Spatial and temporal effects of grazing management and rainfall on the vertebrate fauna of a tropical savanna

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Abstract. Grazing by domestic livestock is one of the most widespread uses of the rangelands of Australia. There is limited information on the effects of grazing by domestic livestock on the vertebrate fauna of Australia and the establishment of a long-term grazing experiment in north-eastern Queensland at Wambiana provided an opportunity to attempt an examination of the changes in vertebrate fauna as a consequence of the manipulation of stocking rates. The aim was to identify what the relative effects of vegetation type, stocking rate and other landscape-scale environmental factors were on the patterns recorded. Sixteen 1-ha sites were established within three replicated treatments (moderate, heavy and variable stocking rates). The sites were sampled in the wet and dry seasons in 1999–2000 (T_0) and again in 2003–04 (T_1). All paddocks of the treatments were burnt in 1999. Average annual rainfall declined markedly between the two sampling periods, which made interpretation of the data difficult. A total of 127 species of vertebrate fauna comprising five amphibian, 83 bird, 27 reptile and 12 mammal species were recorded. There was strong separation in faunal composition from T_0 to T_1 although changes in mean compositional dissimilarity between the grazing stocking rate treatments were less well defined. There was a relative change in abundance of 24 bird, four mammal and five reptile species from T_0 to T_1. The generalised linear modelling identified that, in the T_1 data, there was significant variation in the abundance of 16 species explained by the grazing and vegetation factors. This study demonstrated that vertebrate fauna assemblage did change and that these changes were attributable to the interplay between the stocking rates, the vegetation types on the sites surveyed, the burning of the experimental paddocks and the decrease in rainfall over the course of the two surveys. It is recommended that the experiment is sampled again but that the focus should be on a rapid survey of abundant taxa (i.e. birds and reptiles) to allow an increase in the frequency of sampling and replication of the data. This would help to articulate more clearly the trajectory of vertebrate change due to the relative effects of stocking rates compared with wider landscape environmental changes. Given the increasing focus on pastoral development in northern Australia, any opportunity to incorporate the collection of data on biodiversity into grazing manipulation experiments should be taken for the assessment of the effects of land management on faunal species.

Additional keywords: conservation biology, grazing management, savanna ecology, wildlife ecology.

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Introduction

Grazing by domestic livestock is one of the most globally widespread uses of rangelands and a pervasive means of modifying habitats (Brooks *et al*. 2002). This habitat modification may take two pathways: directly through the process of herbivory, which reduces or changes vegetation structure and which consequently affects the fauna that is associated with the vegetation (Milchunas *et al*. 1988; Goheen *et al*. 2010), or indirectly through management of that domestic stock via the reconfiguration of the landscape through water diversion, spread of introduced pastures or alteration of natural processes such as fire (Kutt and Woinarski 2007; Kutt and Fisher 2011). These changes can potentially have a cascading effect on biodiversity,

although the extent of the effect will depend upon the biology of the species concerned, with some species tolerant and benefitting by disturbance (James *et al*. 1999). Similarly, livestock grazing that changes native fauna assemblages can have flow-on effects on the community trophic structure, such as mammalian predator–prey relationships, which then can affect the abundance of birds, reptiles and invertebrates (McCauley *et al*. 2006; Pringle *et al*. 2007; Waldram *et al*. 2008).

Australia supports vast areas of essentially unmodified environments with relatively low human populations (Garnett *et al*. 2010). There is recent evidence of a pervasive decline in some vertebrate taxa in the apparently least modified tropical savanna biomes (Franklin *et al*. 2005; Woinarski *et al*. 2011).

The pattern of decline varies between species (Perry *et al.* 2011) and regions (Kutt *et al.* 2005). These declines in the fauna of Australian savannas have been attributed to a range of factors, operating alone or in combination, including changed fire regimes, grazing by domestic livestock, predation by feral cats, and poisoning by the introduced cane toad *Rhinella marina* (Fitzsimons *et al.* 2010). Of these, the influence of grazing has received the least attention (Legge *et al.* 2011), although cattle grazing is thought to have a significant effect on biodiversity in other tropical savannas in Africa and North America (Fleischner 1994; Keesing 1998; Salvatori *et al.* 2001; McCauley *et al.* 2006).

There is a relatively large amount of research into the effects of grazing on rangeland dynamics in Australia (MacLeod and McIvor 2006; McIvor 2007; MacLeod *et al.* 2009). For example, there is ample evidence that, at a paddock and local scale, ground vegetation is the strata most changed by grazing of domestic cattle (McIvor 2002) and high stocking rates can lead to reduced projected cover and a change in vegetation composition from perennial to annual species (Ash and Corfield 1998). Long-term reduction in vegetation cover has been linked to declines in the diversity and species-richness of native plant and animal species (Ward and Kutt 2009). Groups, such as small mammals which are dependent on ground cover for shelter and food, may be negatively affected by changes in vegetation biomass, structure and composition due to grazing (Kutt and Woinarski 2007). One challenge facing the interpretation of the effect of management on vertebrate fauna is the relative effect of local changes (i.e. fire history, stocking rate) in comparison to broad spatial and temporal patterns such as the landscape mosaic and long-term weather patterns (Fensham and Fairfax 2008; Price *et al.* 2010; Reside *et al.* 2010).

The establishment of a long-term grazing experiment in north-eastern Queensland provided an opportunity to include vertebrate fauna within the scope of an experimentally manipulated grazing experiment. The experiment was designed with the aim of documenting change in vegetation, soil and livestock variables, and contained sufficiently strong differences in stocking rates to attempt to measure patterns of vertebrate fauna change in response to the manipulation of stocking rates (O'Reagain *et al.* 2011). In this study, the fauna were sampled at the establishment of the experiment and again 5 years later. The aim was to examine three aspects of the data; (1) whether there has been a change in abundance, species richness and composition in the vertebrate fauna assemblage from the first to the second survey; (2) whether changes in the vertebrate fauna were attributable to the different grazing treatments; and (3) what was the relative effects of vegetation type, treatment and other factors, such as weather, in explaining any changes recorded.

Methods

Study area and treatments

The experiment is located on Wambiana Station (20°34′S, 146°07′E), a commercial cattle property ~70 km SW of Charters Towers, northern Queensland, Australia (Fig. 1). The experiment commenced in 1997. Long-term (100-year) mean annual rainfall for Trafalgar Station, 17 km NW of the study area is 643 mm (CV = 39%), with a historical range of 207–1409 mm. Most rain
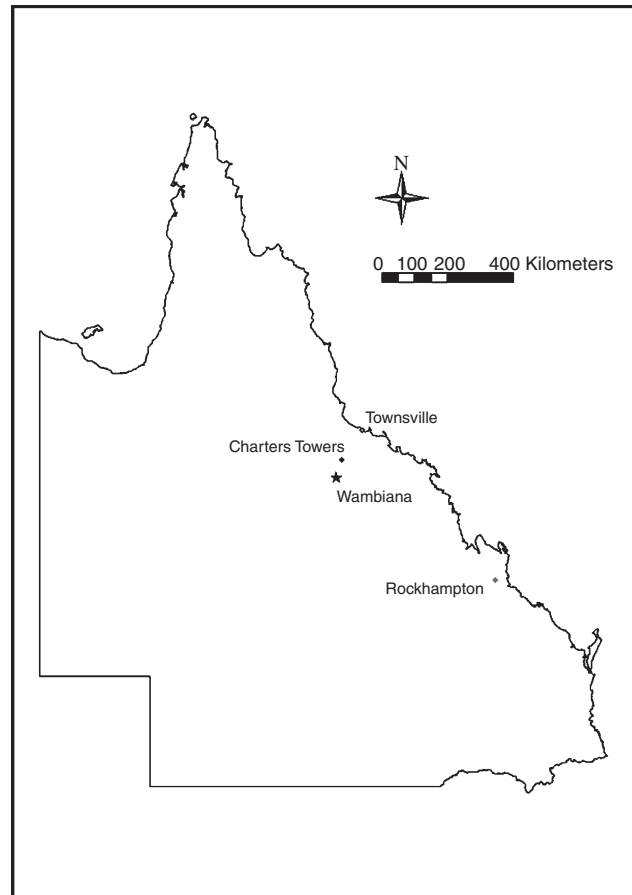

Fig. 1. The location of Wambiana Station grazing experiment in north-eastern Queensland.

(70%) falls in a relatively well defined wet season between December and March (Clewett *et al.* 2003). The vegetation is categorised as an *Aristida–Bothriochloa* pasture community (Tothill and Gillies 1992), and structurally is an open Eucalyptus savanna with smaller areas of *Acacia harpophylla* woodland, overlying relatively infertile kandosol, vertosol and sodosol soils (Isbell 1969; Rogers *et al.* 1999). In each paddock, one site was in Reid River Box vegetation (*Eucalyptus brownii*) and one was in Silver Leaf Ironbark vegetation (*E. melanophloia*). The Reid River Box (*E. brownii*) sites included False Sandalwood (*Eremophila mitchelli*) and, in some places, Black Butt (*E. cambageana*). Moderate to dense stands of *Carissa ovata* were also common. The Box areas occupied gentle slopes and the edges of run-on areas. Soils are generally texture contrast in nature and include sodosols, chromosols, dermosols and sodosol-kandosol gradations. The ground vegetation is commonly dominated by *Bothriochloa ewartiana* with *Dichanthium fecundum*, *Chrysopogon fallax* and various *Aristida* species found locally. The Silver Leaf Ironbark (*E. melanophloia*) sites are on yellow, brown or red kandosols. These relatively well drained but low fertility soils tend to be dominated by unpreferred species, such as *Eriachne mucronata* and *Aristida* species, but may contain appreciable quantities of *C. fallax* and *Heteropogon*

contortus where soils are darker and more fertile. Further descriptions can be found in O'Reagain *et al.* (2009) and O'Reagain and Bushell (2011).

The experimental study area was 1041 ha in area within which there were 10 experimental paddocks of 93–117 ha in size with two blocks of five treatments in a randomised block design. The five treatments comprised five different grazing strategies and stocking rates encompassing typical management options used locally: (1) moderate stocking rate; (2) heavy stocking rate; (3) variable stocking rate; (4) southern oscillation index variable; and (5) rotational spelling. Further details on all the treatments are given in O'Reagain *et al.* (2011). For this study only four of the treatments, treatments 1, 2, 3 and 5, were sampled. Treatments 3 and 5 were combined into a single treatment for several *a priori* and *post-hoc* reasons; (1) we did not intend to analyse the data via orthogonal ANOVA and, instead, took a multivariate and information-theoretic approach given the small number of fauna sites that we could effectively sample; (2) the average annual stocking rate in the variable and rotational paddocks was identical over the time period of sampling; and (3), given the low number of sites and the fact that the design of the paddock structure was not ideal for data collection on fauna, we were more interested in contrasting the extremes and intermediate stocking rates. Initial multivariate exploration of the fauna composition across treatments indicated that the combination of treatments 3 and 5 was an appropriate approach.

Sampling

Sixteen 1-ha sites were established comprising two within each of four replicated treatment paddocks (moderate, heavy, and rotational and variable stocking rates). All sites were sampled in the wet (November–April) and dry (May–October) seasons in 1999–2000 and again in 2003–04, and the seasonal data were combined in subsequent analyses. The 1-ha sites within the treatments will be referred to subsequently in the following manner: T_0 ($n = 16$) as the initial survey and T_1 ($n = 16$) as the second survey; heavy grazing treatment ($n = 4$), variable ($n = 8$, the rotational and variable grazing treatments) and moderate ($n = 4$); and Box ($n = 8$) or Ironbark ($n = 8$). Each site was at least 500 m from another adjacent site.

Faunal sampling used a standardised approach within a 1-ha site (Kutt and Fisher 2011). Nested in the quadrat was 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 pitfall traps (40 cm deep and 25 cm in diameter), 10 m apart and arranged in a 'T' configuration (with 20 m and 10 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: two diurnal and nocturnal searches, each of 30-min duration, conducted within the trapping square. Nocturnal and diurnal counts included active (log-rolling and litter-raking) and passive (looking for eye-shine and listening for nocturnal birds) searches. Within each 1-ha site, eight 5-min wandering diurnal bird counts were conducted over a 4-day period. This method is the most suitable for savanna environments (Kutt *et al.* 2012).

Most of the grazing experiment paddocks were elongate in shape and consist of three different soil–vegetation associations, thus reducing the ability to locate the sites in a truly interspersed manner. Each edge of the 1-ha sites (100 × 100 m) was located at least 100 m from a vegetation boundary and at least 200 m from a watering point.

Change in composition and abundance from T_0 to T_1

We examined if there was any significant compositional change in the fauna from the baseline to the re-sample via multivariate analysis in PRIMER version 6 (Clarke and Gorley 2006). We constructed a site × species table, populated by abundance of each species, and square-root transformed the data and constructed a Bray–Curtis resemblance (similarity) matrix. We then presented this matrix as an ordination via multi-dimensional scaling, labelling the sites as either T_0 or T_1. The variation in species composition across baseline and re-sample was tested via Analysis of Similarity (ANOSIM) using the above resemblance matrix. The characteristic fauna that defined the baseline and re-sample groups were then identified via the SIMPER (similarity percentages) routine in PRIMER (Clarke and Gorley 2006), which decomposes average Bray–Curtis dissimilarities between all pairs of samples into percentage contributions for each species.

As the 16 quadrats were sampled on two occasions (T_0 and T_1), we were able to examine the relative changes in composition and abundance across the two time periods. First, we examined change in abundance of species recorded in the baseline and re-sample using Wilcoxon matched-pair tests. Only species recorded in three or more quadrats over both sampling periods were examined. Second, we calculated, for each quadrat, the dissimilarity in species composition between the two time periods, using the Bray–Curtis dissimilarity index, (which varies from 0, if there is an identical species composition between the two sampling periods and with those species being present in identical proportional abundances, to 100 if there are no species in common). We compared the relative change in composition from the baseline to the re-sample by examining the mean and standard error of dissimilarity between the moderate versus variable stocking rate quadrats, the variable versus high stocking rate quadrats and moderate versus heavy stocking rate quadrats. We examined the change across treatments including all quadrats and then only those within the Box vegetation and the Ironbark vegetation. We tested the significance in the variation between stocking rates via ANOVA.

Grazing and vegetation effects on species abundance

We then investigated the relationship between the abundance of bird, reptile and mammal species, and the grazing and vegetation factors, via generalised linear models assuming a Poisson error distribution and a natural logarithm link function. In this case grazing was tested as a continuous variable, using average stocking rate in the paddocks sampled up until the sampling period, and vegetation as a categorical variable, with Box or Ironbark vegetation as the categories. We used the Kullback–Leibler information-theoretic methods to model the relationship, which assigns relative strengths of evidence to

the different competing models, rather than a significance level (Burnham and Anderson 2002). We tested the baseline and re-sample datasets separately, constructed a set of four alternative models (null, grazing, vegetation and the interaction) and used the Akaike Information Criterion (AIC) as an objective means of model selection (Akaike 1973). We then used information-theoretic methods to select the best set of explanatory variables (Burnham and Anderson 2002). A second-order information criterion was used to correct for bias (termed AIC_c) for each model in a candidate set. The relative likelihood of a set of candidate models was calculated using Akaike weights. The weight of any particular model depends on the entire set of candidate models, and varies from 0 (i.e. no support) to 1 (complete support). To determine which model parameters best fitted the data, we used averaging of the AIC models using the Akaike weights (Burnham and Anderson 2002). For interpretation, the reliability of the model averaged parameter estimates is reported with the aid of confidence intervals and, if the upper and lower confidence intervals do not intersect zero, then the parameter estimate is considered reliable. The direction of the parameter estimate reflects the direction of the effect (positive or negative). All analyses were conducted with the R version 2.9.0 software program (www.r-project.org, accessed 19 April 2012). We compared the influence of each variable by calculating the size of the independent effect of explanatory variables using hierarchical partitioning analysis within the *hier.part* package in R (Chevan and Sutherland 1991; Mac Nally 1996).

Results

Several factors, controlled and uncontrolled, that influenced the entire grazing experiment will have affected the T_0 and T_1 data. First, the entire experiment was deliberately burnt in October 1999 between the wet and dry sampling; second, there was a fire applied to the Ironbark sections in the rotational spell paddocks in November 2001 (affecting only two of the sites), which reduced cover and changed pasture conditions substantially; and, finally, the rainfall over the entire period was highly variable. It was well above average before T_0 (~800 mm) and well below average before T_1 (~400 mm), including an 11-month period of almost no rain. The ground cover also changed dramatically across the experiment study area over the two periods from an average of between 50 (heavy stocking rates) and 70% (moderate stocking rates) in 1999–2000, to between 25 (heavy stocking rates) and 55% (moderate stocking rates). This reduction is a function of the lower than average rainfall combined with the effect of the stocking rates (Orr and O'Reagain 2011).

Over the two periods, we recorded over 2000 individuals representing 127 species of vertebrate fauna comprising five amphibian, 83 bird, 27 reptile and 12 mammal species. The ANOSIM results indicated that there was strong separation in the fauna composition from the baseline to the re-sample (Global $r = 0.48$ ***, Fig. 2). The characteristic fauna that best defined (>5% contribution) the T_0 and T_1 groups were Australian owlet-nightjar (*Aegotheles cristatus*), rufous whistler (*Pachycephala rufiventris*), black-faced cuckoo-shrike (*Coracina novaehollandiae*), pied butcherbird (*Cracticus*
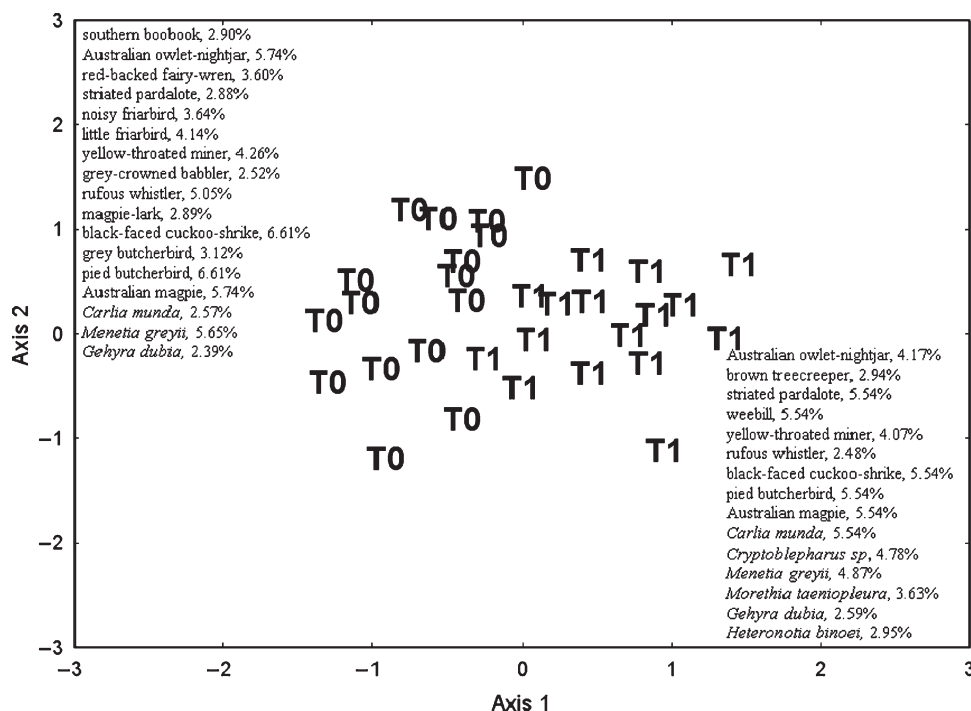

Fig. 2. Two-dimensional multi-dimensional scaling of vertebrate fauna composition at each survey site. T_0 is the initial sampling and T_1 is the re-sampling. The abundance data were square-root transformed and the ordination utilised a Bray–Curtis similarity matrix. The list of species in the top left corner indicate those that were identified as contributing to the T_0 group and those in the bottom right the T_1 group (as identified by the SIMPER routine in Primer). The scores are the percentage contribution to the degree of similarity.

nigrogularis), Australian magpie (*Cracticus tibicen*) and common dwarf skink (*Menetia greyii*) (baseline group) and striated pardalote (*Pardalotus striatus*), weebill (*Smicrornis brevirostris*), black-faced cuckoo-shrike, pied butcherbird, Australian magpie and shaded-litter rainbow-skink (*Carlia munda*) (re-sample) (Fig. 2). The changes in mean compositional dissimilarity across the grazing stocking rate comparisons were on the whole not significant except for the moderate versus variable stocking rate comparison (fauna became slightly more similar) and the same comparison for Box vegetation only (fauna became clearly more similar) (Table 1).

There was a relative change in abundance of 25 birds, four mammal and five reptile species from the T_0 to the T_1 sampling (Table 2). Of these, nine species of birds increased and 15 species of birds decreased in abundance, three species of mammals increased and one mammal species decreased in abundance, and three species of reptiles increased, one species of reptile decreased in abundance and the abundance of one species of reptile was mixed in pattern (Table 2). The strongest patterns in abundance were for the galah (*Eolophus roseicapillus*), which increased under the variable stocking rates, the pheasant coucal (*Centropus phasianinus*) and Southern boobook (*Ninox novaeseelandiae*), which decreased under the moderate and variable stocking rates, striated pardalote and weebill, which increased under high and moderate/variable stocking rates, respectively, noisy friarbird (*Philemon corniculatus*) and little friarbird (*P. citreogularis*), which decreased under the variable stocking rate, grey butcherbird (*Cracticus torquatus*) and pied butcherbird, which decreased under the moderate stocking rate, and fire-tailed skink (*Morethia taeniopleura*), which increased under the high stocking rate. The response in mammals was generally weak but the abundance of the common planigale (*Planigale maculate*) increased under the high stocking rate, that of the eastern grey kangaroo (*Macropus giganteus*) increased under the variable stocking rates and that of the northern short-tailed mouse (*Leggadina lakedownensis*) increased under the moderate and variable stocking rates. Other notable changes in the abundance of species were a decrease in that of the yellow-throated miner (*Manorina flavigula*) in the high and variable stocking rates and a decrease in that of the terrestrial gecko (*Diplodactylus conspicillatus*) at the high stocking rate (Table 2).

The generalised linear modelling revealed that there were nine species that were already distributed in significantly different abundances across the grazing and vegetation treatments at the time of the baseline survey (Table 3). The abundance of four of these was associated with the interaction term. The most notable species were the cockatiel (*Nymphicus hollandicus*) (positive grazing effect), red-backed fairy-wren (*Malurus melanocephalus*) (negative grazing effect), rufous whistler (less abundant in Box vegetation), shaded-litter rainbow-skink (more abundant in Box) and common dwarf skink (less abundant in Box) (Table 3). There was a strong interactive effect of grazing and vegetation on the brown tree creeper (*Climacteris picumnus*) and jacky winter (*Microeca fascinans*). In the dataset for T_1, the abundance of 16 species could be explained by the grazing and vegetation factors. Five of these had a strong positive grazing association – crested pigeon (*Ocyphaps lophotes*), weebill, yellow-throated miner, magpie-lark (*Grallina cyanoleuca*), apostlebird (*Struthidea cinerea*) and three of these had a strong negative effect – variegated fairy-wren (*Malurus lamberti*), red-backed fairy-wren and double-barred finch (*Taeniopygia bichenovii*). Many more species than in the T_0 sampling displayed a vegetation effect, including the galah (increased abundances in Ironbark), and dubious gecko (*Gehyra dubia*) and Binoe's prickly gecko (*Heteronotia binoei*) (decreased in Box).

Discussion

Limitations of the study

In this study we have demonstrated that the composition of the vertebrate fauna and the abundance of many species altered across the Wambiana grazing experiment. A majority of species decreased in abundance over the two sampling periods. Some of the reconfiguration of the fauna can be attributed to the grazing treatment and vegetation types and, although not directly tested, concomitant structural changes in the vegetation such as the reduction in ground cover (Orr and O'Reagain 2011). Other variation is seemingly in response to broader landscape-scale changes, such as the reduction in rainfall over the two periods of the survey, and management actions such as the burning of the entire experiment in 1999 and in two small sections affecting two sites in 2001. The data from the T_0 sampling indicated there was some pre-existing variation in composition and abundance of the fauna at the beginning of the grazing experiment and this subtle spatial heterogeneity will have had some consequence for the pattern of changes in fauna over time (Price *et al.* 2010). Because of the low level of replication of sites and the clustering of the sites within an ~1000-ha area, we were unable to clearly identify the relative effect of the site-scale responses from more large-scale effects of rainfall and fire. As changes in rainfall and the large fire affected the entire experimental area, we can

Table 1. Change in mean fauna compositional dissimilarity (Bray–Curtis index) from the T_0 baseline sampling to the T_1 re-sampling for all sites, Red River Box (Box) and Silver leaf Ironbark (Ironbark) sites

Comparisons are the moderate versus variable stocking rate (M v. V), variable versus high stocking rate (V v. H) and moderate versus heavy stocking rate (M v. H). Variation between T_0 and T_1 examined via ANOVA (*F*-value given). Actual significance levels (*P*) are listed

Comparison	All sites				Box				Ironbark			
	T_0	T_1	*F*	*P*	T_0	T_1	*F*	*P*	T_0	T_1	*F*	*P*
M v. V	43.8 (1.2)	43.4 (1.5)	0.04	0.84	43.2 (2.4)	37.2 (2.4)	3.16	0.09	44.7 (3.1)	43.4 (3.8)	0.07	0.78
V v. H	46.5 (1.6)	42.6 (1.4)	3.34	0.07	43.4 (4.1)	35.4 (3.1)	2.42	0.14	50.8 (2.1)	46.3 (2.2)	2.23	0.15
M v. H	47.3 (3.2)	42.7 (2.2)	1.43	0.23	45.9 (6.9)	39.5 (3.4)	0.68	0.44	45.9 (5.8)	37.5 (1.5)	1.94	0.21

Table 2. The differences in abundance of species at the Wambiana grazing trial over the two sampling periods (T_0 baseline sampling and T_1 re-sampling)

n is the number of quadrats the species was recorded in over the two sampling periods and only species recorded in three or more quadrats were considered. Data within the T_0 and T_1 columns are the mean (and standard error) of abundances for each sampling period. T_0 *v.* T_1 indicates the direction of change in abundance [increase (Inc.) and decrease (Dec.)] and in which treatments the change occurred. M = moderate, V = variable and H = high stocking rate. Data within these columns is the relative change in abundance in the T_0 and T_1 samples for each stocking rate. Z is the Wilcoxon matched-pairs test statistic, and *P* is the probability levels with n.s., not significant; *, $P < 0.05$; **, $P < 0.01$; and ***, $P < 0.001$. Only species with significant Wilcoxon scores are tabulated

Species	*n*	T_0	T_1	T_0 *v.* T_1	Z	*P*	M	V	H
Birds									
Brown falcon (*Falco berigora*)	4	0	0.3 (0.1)	Inc. (LMH)	1.82	n.s.	0.3	0.3	0.3
Nankeen kestrel (*Falco cenchroides*)	5	0	0.5 (0.2)	Inc. (H)	2.02	*	0.3	0.3	0.5
Peaceful dove (*Geopelia striata*)	11	3.6 (1.2)	0.6 (0.4)	Dec. (M)	2.31	*	−0.1	−0.5	−0.3
Galah (*Eolophus roseicapillus*)	11	0.4 (0.3)	2.4 (0.9)	Inc. (M)	2.65	**	0.5	0.7	0.1
Pale-headed rosella (*Platycercus adscitus*)	17	1.6 (0.5)	4.1 (1.2)	Inc. (L)	1.68	n.s.	0.6	0.1	0.1
Budgerigar (*Melopsittacus undulates*)	7	0	4.8 (2.0)	Inc. (LM)	2.36	*	0.5	0.5	0.3
Pheasant coucal (*Centropus phasianinus*)	10	2.1 (0.6)	0	Dec. (L)	2.80	**	−0.8	−0.6	−0.5
Southern boobook (*Ninox novaeseelandiae*)	13	1.1 (0.2)	0.1 (0.1)	Dec. (LM)	2.93	**	−0.6	−0.6	−0.5
Australian owlet-nightjar (*Aegotheles cristatus*)	29	1.7 (0.3)	0.9 (0.1)	Dec. (H)	2.31	*	0.0	−0.1	−0.2
Blue-winged kookaburra (*Dacelo leachii*)	12	1.8 (0.6)	0.5 (0.2)	Dec. (H)	2.07	*	−0.2	−0.2	−0.4
Forest kingfisher (*Todiramphus macleayii*)	3	0.4 (0.2)	0	Dec. (MH)	1.60	n.s.	0.0	−0.3	−0.3
Red-backed fairy-wren (*Malurus melanocephalus*)	18	13.9 (3.5)	3.4 (1.9)	Dec. (L)	2.39	*	−0.8	−0.7	−0.2
Striated pardalote (*Pardalotus striatus*)	27	5.1 (1.2)	15.5 (2.7)	Inc. (H)	3.18	**	0.6	0.5	0.7
Weebill (*Smicrornis brevirostris*)	20	2.3 (1.4)	18.5 (2.3)	Inc. (LM)	3.51	***	0.9	0.9	0.6
Noisy friarbird (*Philemon corniculatus*)	15	5.6 (1.3)	0.3 (0.2)	Dec. (M)	2.93	**	−0.6	−0.8	−0.4
Little friarbird (*Philemon citreogularis*)	19	6.2 (1.4)	1.4 (0.3)	Dec. (M)	3.11	**	−0.6	−0.8	−0.3
Blue-faced honeyeater (*Entomyzon cyanotis*)	5	0	0.6 (0.3)	Inc. (H)	2.02	*	0.3	0.3	0.5
Yellow-throated miner (*Manorina flavigula*)	27	7.0 (1.9)	3.3 (1.1)	Dec. (H)	2.07	*	0.0	−0.2	−0.3
Grey-crowned babbler (*Pomatostomus temporalis*)	18	7.6 (1.8)	2.7 (1.0)	Dec. (M)	2.55	*	0.0	−0.4	−0.3
Rufous whistler (*Pachycephala rufiventris*)	25	5.8 (1.3)	1.9 (0.5)	Dec. (L)	2.44	*	−0.8	−0.1	−0.6
Magpie-lark (*Grallina cyanoleuca*)	20	1.9 (0.4)	0.7 (0.2)	Dec. (L)	2.24	*	−0.9	−0.2	0.3
White-browed woodswallow (*Artamus superciliosus*)	6	0	1.4 (0.6)	Inc. (L)	2.20	*	0.8	0.3	0.3
Grey butcherbird (*Cracticus torquatus*)	17	1.8 (0.3)	0.4 (0.1)	Dec. (L)	2.83	**	−0.6	−0.4	−0.1
Pied butcherbird (*Cracticus nigrogularis*)	32	11.5 (0.8)	4.9 (0.8)	Dec. (L)	3.29	***	−0.5	−0.3	−0.4
Australian magpie (*Cracticus tibicen*)	31	5.6 (1.0)	3.6 (0.9)	Dec. (M)	1.88	n.s.	0.0	−0.4	0.0
Mammals									
Planigale maculata	5	0.1 (0.1)	0.3 (0.1)	Inc. (H)	1.60	n.s.	0.0	0.1	0.5
Macropus giganteus	10	0.2 (0.1)	1.3 (0.4)	Inc. (M)	2.09	*	0.0	0.6	0.3
Leggadina lakedownensis	3	0	0.6 (0.4)	Inc. (LM)	1.61	n.s.	0.3	0.3	0.0
Mus musculus	3	0.3 (0.2)	0	Dec. (M)	1.61	n.s.	0.0	−0.4	0.0
Reptiles									
Diplodactylus conspicillatus	5	0.5 (0.2)	0.1 (0.1)	Dec. (H)	2.02	*	0.0	−0.3	−0.4
Gehyra dubia	21	1.4 (0.3)	2.8 (0.7)	Inc. (M)	2.13	*	0.0	0.3	0.2
Heteronotia binoei	21	1.2 (0.3)	4.2 (1.1)	Inc. (MH), Dec. (L)	2.07	*	−0.2	0.5	0.5
Carlia munda	26	1.8 (0.5)	7.1 (2.0)	Inc. (M)	2.51	*	0.7	0.8	0.5
Morethia taeniopleura	14	0.1 (0.1)	1.8 (0.3)	Inc. (H)	3.18	**	0.8	0.7	1.0

assume that these effects were similar for the entire fauna allowing some interpretation of the effect of stocking rate. For example, the decline in annual rainfall in the early period of the experiment reduced herbage mass and ground cover across all stocking rates although pasture condition severely declined in the heavily stocking treatment. In contrast, the fire had little effect on the density of trees but promoted seedling recruitment, a majority of which died in the subsequent 2 years (O'Reagain and Bushell 2011).

In many respects this study reflects the value of small-scale experimental work versus the value of landscape-scale 'space for time' correlational studies and highlights several issues. First, although grazing experiments can manipulate stocking numbers and vegetation, identifying the effects on a natural,

mobile population of species may be difficult to achieve within such as small scale. Cattle can be moved annually, counted, weighed and measured accurately whereas obtaining reliable estimates of native fauna populations is much more resource-intensive (Eyre *et al.* 2011). Second, despite the large capital investment in setting up the treatments in the experiment, the pre-existing and on-going fauna pattern will be in part spatially auto-correlated due to other effects of historical management and the relatively small size of the experiment and close proximity of the sample sites for mobile fauna; it might take longer time periods to fully identify lasting effects on species as a direct result of the grazing treatments as compared with matrix of vegetation pattern at the site (Eyre *et al.* 2009). Finally, in largely intact continuous tropical savanna woodlands, landscape-

Table 3. The outcomes of the Akaike Information Criteria model averaging for the two sampling periods (T_0, baseline; and T_1, re-sampling)
Only species with model terms having confidence limits not intersecting zero are shown. (–) or (+) indicates the direction of the effect. n is the number of sites the species was recorded. Graze is a test of the grazing factor alone, Veg is the vegetation factor and Graze × Veg is the interaction term. % is the independent effect of the variable as identified from hierarchical partitioning

Species	n	T_0						T_1					
		Graze	%	Veg	%	Graze × Veg	%	Grazing	%	Veg	%	Graze × Veg	%
Birds	–	–	–	–	–	–	–	–	–	–	–	–	–
Crested pigeon (*Ocyphaps lophotes*)	8	–	–	–	–	–	–	(+)	20	–	–	–	–
Galah (*Eolophus roseicapillus*)	11	–	–	–	–	–	–	–	–	(+)	41	–	–
Cockatiel (*Nymphicus hollandicus*)	18	(+)	26			–	–	–	–	(–)	26	(+)	67
Blue-winged kookaburra (*Dacelo leachii*)	12	–	–	(+)	28	–	–	–	–	–	–	–	–
Variegated fairy-wren (*Malurus lamberti*)	10	–	–	–	–	–	–	(–)	31	–	–	–	–
Red-backed fairy-wren (*Malurus melanocephalus*)	18	(–)	15	–	–	(–)	55	(–)	9	–	–	–	–
Brown tree creeper (*Climacteris picumnus*)	20	–	–	(+)	4	(–)	80	–	–	–	–	–	–
Striated pardalote (*Pardalotus striatus*)	27	–	–	–	–	–	–	(+)	6	(–)	25	–	–
Weebill (*Smicrornis brevirostris*)	20	–	–	–	–	(+)	75	–	–	–	–	–	–
Little friarbird (*Philemon citreogularis*)	19	–	–	–	–	–	–	(+)	18	–	–	–	–
Yellow-throated miner (*Manorina flavigula*)	27	–	–	–	–	–	–	(+)	16	–	–	–	–
Rufous whistler (*Pachycephala rufiventris*)	25	–	–	(–)	32	–	–	–	–	–	–	–	–
Jacky winter (*Microeca fascinans*)	17	–	–	(–)	10	(+)	77	–	–	(–)	16	–	–
Magpie-lark (*Grallina cyanoleuca*)	20	–	–	–	–	–	–	(+)	30	–	–	–	–
Apostlebird (*Struthidea cinerea*)	7	–	–	–	–	–	–	(+)	36	–	–	(+)	62
Double-barred finch (*Taeniopygia bichenovii*)	8	–	–	–	–	–	–	(–)	12	(–)	27	(+)	61
Mammals	–	–	–	–	–	–	–	–	–	–	–	–	–
Leggadina lakedownensis	3	–	–	–	–	–	–	–	–	(+)	19	–	–
Reptiles	–	–	–	–	–	–	–	–	–	–	–	–	–
Gehyra dubia	21	–	–	–	–	–	–	–	–	(–)	38	–	–
Heteronotia binoei	21	–	–	–	–	–	–	–	–	(–)	39	(+)	81
Carlia munda	26	–	–	(+)	45	–	–	–	–	(+)	18	–	–
Menetia greyii	30	–	–	(–)	36	–	–	–	–	–	–	–	–

scale patterns of climate, land type and fire can be more significant drivers of fauna pattern than local, small-scale perturbation (Woinarski *et al*. 2005; Kutt and Woinarski 2007; Reside *et al*. 2010). Despite these caveats, some of the patterns recorded in this study seem sensible and interpretable.

Changes in the vertebrate fauna

Many of the changes recorded over the two sampling periods of this study seem to reflect landscape-scale perturbation to the fauna rather than patterns derived from the imposition of the grazing treatments. This is understandable for vagile fauna. Tropical savanna bird communities, for example, are influenced by climate seasonality and longer-term weather patterns (Reside *et al*. 2010), changing fruiting and flowering resources across the landscape (Franklin 1997) and subtle gradients in the ground and woody vegetation (Price *et al*. 2009). Some of the variation recorded seemed compelling such as the decline in yellow-throated miner from the T_0 sampling and the corresponding increase in small-canopy passerines, the weebill and striated pardalote. There is increasing evidence to show that an increased abundance of miners (*Manorina* spp.) corresponds with a decline in small passerine birds, as the miners are hyper-aggressive and mob the smaller birds (Maron *et al*. 2011). This is most apparent where habitat is disturbed through grazing, logging or clearing (Eyre *et al*. 2009). The results from the re-sampling period reflected this in part – yellow-throated miners were most abundant in the heavily grazed treatments.

Other species are nomadic or partially migratory across the landscape, for example the granivorous and ground-feeding budgerigar (*Melopsittacus undulates*) and pale-headed rosella (*Platycercus adscitus*). These species move in response to seed flushes and deficits mediated by fire (Kutt and Woinarski 2007) and rainfall or drought (Chan 1999; Franklin 1999). Other changes might be a consequence of unintended factors; each grazing paddock had permanent water points and these might have encouraged the local increase in the eastern grey kangaroo and birds strongly associated with artificial waters such as crested pigeon and apostlebird (Landsberg *et al*. 1997).

The pattern of the avifauna in the T_1 data agrees with some typically reported responses to pastoral disturbance. The crested pigeon, apostlebird, yellow-throated miner and magpie-lark all increased due to grazing and habitat disturbance, the mechanisms being the loss of ground cover, increase in artificial water and changes in woody vegetation structural (Kutt and Woinarski 2007; Price *et al*. 2009). Similarly, the negative response of grass and shrub foraging and nesting species, such as the variegated and red-backed fairy-wrens and the double-barred finch, to heavy grazing simply reaffirms the link between ground cover and abundance of these species (Tassicker *et al*. 2006; Kutt and Martin 2010). In this study, cover was lowest in the most heavily stocked paddocks (O'Reagain *et al*. 2009) and we recorded a reduction in these species due to a grazing effect.

Although there were several reptile species that changed in relative abundance from the baseline to the re-sample, there was no universal relationship between the grazing treatments and total

reptile abundance or species richness in the re-sample. Species, such as the fat-tailed gecko (*Diplodactylus conspicillatus*), did decrease on the heavily grazed sites and there is some link between the decline in terrestrial burrowing species and reduced ground cover (Kutt and Woinarski 2007) although no clear pattern was revealed by the present study. Other small ground-dwelling reptiles increased substantially from T_0 to T_1 in the variable (shaded-litter rainbow-skink) and heavily grazed sites (fire-tailed skink), while Binoe's prickly gecko increased in variable and decreased in moderately grazed sites. The lack of definitive change in the dubious gecko may relate to this species being arboreal and hence unaffected by changes in ground cover. Reptiles, when compared with mobile and wide-ranging species, such as birds, respond to fine-scale heterogeneity in the grass and tree cover (Price *et al*. 2010) and broad-scale scale changes in soil and landscape structure (Woinarski *et al*. 1999). The changes caused by the grazing treatments may not have been sufficiently strong or widespread to affect local resources of litter, fallen timber or woody vegetation cover. Indeed the ground cover of *Carissa* spp. of shrubs increased dramatically after the fire in 1999 (O'Reagain *et al*. 2011).

As with many areas of north-eastern Queensland, and especially in areas with historically long periods of pastoral management (Ward and Kutt 2009), the mammals were recorded in very low numbers in this study. The results from this experiment provided some equivocal and slightly conflicting responses, such as the rodent *Leggadina lakedownensis* increasing in relative abundance from the baseline to the re-sample in the moderate and variable stocking rate treatments, but, due to an effect of vegetation type, not to grazing. The decline of mammals in northern Australia is considered a significant conservation issue (Woinarski *et al*. 2011) but this study highlights the difficulty in providing clear data on cause; the current data is sparse (or at least highly variable) and the decline may have been historical in Queensland and now is difficult to accurately ascribe to a cause (Kutt and Gordon 2012).

Improving design of future grazing experiments for measuring changes in the abundance of fauna

Despite the large area devoted to livestock grazing in northern Australia, effects of livestock grazing on fauna have received only moderate attention (James 2003; Martin *et al*. 2005) due to the limited prospects of correlative studies (i.e. the ubiquity of grazing across the landscape) and difficulty in undertaking experimental manipulations at an appropriate scale where the grazing response can be teased apart from other confounding effects (Kutt and Gordon 2012). These factors were influential limitations in this study and, although we recommend that the Wambiana grazing experiment be surveyed again for vertebrate fauna, there are opportunities to learn from the previous sampling strategy and modify it. Key changes suggested are: (1) an increase in the replication of sites sampled within the experimental paddocks; (2) a focus on abundant, easily sampled taxa (i.e. reptiles and birds) that might respond rapidly to changes caused by stocking rates; and (3) a use of rapid survey methods that allow an increase in the spatial and temporal spread of the survey data (i.e. active searches and bird counts). As taxa,

such as mammals, are clearly at very low abundances, yet of high conservation concern in northern Australia rangelands (Kutt and Gordon 2012), this presents a challenge for understanding grazing effects on these species. These suggested changes to the sampling should be in addition to the existing monitoring program and the combination of detailed surveillance surveys with more frequent rapid surveys for key taxa is recommended for rangelands generally (Eyre *et al*. 2011). In the future, dedicated experimental work that manipulates grazing effect at scales relevant to mobile fauna should be considered, or at least more formally incorporated in experimental designs (rather than an afterthought) given the value of landscape-scale investigations that use natural contrasts in management at property scales (Fischer *et al*. 2005).

Conclusion

Declines in the fauna of tropical savannas in Australia have been attributed to the singular effect or interaction of fire regimes, grazing by introduced herbivores and predation by feral cats (Legge *et al*. 2008, 2011; Kutt 2011). In this study we identified some clear changes in the composition and abundance of fauna across the Wambiana grazing experiment and, although some of the shifts were attributable to a grazing effect, others were clearly influenced by landscape-scale management and environmental effects. Previously the response of fauna to the removal of cattle has been reported as significant (Legge *et al*. 2011) to muted (Silcock and Fensham 2012), and the intensity and history of pastoral land use at any particular site is probably a key influence on the amplitude of change (Ward and Kutt 2009). The increasing focus on pastoral development in northern Australia under changing climates and rainfall patterns (Cobon *et al*. 2009) means any opportunity to incorporate data collection on biodiversity into grazing manipulation experiments is critical for the assessment of the effects of different land management scenarios on native species.

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