campylocaulon*, *Neptunia gracilis*, *Rhynchosia minima*, *Convolvulus erubescens* and *Boerhavia domini*) or by climbing on taller species (e.g. *Einadia nutans*). A third trait is having large or long-lived seeds with dormancy cues (e.g. *Cullen tenax*, *Acacia* spp., *Goodenia fascicularis* and *Solanum esuriale*). Large seeds hold more resources and may give seedlings a better chance of

emerging above the grass canopy. Long-lived seeds that are able to lie dormant until conditions are favourable for growth (e.g. after fire) would allow plant species to establish at times when competition is less intense (e.g. Gill 1981). A fourth trait is the ability of species to grow opportunistically or seasonally (e.g. *Wahlenbergia communis*, *Goodenia fascicularis*, *Phyllanthus virgatus*, *Sida trichopoda* and many other forb and grass species). Plants that are able to germinate and grow rapidly during times when conditions are favourable (e.g. after rainfall) are likely to suffer less intense competition. Growth of species at different times of the year allows a greater number of species to coexist in the same area, as they do not compete directly for resources (Fowler 1986; Bullock 1996; Tokeshi 1999).

Resilience to grazing

The lack of a species richness response to grazing suggests that these grasslands are similar to those in other parts of the world with long histories of grazing (Milchunas & Lauenroth 1993; Milchunas *et al.* 1998; Grace 1999). Approximately 80% of the species recorded in this study were present at the grazed sites. Many native species on these floodplain grasslands appear to be resilient to livestock grazing, perhaps because of their abilities to be reduced to rootstock during unfavourable conditions (e.g. during drought). Olf and Ritchie (1998) suggested that dry environments on fertile soils often support competitively dominant plant species that are able to tolerate grazing. In such areas, exclusion of herbivores may have a small positive effect on richness due to the persistence or return of a few plants that are intolerant of grazing (Olf & Ritchie 1998). The evidence of past heavy livestock grazing at Kirramingly (P. Wall, pers. comm., 2002) suggests that these grasslands are able to recover well in terms of native species richness after such a disturbance and that some grazing-sensitive species (e.g. species associated with ungrazed sites in Appendix I) are able to persist in grazed areas. The resilience of many native species to livestock grazing is in accordance with the suggestion that Mitchell grasslands are resilient communities (Orr & Holmes 1984). However, it is possible that certain grazing-sensitive species have already been eliminated from the plant assemblage, despite the fact that Australia has a short history of relatively light ungulate grazing, compared with some other parts of the world (Landsberg *et al.* 1999).

Cultivation and abandonment

Both the floristic composition and species richness of previously cultivated sites were markedly different to adjacent uncultivated sites. As expected, the culti-

vated sites had more introduced and annual species, and several winter-growing introduced species were more abundant in cultivated areas in November 1999 and December 2001 (Lewis 2006). Nevertheless, perennial native grasses had re-established dominance in cultivated areas after a decade or more of abandonment. McIntyre *et al.* (1995) reported that wind-dispersed species occurred in higher proportions at soil-disturbed sites and we found that most of dominant grasses in these sites had open panicles that are easily moved by wind. Mitchell grass (*Astrebla* spp.) was not common at cultivated sites, suggesting it may take some time (i.e. more than 22 years) for these species to reach the same abundance as in uncultivated areas. The seeds of *Astrebla* spp. would not be easily dispersed by wind and may rely on animal dispersal.

There was no evidence to suggest that cultivated and uncultivated sites were converging in richness through time. Although species richness increased over time at cultivated sites, similar increases in richness were observed at uncultivated sites. Hence, native species richness was still lower at cultivated sites despite 13–22 years of recovery. The lower native species richness at cultivated sites appeared to be due to combined reductions in forb, grass, graminoid and shrub richness. Only grass species richness appeared to increase more at cultivated sites between 1998 and 2004, possibly due to colonization of wind-dispersed species. The richness and abundance of introduced species in previously cultivated areas appeared to fluctuate, probably depending on climatic conditions and the persistent seed bank (Lunt 1990). With increasing colonization and competition from native species, introduced species richness should decrease in previously cultivated areas over time.

Cultivated areas in the nature reserve were cropped for between 15 and 34 years before the last cultivation. Although there were some breaks between cultivation (P. Wall, pers. comm., 2002), the extent of these is unknown. The length of persistence of soil seed banks within previously cultivated areas is not known for these grasslands, but given the length of cultivation, it is unlikely many species survived, if any (Graham & Hutchings 1988a,b). Studies on the seed banks of grasslands in England have shown ruderal species reappear after cultivation (Graham & Hutchings 1988a); however, the survival of seed banks in previously cultivated paddocks requires further investigation in Australia. Recovery of seed banks after cultivation is probably heavily influenced by grazing animals. The influence of grazing on composition might be positive, through the spread of seed (Montalvo *et al.* 1993; Römermann *et al.* 2005), or negative, due to lack of re-establishment of palatable perennial species (Robson 1995).

Synthesis and application

This research suggests that disturbance in the form of livestock grazing is not necessary to maintain plant species richness in Kirramingly Nature Reserve and perhaps in other grassland reserves dominated by Mitchell grass. In fact, at larger spatial scales, floristic composition varied due to the absence of grazing-sensitive species in grazed grasslands. Some of these species were also less abundant or absent in cultivated areas, suggesting they may be sensitive to anthropogenic disturbance in general. We suggest that the high variability in available moisture plays an important role in the coexistence of species by negating competitive exclusion and allowing interstitial species to persist in these grasslands. Phylogenetic diversity may also be important and comparative data are required before models are developed about the interactive effects of grazing and productivity on the diversity of Australian grasslands. Cultivation had a more pronounced influence on species composition and richness than removal of livestock grazing and measuring the recovery of these sites will provide insights into the influence of cropping on plant diversity. Cultivation can result in the removal of the dominant perennial grasses (e.g. *Astrelba* spp.) and other species that are able to tolerate natural disturbances (e.g. grazing and drought) and will have a greater effect on the conservation value of these grasslands.

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