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The effects of grazing and fire on vegetation and the vertebrate assemblage in a tropical savanna woodland in north-eastern Australia

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Abstract We studied the response of vegetation and vertebrate assemblages to fire and grazing, and their interacting effects, in *Eucalyptus* woodland in north-eastern Australia. In this vegetation type, many pastures remain free of cattle grazing due to the occurrence of a native shrub poisonous to livestock. Vegetation (floristic data and 22 habitat variables) and vertebrate fauna (birds, mammals, reptiles) were sampled in 29 standardized 50 × 50-m quadrats in the 2001 wet season, representing four treatments: sites burnt recently (within 2 y) and grazed by cattle (4–8 ha per livestock unit); sites unburnt (last burnt >2 y ago) and grazed; sites burnt recently and ungrazed; and unburnt and ungrazed sites. Fire and grazing had a significant influence on vegetation: both grazing and fire reduced ground cover (fire in grazed sites 51–23%, fire in ungrazed sites 68–39%) and increased the cover of forbs (8% in burnt and grazed sites, 3% if ungrazed) and tussock grasses (20% in grazed and unburnt sites and 5% when ungrazed). Grazing caused a shift in floristic composition from the perennial hummock grass *Trioda pungens* to tussock grasses (e.g. *Aristida* spp., *Enneapogon* spp.), forbs (e.g. *Phyllanthus* spp.) and shrubs (e.g. *Acacia* spp.). Of the vertebrate groups, birds responded more to fire effects (9 species), reptiles to grazing effects (6 species) and mammals to the interaction (2 species). Species reacted to increases in bare ground (e.g. crested pigeon *Ocyphaps lophotes*, hooded robin *Melanodryas cucullatus*, *Ctenophorus nuchalis*) and to the dominant ground cover (e.g. *Ctenotus pantherinus*) or change in vegetation architecture (e.g. singing honeyeater *Lichenostomus virescens*, variegated fairy-wren *Malurus lamberti*). The clearest example of an interacting effect was the cycle of complementary dominance between the rodents *Pseudomys delicatulus* and *P. desertor*, the latter's post-fire recovery becoming more muted in sites where cattle grazed (modelled time for population recovery twice as long as in ungrazed sites).

Key Words: Australia, Desert Uplands, fauna, fire, grazing, interaction, management, rangelands, vegetation

INTRODUCTION

Vegetation pattern(and consequently faunal assemblages) in the world's tropical savannas is driven primarily by water availability and soil nutrients (Scholes & Archer 1997, Walker & Langridge 1997). Superimposed upon this, fire and grazing (by livestock and native herbivores) are major secondary drivers, and those most manipulated by human management (Bond & van Wilgen 1996, Bond *et al*. 2003, Enslin *et al*. 2000, McNaughton 1985, Oliveira & Marquis 2002, Walker & Menaut 1988, Walker *et al*. 1981). While, in most of the world's tropical savannas, there has been considerable research directed at the ecological impacts of fire (Bond & van Wilgen 1996) or grazing (Fleischner 1994, Olff & Ritchie 1998), there have been far fewer studies directed at the relative, interactive or compounding influence of both factors (Buechner & Dawkins 1961, Fuhlendorf & Engle 2004, Harrison *et al*. 2003, Roques *et al.* 2001, Salvatori *et al.* 2001).

As in other tropical savanna regions (Bond & van Wilgen 1996), fire has profoundly influenced the historical evolution and current patterns of biota in Australia (Kershaw *et al.* 2002, Williams & Gill 1995). There is also strong evidence of a long history of prescribed burning by Aboriginal land managers (Crowley & Garnett 2000, Hallam 1985): however the onset of European settlement produced a rapid cessation of pre-existing regimes and a shift to regimes dictated by pastoral land-use that have caused changes to vegetation and faunal assemblage (Bowman 2001, Crowley & Garnett 2000,

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Yibarbuk *et al.* 2001). The historical effects of grazing on Australian ecosystems contrast with those of fire, as Australia lacks large native herbivores. European settlement brought a massive influx of exotic herbivores, within and beyond fenced areas (Lunney 2001). Loss of ground cover and diversion of primary productivity has been directly linked to bird and small-mammal population decline (Burbidge & McKenzie 1989, James *et al.* 1999, Woinarski *et al.* 2001a).

Though there is broad acceptance that both fire and grazing have affected many Australian species over very extensive areas (Franklin *et al.* 2005), examination of the explicit interaction between the two factors has been rare (Hill & French 2002, Sharp & Whittaker 2003). Most studies consider only sites where cattle and/or fire have been removed or are stable (Andersen *et al.* 2005, James *et al.* 1999, Pettit & Froend 2001, Woinarski *et al.* 2004). Grazing and the suppression of fire (deliberately or through lack of fuel) have been linked to woody vegetation changes in Australia, South Africa and America (Roques *et al.* 2001, Sharp & Whittaker 2003, Van Auken 2000).

In the Desert Uplands Bioregion in north-central Queensland, pastoralism has been the dominant land-use (Smith 1994) and one particular vegetation type – open *Eucalyptus similis* woodland – is notable for having large cattle properties with long-term or permanently ungrazed paddocks due to the presence of *Gastrolobium grandiflorum*, a native plant that is toxic to cattle. The ground cover of this vegetation is dominated by a highly flammable species (spinifex *Triodia pungens*). Because of these distinctive landscape factors, clear grazing and fire histories can be identified for properties, allowing the design of a landscape-scale experiment. We investigated three key questions: (1) What is the influence of fire and grazing on vertebrate assemblages and vegetation? (2) Was there any variation in the nature of response by different taxa and species? (3) Is there an interacting effect between fire and grazing that causes amplification or muting of any responses to these single factors alone? Understanding the patterning of non-equilibrium systems (for example where both fire and grazing co-occur) is important for both ecology and conservation management (Fuhlendorf & Engle 2004, Wiens *et al.* 2002).

METHODS

Study area

The study was conducted within the Desert Uplands bioregion in north-central Queensland (Figure 1). The climate is semi-arid, with rainfall averaging between 350 and 600 mm y^{-1}. Vegetation consists predominantly of *Acacia* and *Eucalyptus* woodlands, ephemeral lake habitats and grasslands.

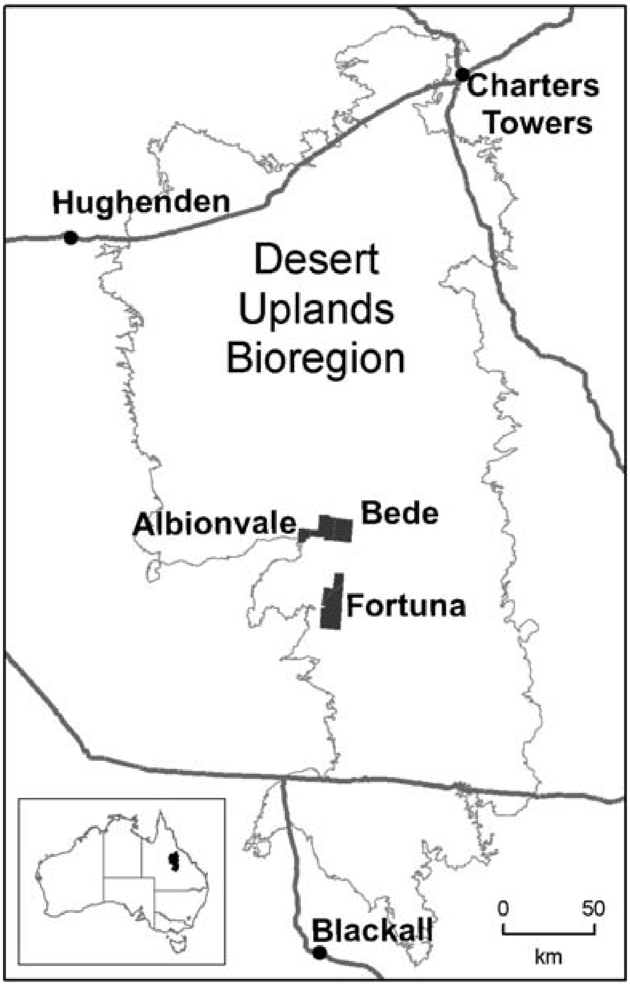


Figure 1 The Desert Uplands bioregion study area indicating the location of Fortuna, Albionvale and Bede Stations where the sampling was undertaken.

Sampling was conducted on three properties, Fortuna (22° 45′S, 145° 36′E), Bede (22° 24′S, 145° 36′E) and Albionvale (22° 18′S, 145° 24′E) Stations, which lie 50–100 km north of Aramac (Figure 1). The latter two share a boundary while Fortuna is 50 km further south. All sampling sites were located within the same vegetation type; *Eucalyptus similis* open woodland on deep red earths of the Tertiary sand-plain, which includes small areas of *Eucalyptus melanophloia* on low rises and *Corymbia brachycarpa* in depressions (Sattler & Williams 1999).

Sampling

Four treatment classes were identified for survey: sites burnt recently (within 2 y) and grazed by cattle (F + G); sites unburnt (last burnt > 2 y ago, but typically at least 5 y prior to sampling) and grazed (N + G); sites burnt recently (as above) and ungrazed (F + U); and unburnt (as above) and ungrazed sites (N + U). The properties sampled were all large (> 20 000 ha), and therefore grazing and fire treatments were of a large paddock scale (> 2000 ha). Twenty-nine sites were sampled in the wet season (January–February) 2001.

The carrying capacity and stocking rate (4–8 ha per livestock unit) for this type of vegetation was consistent across these properties; therefore the grazing treatment was simply categorical (present or absent) rather than an assessment of varying intensity. Ungrazed sites are paddocks where cattle are completely excluded. Fire age for the paddocks was determined by reference to landholders, who had clear knowledge of the recent history of burning of these sites. Fires are a mix of wildfire or fires lit by pastoralists to provide 'greenpick' (post-fire growth flush) for cattle. As such, fire followed by grazing is often the preferred management. The range of treatment classes examined in this study was relatively modest: pastoral management in this region is less intensive than many other parts of the north Australian rangelands. Fire regimes in this region include neither annual burning nor complete exclusion – extremes that are present in many other parts of these rangelands. As such, responses may be more muted in our study than is typical for the wider region.

The sampling of vegetation and fauna was conducted simultaneously. Faunal sampling used a standardized 1-ha quadrat (Woinarski & Ash 2002). Nested in the quadrat is a 50 × 50-m trap array comprising 20 Elliott traps (for small mammals) placed 10 m apart along the perimeter, two cage traps placed at opposing corners, and four pitfalls (60 cm deep and 25 cm diameter), 10 m apart and arranged in a 'T' configuration (30 m and 20 m of drift fence). Elliott and cage traps were baited with peanut butter, honey and oats, and alternatively with dog biscuits. Traps were checked in the morning and afternoon and opened for a 96-h period. Trapping was supplemented by timed searches: four 10-min morning bird counts within the 1-ha quadrat and two diurnal and nocturnal searches each of 30-min duration conducted within the trapping square. Nocturnal and diurnal counts included active (log rolling, litter raking) and passive (looking for eye-shine, listening for nocturnal birds) searches.

A range of habitat variables was measured in the 50 × 50-m trap array area. Average canopy height was visually estimated, and foliage projective cover (FPC) was estimated and scored for four height classes (1–3 m, 3–5 m, 5–10 m and >10 m) using the categories 0 = 0, 1 = 0.1–5%, 2 = 5–10%, 3 = 10–25%, 4 = 25–50%, 5 = 50–75%, 6 ≥ 75%. Total basal area of dead and live trees was calculated by averaging three measurements (two from diagonal corners and one from the centre) using the Bitterlich method (Mueller-Dombois & Ellenberg 1974). Measures of percentage cover of each of bare earth, rock, litter, hummock grass, tussock grass, sedges and forbs were derived by taking 100 random paces within the 50 × 50-m quadrat and recording the dominant cover at each step. The total number of logs (>10 cm diameter) along total quadrat perimeter (200 m length), and the total number of fallen trees (>10 cm diameter), termite mounds and the modal height (m) were counted within the 50 × 50-m area. All ground stratum plant species estimated to have >2% FPC within the 50 × 50-m area were recorded, and given a FPC score using the same categories as those for canopy species above. Average height of each species and total number of species was recorded and the average height (m) of the ground stratum was estimated. Plant species that could not be identified in the field were collected and sent to the Queensland Herbarium (Mt Coot-tha, Brisbane) for verification.

All quadrats were situated in typical examples of the vegetation type, and were positioned more than 500 m from the nearest unit edge, more than 200 m from fence-lines or tracks, and 3–5 km from water-points. Quadrats were separated by at least 500 m, but generally the distance between sites was 1–2 km.

Common names, scientific names and authorities for fauna follow Clayton *et al.* (2006). Scientific names and authorities for plants follow Henderson (2002).

Analysis

The variation in cover (for individual plant species) and abundance (for individual vertebrate species) between the four treatment classes was examined using non-parametric one-way analysis of variance, with analysis restricted to only those species recorded from five or more quadrats.

The composition of plant species and vertebrate species in the quadrats was each examined with ordination on two axes using semi-strong hybrid multi-dimensional scaling derived from Bray–Curtis association (dissimilarity) indices (Belbin 1995). Only species recorded in more than one quadrat were included and all abundance data were range transformed. Principal axis correlation (PCC) was used to examine the correlation between environmental and habitat measures with the ordination pattern (Belbin 1995). The resultant output identifies the direction of best fit, and a correlation coefficient that is a rough indicator of significance. A Monte Carlo randomization technique (MCAO) using 999 permutations was undertaken to test the statistical significance of the correlation coefficient of each PCC vector (Belbin 1995). Analysis of similarity (Clarke & Gorley 2001) was used to examine the relationship of variation in species composition among sites with a priori site classifications, in this case the grazing and fire classes.

Table 1. The variation between treatments for all habitat factors identified as significant vectors in the fauna ordination. Data tabulated are the mean score for that treatment. Bold indicates highest value. H is the Kruskal–Wallis analysis of variance statistic. Probability levels are * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$, ns = not significant. N = no fire, F = fire, G = grazed, U = ungrazed.

Variable	N + G	F + G	N + U	F + U	H
Bare earth cover	40.6	**70.0**	25.0	55.7	22.6^{***}
Hummock grass cover	27.5	12.5	**60.6**	30.0	18.6^{***}
Tussock grass cover	**20.5**	3.7	4.8	6.3	7.2^{*}
Litter cover	**7.5**	5.8	6.9	5.0	5.2^{ns}
Forb cover	3.9	**8.0**	2.8	3.0	8.1^{*}
Logs > 10 cm	2.5	**4.0**	1.8	2.1	5.4^{ns}
Fallen trees diameter > 10 cm	6.3	**9.7**	4.6	5.0	5.0^{ns}
Number of termite mounds	6.0	**11.8**	5.8	4.6	8.8^{*}
Modal height of termite mounds	0.2	**0.3**	0.2	0.2	1.2^{ns}
Canopy height	**9.5**	7.2	7.9	7.6	5.5^{ns}
Canopy cover	**13.1**	6.7	12.5	9.3	7.4^{ns}
Ground cover height	0.5	0.2	**0.6**	0.4	15.9^{**}
Ground cover plant richness	9.9	**12.8**	5.6	10.4	12.0^{**}
Ground cover total	51.9	23.3	**68.1**	39.3	22.3^{***}
Foliage projective cover > 10 m	**0.6**	0.2	0.3	0	7.7^{ns}
Foliage projective cover 5–10 m	1.0	1.0	**1.2**	1.0	2.6^{ns}
Foliage projective cover 1–3 m	**2.1**	1.2	1.8	1.3	8.3^{*}
Foliage projective cover < 0.5 m	3.5	2.0	**4.8**	3.1	18.1^{***}
Live basal area (m^2)	**5.8**	**5.8**	4.5	4.7	4.6^{ns}
Dead basal area (m^2)	**1.7**	1.0	0.9	1.6	0.9^{ns}

Generalized linear modellingwas used to examine the variation in occurrence of species richness for broad taxonomic groupings, and individual vertebrate species, in relation to grazing; fire age; and the interaction between grazing and fire age. From these a minimum adequate model was derived using a backwards-stepwise procedure, and a Poisson (log-linear) error distribution (Crawley 1993). Grazing was treated as a categorical factor (grazing present or absent, and fire as continuous (months since last burn).

Plant species responses were not modelled due to the high number of species with low cover abundance, the high number of species recorded in fewer than five quadrats, and the predominant focus of this study on fauna response.

RESULTS

Analysis of variance indicated that bare ground was most extensive in burnt, grazed sites, and least extensive in unburnt ungrazed sites, with this difference nearly three-fold. Forb cover was likewise most extensive in burnt grazed sites. Tussock grass cover was most extensive in the grazed unburnt sites, and at a magnitude of at least four-times higher than any other treatment. Hummock grass cover was by far most extensive in unburnt ungrazed sites (Table 1).

A total of 98 plant species was recorded from all quadrats, of which only 39 occurred in five or more. Almost half (18) of these 39 individual plant species varied significantly in cover amongst the four combinations of grazing and fire treatments (Table 2). Ungrazed and unburnt quadrats were characterized by the hummock grass *Triodia pungens* and the shrubs *Persoonia falcata* and *Acacia stipuligera*; burnt quadrats had more extensive cover of the grasses *Aristida contorta*, and *A. holathera*, the forb *Evolvulus alsinoides*, and the shrub *Dodonaea viscosa*; and grazed and burnt quadrats had extensive cover of the forbs *Tephrosia simplicifolia*, *Bonamia media* and *Sida rohlenae*, the grass *Enneapogon polyphyllus*, and the shrub *Acacia leptostachya*; grazed and unburnt quadrats had extensive cover of the grasses *Eriachne obtusa*, *Paraneurachne muelleri*, *Aristida calycina*, the forb *Sida fibulifera* and the shrubs *Senna artemisioides* and *Petalostigma pubescens.* Perversely *Gastrolobium grandiflorum* remained unrecorded in all quadrats.

In general, variation in vegetation composition was highly significantly associated with fire and grazing factors (Table 3). The single exception was for canopy plants, for which variation in species composition was strongly related to fire treatment but not significantly associated with grazing effects. The influence of grazing was far more marked for variation in ground-layer plants, shrubs and all plants than it was for any vertebrate group.

Ordination of plant species composition indicated segregation according to grazing along the first axis and to fire class on the second axis (Figure 2), and reiterated many of the relationships identified above between fire, grazing and associated vegetation structural and life-form features.

Table 2. Variation between treatments in mean foliage projective cover score (ranging from 0 = 0% to 6 ≥ 75%) of plant species recorded in five or more quadrats. Bold indicates highest value. H is the Kruskal–Wallis analysis of variance statistic. H values are given only where a significant result occurs. Probability levels are * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$. N = no fire, F = fire, G = grazed, U = ungrazed. Letter in parentheses after species indicates life form (V = vine, G = graminoid, F = forb, S = shrub/small tree, T = tree).

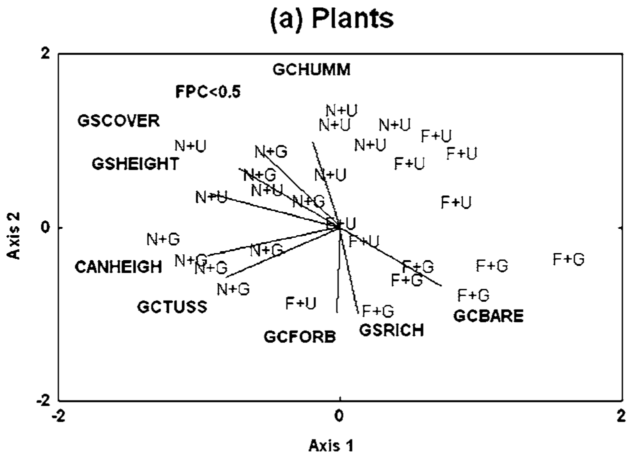
Species	n	N + G	F + G	N + U	F + U	H
Asclepiadaceae						
Parsonsia lanceolata (V)	6	0.25	**0.33**	0.25	0	
Caesalpiniaceae						
Senna artemisioides (S)	8	**0.75**	0	0.13	0.14	12.8**
Senna costata (S)	9	0.38	**0.50**	0.38	0	
Celastraceae						
Maytenus cunninghamii (S)	6	0.25	0	**0.50**	0	
Convolvulaceae						
Bonamia media (F)	8	0	**1.50**	0	0.29	21.8***
Evolvulus alsinoides (F)	7	0.13	0.33	0	**0.57**	
Erythroxylaceae						
Erythroxylum australe (S)	5	**0.38**	0	0	0	8.7*
Euphorbiaceae						
Petalostigma pubescens (S)	8	**0.88**	0	0	0.29	20.3***
Phyllanthus fuernrohrii (F)	7	0.13	**0.67**	0	0.43	
Phyllanthus virgatus (F)	6	**0.38**	0.33	0.13	0	
Fabaceae						
Tephrosia simplicifolia (F)	8	0	**0.83**	0	0.43	16.2***
Lamiaceae						
Clerodendrum floribundum (S)	7	0	**0.67**	0.13	0.14	10.3*
Malvaceae						
Sida fibulifera (F)	6	**0.50**	0	0	0.29	8.1*
Sida rohlenae (F)	14	0.75	**0.83**	0.13	0.29	10.4**
Mimosaceae						
Acacia coriacea (S)	25	**0.88**	0.83	**0.88**	0.86	
Acacia leptostachya (S)	14	0.50	**1.17**	0.38	0.43	8.6*
Acacia melleodora (S)	12	**0.63**	0.50	0.25	0.43	
Acacia stipuligera (S)	9	0.25	0	**1.13**	0.43	8.1*
Acacia tenuissima (S)	7	**0.63**	0.17	0.13	0	9.4*
Myrtaceae						
Corymbia brachycarpa (T)	14	**0.75**	0.17	0.50	0.57	
Corymbia setosa (T)	8	0.13	0.33	**0.38**	0.29	
Eucalyptus similis (T)	26	**1.0**	**1.0**	0.88	**1.0**	
Poaceae						
Aristida calycina (G)	9	**0.75**	0	0.13	0.43	8.1*
Aristida contorta (G)	5	0	0	0.13	**0.57**	10.8**
Aristida holathera (G)	9	0.25	0.33	0.13	**0.71**	
Aristida ingrata (G)	21	**0.88**	0.33	0.63	1.0	
Cenchrus ciliaris (G)	7	0	**0.50**	0.25	0.29	
Enneapogon lindleyanus (G)	15	**1.0**	0.33	0.50	0.29	
Enneapogon polyphyllus (G)	7	0.25	**0.83**	0	0	16.2***
Eriachne obtusa (G)	6	**0.63**	0.50	0	0	8.4*
Panicum effusum (G)	9	**0.63**	0	0.25	0.29	
Paraneurachne muelleri (G)	5	**1.50**	0	0	0	10.8**
Triodia pungens (G)	29	3.0	1.83	**4.25**	3.0	13.6**
Proteaceae						
Persoonia falcata (S)	6	0	0	**0.50**	0.29	8.1*
Rhamnaceae						
Alphitonia excelsa (S)	23	**1.13**	0.17	1.0	1.0	
Rubiaceae						
Canthium attenuatum (S)	15	**0.88**	0	0.75	0.29	
Santalaceae						
Santalum lanceolatum (S)	6	**0.25**	0.17	**0.25**	0.14	
Sapindaceae						
Dodonaea viscosa (S)	9	0.38	0	0.38	**0.57**	
Sterculiaceae						
Brachychiton populneus (T)	6	0.13	**0.33**	0.25	0.14	

Table 3. Analysis of similarity for two treatment classifications across all sample sites. Variation in the composition (using Bray–Curtis dissimilarity matrices) is examined for vertebrate taxa, and plant structural groups. Ground plants are all those less than 1.5 m in height. Probability levels are * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$, ns = not significant.

Taxon	Fire (n = 2)	Grazing (n = 2)
All vertebrates	0.36***	Ns
Birds	0.20**	Ns
Mammals	0.53***	Ns
Reptiles	0.10*	0.15**
All plants	0.27***	0.38***
Canopy plants	0.30***	Ns
Mid-storey plants	0.13**	0.24***
Ground plants	0.30***	0.29***

A total of 113 vertebrate species (74 birds, 32 reptiles and seven mammals) was recorded from the sampled quadrats. Of these, 57 were recorded in five or more quadrats and hence included in modelling response to grazing and fire effects.

The total number of birds was greatest in burnt quadrats, although the mean bird species richness showed no significant variation across treatment classes (Table 4). Of the 35 individual bird species modelled (i.e. those recorded from 5 or more quadrats), 12 species were significantly related to fire or grazing treatment (and/or their interaction), as determined either through generalized linear modelling or through analysis of variance. Black-faced woodswallow *Artamus cinereus*, red-browed pardalote *Pardalotus rubricatus*, crested pigeon *Ocyphaps lophotes*, hooded robin *Melanodryas cucullata*, red-backed kingfisher *Todiramphus pyrrhopygia* and singing honeyeater *Lichenostomus virescens* recorded a significant response to fire only, the first five were more common in recently burnt quadrats and the singing honeyeater was less common in recently burnt quadrats (Table 4). Only one species showed a main grazing effect: the cockatiel *Nymphicus hollandicus* was less abundant in grazed quadrats.


(a) Plants

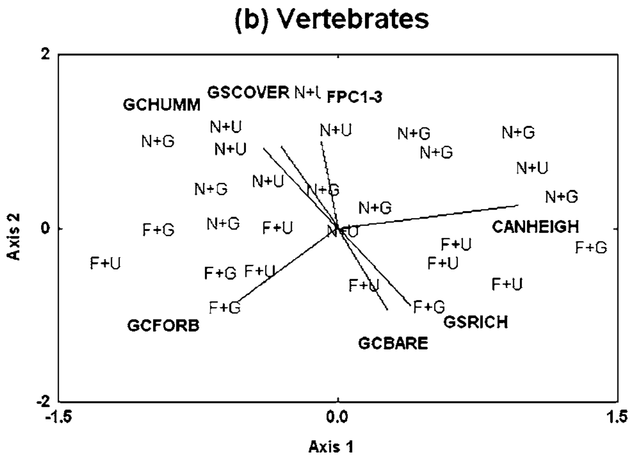

(b) Vertebrates

Figure 2 Semi-strong hybrid two-dimensional ordination of survey quadrats, labelled with significant environment vectors as identified by principal axis correlation. Significance level derived from permutation test, and labelled as * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$. (a) plant composition (stress = 0.24) labelled with fire (F = Fire/burnt < 2 y, N = No Fire/unburnt > 5 y) and grazing (G = Grazed, U = Ungrazed) treatment. Environmental vectors presented are: hummock grass cover (GCHUMM) r = 0.83***, bare ground cover (GCBARE) r = 0.82***, total ground cover (GSCOVER) r = 0.81***, foliage projective cover < 0.5 m (FPC < 0.5 m) r = 0.79***, tussock grass cover (GCTUSS) r = 0.77***, ground cover height (GSHEIGHT) r = 0.76***, GCFORB, 0.72***, ground cover richness (GSRICH) r = 0.67***, canopy height (CANHEIGH) r = 0.56***. (b) fauna composition (stress = 0.31). Vertebrate fauna labelled as for plants. Environmental vectors presented are: bare ground cover (GCBARE) r = 0.76***, hummock grass cover (GCHUMM) r = 0.51**, forb cover (GCFORB), r = 0.45*, canopy height (CANHEIGH) r = 0.52**, ground cover plant species richness (GSRICH) 0.53**, ground cover total (GSCOVER) r = 0.74***, foliage projective cover 1–3 m (FPC1–3), r = 0.62***.

Pallid cuckoo *Cuculus pallidus*, jacky winter *Microeca fascinans*, rufous whistler *Pachycephala rufiventris* and rainbow bee-eater *Merops ornatus* responded to the interaction of fire and grazing (Table 4); with pallid cuckoo and jacky winter also showing a significant main fire effect (both more common in recently burnt areas), and rufous whistler and rainbow bee-eater also showing a significant main grazing effect (both more common in grazed areas) (Figure 3). Jacky winters decreased in abundance with time since fire, but more dramatically when the quadrats were also grazed. Pallid cuckoos similarly declined in abundance with time since fire, but remained at higher abundances if the quadrats were also grazed. Both rainbow bee-eaters and rufous whistlers increased rapidly with increasing fire age in grazed sites, but remained at stable numbers if grazing was absent. Variegated fairy-wrens *Malurus lamberti* also demonstrated a relationship with both fire and grazing, with abundance increasing with time since fire and with less grazing (Table 4).

The abundance of mammals varied significantly with the grazing term. Mammals were most abundant after fire in grazed sites, but remained constant and high across fire ages in the absence of grazing (Table 4). Of the six mammal species modelled, two species showed no

Table 4. Minimum adequate models derived for fauna species and groups utilizing GLIM and Poisson (log-link) distribution error and four model terms (grazing, fire, grazing and fire interaction and site). Table indicates parameter estimate and significance (Wald statistic * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$), the number of quadrats from which the species was recorded (n) and total deviance explained (%). The mean abundance is given for each of the four combinations of grazing and fire treatments (N = no fire, F = fire, G = grazed, U = ungrazed). H is the Kruskal–Wallis analysis of variance statistic. Bold indicates highest value. Probability levels as above including $P < 0.1$. Letter in parentheses for birds indicates feeding guild. I = insectivore (aerial or arboreal), G = granivore, NI = nectarivore/insectivore, TIO = terrestrial or pouncing insectivore/omnivore. Note that species are listed only if they demonstrated a significant response to one or more factors.

Species	n	%	Intercept	Grazing	Fire	F × G	N + G	F + G	N + U	F + U	H
Bird abundance	29	11	3.96		−0.002***		43.5	**55.5**	41.6	45.7	
Mammal abundance	29	2	2.87	−0.11*			11.5	**21.5**	19.8	19.5	
Reptile abundance	29	36	2.76	−0.18***			14.0	12.3	18.5	**19.6**	9.1*
Reptile richness	29						7.4	6.0	7.6	**8.9**	7.3 (0.1)
Pallid cuckoo *Cuculus pallidus* (I)	17	25	0.79		−0.01*	0.006*	0.5	2.3	1.5	**1.6**	
Red-browed pardalote *Pardalotus rubricatus* (I)	9	31	0.91		−0.03***		0.1	**2.3**	0.1	1.3	6.9 (0.1)
Rufous whistler *Pachycephala rufiventris* (I)	27	18	1.46	0.41**		0.006*	3.9	**6.2**	5.0	3.1	6.4 (0.1)
Cockatiel *Nymphicus hollandicus* (G)	5	11	−0.46	−0.79**			0	0.7	**1.5**	1.3	
Crested pigeon *Ocyphaps lophotes* (G)	6	52	1.68		−0.07***		0	**4.3**	0	0.3	18.3***
Black-faced woodswallow *Artamus cinereus* (I)	11	31	1.34		−0.03***		0.1	**3.5**	0.5	2.0	7.4 (0.1)
Singing honeyeater *Lichenostomus virescens* (NI)	25	17	0.85		0.007**		**5.1**	3.0	4.4	2.4	
Hooded robin *Melanodryas cucullatus* (TIO)	5	44	0.92		−0.05**		0	0.7	0	**1.9**	10.5*
Jacky winter *Microeca fascinans* (I)	20	34	1.46		−0.007***	−0.007**	**3.3**	2.3	0.8	3.0	6.9 (0.1)
Rainbow bee-eater *Merops ornatus* (I)	10	47	−0.42	1.76***		0.02**	0.3	**3.2**	0.9	0.3	11.8**
Variegated fairy-wren *Malurus lamberti* (TIO)	6	21	−10.83	−0.73**	0.12*		0.8	0	**3.3**	0	11.4**
Red-backed kingfisher *Todiramphus pyrrhopygia* (TIO)	6	30	−0.04		0.03*		0	**1.2**	0.1	0.1	10.7*
Macropodidae *Macropus giganteus*	17	7	1.52	0.17*			3.0	**8.7**	3.5	4.3	
Macropodidae *Macropus robustus*	16	7	2.46	−0.27**	−0.18***		0.5	9.5	3.4	**9.7**	9.4*
Muridae *Pseudomys delicatulus*	16	45	1.59	−0.63**	−0.03***	−0.02**	1.4	2.5	0.3	**3.3**	8.5*
Muridae *Pseudomys desertor*	16	76	−8.84	−7.80**	0.12***	−0.79*	5.9	0	**11.4**	1.0	19.9***
Agamidae *Ctenophorus nuchalis*	6	45	0.29		−0.03**		0	0.7	0.1	1.0	
Agamidae *Pogona barbata*	8	26	−1.52	−1.12*			0.1	0	0.6	**0.7**	6.4 (0.1)
Gekkonidae *Diplodactylus conspicillatus*	7	37	−1.04	−0.90*			0.1	0.2	0.8	**1.0**	
Scincidae *Ctenotus hebetior*	19	4	0.99	−0.23*			2.3	2.0	2.6	**4.3**	
Scincidae *Ctenotus pantherinus*	17	47	−0.82	−0.71***	0.02***		1.3	0	**4.4**	1.4	15.8**
Scincidae *Ctenotus rosarium*	14	33	−0.19	−0.84***			0.6	0	**2.0**	1.9	8.5*
Scincidae *Menetia greyii*	8	43	−0.94	1.07***			**1.3**	1.0	0	0.3	

association with any factor; and three species had complex fire and grazing relationships. *Macropus giganteus* was clearly most abundant in sites both grazed and burnt. The abundance of *Macropus robustus* declined with increasing time after fire and decreased in grazed sites. There was a fire/grazing interaction for both *Pseudomys delicatulus* and *P. desertor*. *Pseudomys delicatulus* was most abundant in recently burnt quadrats, and in ungrazed quadrats; but also showed a significant fire/grazing interaction. Conversely *P. desertor* was almost entirely absent from quadrats recently burnt, and did not appear again until over 3 y post-fire. In quadrats that were also grazed, re-establishment was strongly suppressed and they did not reappear until about 6 y post-burn (Figure 3).

Reptiles were more abundant in the ungrazed sites. Of 18 species modelled, seven showed a significant fire or grazing effect, but none an interaction. The abundance of *Pogona barbata*, *Diplodactylus conspicillatus*, *Ctenotus hebetior*, *C. rosarium* and *Menetia greyii* all varied significantly in response to grazing alone, with all except the *Menetia* decreasing in abundance. *Ctenophorus nuchalis* demonstrated a strong negative response to fire age (Table 4). The only species to demonstrate a grazing and fire effect was the large-bodied *Ctenotus pantherinus* which significantly decreased in response to fire, and this decrease was compounded with the input of grazing (Table 4).

Variation in vertebrate composition across the set of sampled quadrats is illustrated in Figure 2. The segregation of quadrats showed a highly significant ecological patterning, with especially good correlation with fire class (on axis 2). Environmental variables significantly associated with the ordination pattern (Figure 3) indicate that vertebrate assemblages in sites that were unburnt lie on the upper end of a gradient associated with hummock grass and total ground cover,

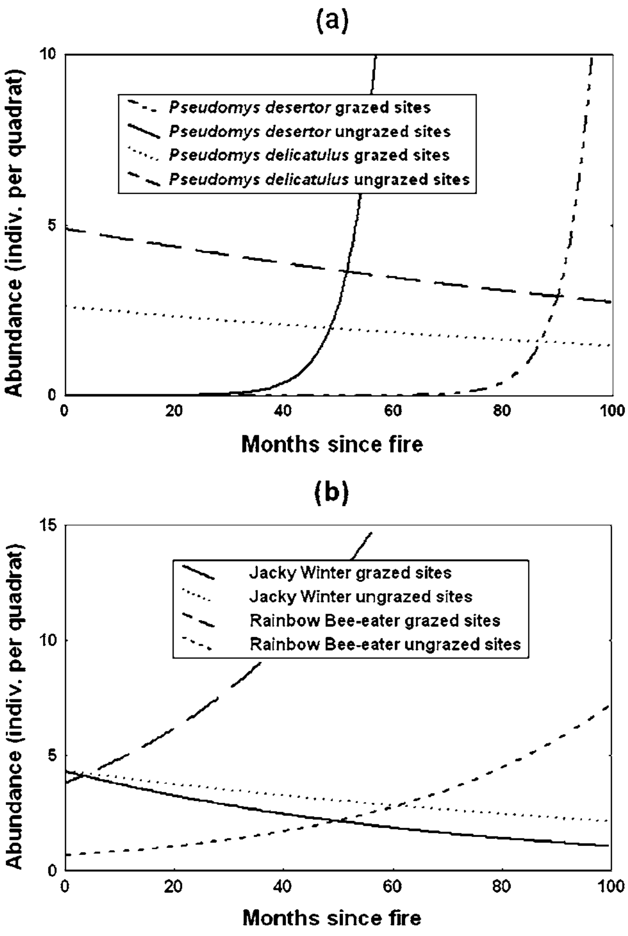


Figure 3 Two examples of the modelled relationship between the mean abundance (individuals per quadrat) of vertebrate species and increasing time since fire. (a) *Pseudomys delicatulus* and *P. desertor* (b) jacky winter and rainbow bee-eater. Model terms (variable, intercept, estimates and significance levels) are listed in Table 4.

and cover of plants in the 1–3 m height class. A vector for canopy height lies parallel with the first ordination axis, indicating general independence from fire age.

Analysis of similarity indicated that the total vertebrate assemblage was most strongly segregated by fire treatment (Table 3). This response was similar for bird species composition, an unsurprising result given that bird species contributed most to the total fauna. Mammal species composition was related strongly to fire, but not to grazing treatment. In contrast, variation in reptile communities was associated mostly with grazing treatment, and less strongly (albeit still significantly) to fire treatment.

DISCUSSION

Before interpreting the results of this study further, we acknowledge some constraints in the design. It is recognized that the sample size is modest, from a single season and restricted to a small geographic area. Additionally past reviews have indicated that local factors such as climate and long-term fire and grazing history can markedly influence the nature of biotic response (Gill *et al.* 1999, Roques *et al.* 2001). However we endeavoured to simplify the design to look at responses to management (fire, grazing or not) and by attempting to eliminate the noise of landscape variation (geographic, climate and vegetation types). The wet season in Australian tropics is the ideal time to survey, as faunal activity and vegetation diversity is at its premium (Neldner *et al.* 2004).

Although this study was designed to attempt to minimize variation in factors other than fire and grazing, there may have been some pre-existing differences between the sites unrelated to treatment. For example, the grazed paddocks may have always had fewer *Gastrolobium* and hence possibly some other floristic differences which may relate to subtle edaphic factors (Harrison *et al.* 2003). Also the mechanical removal of *Gastrolobium* from some paddocks that are grazed may have had some influence. The results indicated a lack of *Gastrolobium* in the sites, though in the region this plant occurs typically in low abundance. Paddocks are locked up for precautionary reasons, as most properties are of large size (>20 000 ha) and have ample other exploitable land for cattle. These landscape-scale constraints are almost unavoidable in any regional correlative study: indeed, the study area considered here provided us with an unusual opportunity to minimize these problems within a non-experimental format.

Vegetation

Studies of the impact of grazing on vegetation in savannas worldwide have identified shifts in perennial plant species dominance and increases in unpalatable and annual species (Crowley & Garnett 1998, Fensham & Skull 1999, Friedel *et al.* 1990, James *et al.* 1999, Olff & Ritchie 1998, Van Auken 2000). At intermediate grazing levels within-habitat species diversity can increase or remain stable (Fensham & Skull 1999, Landsberg *et al.* 1997), though heavy grazing cause declines and local losses of some species (McIvor 1998, Van Auken 2000). The results of this study indicate that grazing in the absence of fire also creates a structural and floristic shift, most notably a reduced ground cover (especially of *Triodia*), and alteration in composition with increases in annual and perennial tussock grass species (*Aristida* spp., *Enneapogon* spp., *Eriachne obtusa*, *Paraneurachne muelleri*, *Panicum effusum*), forbs (*Phyllanthus* spp., *Sida* spp.) and shrubs (*Senna* spp., *Acacia* spp.).

This study is also consistent with previously reported work that has demonstrated that fire can increase plant species richness (Bowman *et al.* 1990, Griffin & Friedel 1984, Harrison *et al.* 2003), or through exclusion, increase woody shrub density (Hill *et al.* 1992, Van Auken 2000). Here, fire reduced the cover of *Triodia* and canopy species, and increased the richness of the ephemeral and perennial species, creating a more patchy environment. Fire in ungrazed sites caused a shift from a vegetation community with a tall, dense ground cover dominated by *Triodia pungens* and more mid-storey species (e.g. *Persoonia falcata*, *Maytenus cunninghami*, *Alphitonia excelsa*), to one with a patchy but diverse ground cover, comprising a mixture of forbs, tussock and hummock grasses (e.g. *Phyllanthus* spp., *Tephrosia simplicifolia*, *Evolvulus alsinoides*, *Aristida* spp.).

More importantly in our study, fire and grazing is shown to have a major interactive (compounding) effect on floristic composition and structure. Bare ground was far more extensive at burnt grazed quadrats than in either burnt ungrazed or unburnt grazed quadrats, and the ground cover at these burnt grazed sites was far more likely to comprise a high diversity of annual grasses and herbs and shrubs known to be favoured by disturbance (e.g. *Bonamia media*, *Tephrosia simplicifolia*, *Clerodendrum floribundum*, *Sida rohlenae* and *Enneapogon polyphyllus*), rather than perennial hummock grass. This suggests that vegetation patterns resulting from a long history of frequent fire will not be reproduced if grazing replaces fire as the primary agent of disturbance. Previous work in a variety of savanna and woodlands indicate a suppression of fire in grazed systems can alter the dominance of grasses and herbs, promoting exotic and unpalatable species (Harrison *et al.* 2003, Zimmerman & Neunschwander 1984). In other Australian hummock grasslands, cattle grazing reduces the cover, height and species richness of vegetation regrowing after fire (Letnic 2004).

Fauna

In this study, the most conspicuous feature of the response of birds to fire and grazing treatments was the prevalence of a set of mainly terrestrial species (including red-backed kingfisher, crested pigeon and hooded robin) in recently burnt quadrats. Insectivorous and pouncing omnivorous species in this set (such as red-backed kingfisher and hooded robin) may be attracted to recently burnt areas by increased foraging efficiency in the more open habitats in such burnt sites (e.g. low shrub and ground cover) (Woinarski 1990, Woinarski & Recher 1997). Some granivorous bird species may also be attracted to recently burnt sites, because of greater ease of foraging and/or because the relatively high diversity of annual grasses and herbs in such sites may provide a greater variety and availability of seed resources than in unburnt sites (Woinarski 1990). In contrast, a smaller set of bird species (notably variegated fairy-wren and singing honeyeater) was more common at unburnt sites. Habitat suitability for these species is largely dictated by the presence of a relatively dense and tall shrub layer and ground cover for foraging and nesting (Brooker 1998), a pattern noted for similar guilds in other fire-driven savannas systems such as those in southern Africa (Skowno & Bond 2003).

In contrast, there was less evident response to grazing as a main factor structuring this bird community. Only one species, the granivorous cockatiel, showed a significant response to grazing alone, being more abundant in ungrazed sites. This relatively subdued response contrasts somewhat with the few previous studies that have considered impacts of pastoralism upon bird communities in tropical savannas (Landsberg *et al.* 1997, Woinarski & Ash 2002). A predominant grazing effect on habitat and key bird functional groups (e.g. grassland, ground-nesting species) has been identified in previous studies in non-Australian ecosystems (Fondell & Ball 2004, Krueper *et al.* 2003).

Our study suggests that there may be substantial interactive and compounding impacts, with significant interaction terms for four bird species (pallid cuckoo, rufous whistler, jacky winter, rainbow bee-eater) and significant main effects for both grazing and fire for variegated fairy-wren. Most patterns correspond to known foraging behaviour and habitat, and the effect of grazing and fire on the architecture of the vegetation (e.g. the variegated fairy-wren associated with more extensive ground cover; the rainbow bee-eater, a gregarious sallying insectivore, occurring in more open burnt and grazed vegetation; the jacky winter, a smaller, more secretive perching, insectivore, preferring an intermediate vegetation density). These responses suggest that previous research results, and management advice, relating to responses to either fire or grazing alone should be more properly interpreted within a context including the other factor (Wiens *et al.* 2002).

In contrast to birds, the level of mammal responses to grazing was similar to that of fire, and only one mammal *Macropus giganteus* indicated a significant response to a single factor (grazing). Despite the simplicity of the mammal community structure, the pattern of the rodent species recorded in relation to fire provided the most concise illustration of how fire-driven population cycles may be modified or subverted by grazing effects. In this study, both grazing and fire caused significant decline of *P. desertor*. The extinction of *P. desertor* in western New South Wales has been clearly linked to overgrazing (Dickman 1993, Krefft 1866). These results are also consistent with other evidence that *P. desertor* decreases in abundance after burning (Masters 1993, Sutherland & Dickman 1999) and its congener *Pseudomys delicatulus* is irruptive and extremely well adapted to sparsely vegetated post-fire environments (Braithwaite & Brady 1993). However, our study also suggests that it is not disturbance per se that favours this species, as it has a negative relationship with grazing: while grazing, like fire, may increase the prevalence of bare ground, it does not necessarily mimic fire in producing a flush of new vegetation growth and seeds of annual grasses and herbs. In African savannas, community simplification and population declines have been recorded in small-mammal populations, in response to intense native ungulate grazing and/or fire causing a change in habitat structure and available food quality (Keesing 1998, Salvatori *et al.* 2001).

Grazing, more than fire, influenced the reptile community in this study, and the most conspicuous feature of the responsive species was for a set of species (*Pogona barbata, Diplodactylus steindachneri, Ctenotus herbetior, C. pantherinus* and *C. rosarium*), that declined in abundance in grazed sites. These results are broadly consistent with some previous studies in reptile-rich Australian savannas that have considered responses of reptile communities to fire and grazing effects alone (Woinarski & Ash 2002).

Our study showed few significant responses in the reptile community to fire alone, with the dragon *Ctenophorus nuchalis* the only species linked to fire effect and increasing in grazed and ungrazed recently burnt areas, a pattern observed in other Australian savannas (Woinarski *et al.* 1999). This has been linked to its known heat tolerance and burrowing behaviour (Bradshaw & Main 1968, Read 2002). In contrast, the large skink *Ctenotus pantherinus* was less abundant in recently burnt areas (as it was also in grazed areas), again consistent with previous work (Masters 1996, Reid *et al.* 1993), and consistent with its known association with cover of hummock grasses, and the propensity of large skinks to be vulnerable to rapid over-heating without adequate shelter (Heatwole & Taylor 1987).

CONCLUSION

This study demonstrates that though both fire and grazing alone can change the vegetation structure and relative vertebrate species abundance, there was an important interacting influence. As habitat heterogeneity shifted with the imposition of grazing on typical fire pattern, so too did the relative abundance of some species, and to the detriment or advantage of species tolerant or vulnerable to the shifting habitat states. Understanding how fire and grazing disturbances shift the habitat patterns, succession and the landscape mosaic, is recognized as critical to understanding the functioning of rangeland ecosystems and therefore integrating conservation biology with pastoral systems (Ludwig & Tongway 1995, Fuhlendorf & Engle 2001). In the rangelands of tropical northern Australia there is recent and continuing evidence of broad-scale decline in many components of the distinctive vertebrate fauna (e.g. granivorous birds, small mammals) (Franklin 1999, Franklin *et al.* 2005, Woinarski *et al.* 2001b). This study suggests that the interpretation of current and historical land management impacts, and subsequent conservation management, needs to consider the spatial and temporal integration of fire and grazing effects, rather than each alone as a static operator (Fuhlendorf & Engle 2001).

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