Buffel grass in Queensland's semi-arid woodlands: response to local and landscape scale variables, and relationship with grass, forb and reptile species

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Abstract.   Buffel grass [*Pennisetum ciliare* (L.) Link] has been widely introduced in the Australian rangelands as a consequence of its value for productive grazing, but tends to competitively establish in non-target areas such as remnant vegetation. In this study, we examined the influence landscape-scale and local-scale variables had upon the distribution of buffel grass in remnant poplar box (*Eucalyptus populnea* F.Muell.) dominant woodland fragments in the Brigalow Bioregion, Queensland. Buffel grass and variables thought to influence its distribution in the region were measured at 60 sites, which were selected based on the amount of native woodland retained in the landscape and patch size. An information-theoretic modelling approach and hierarchical partitioning revealed that the most influential variable was the percent of retained vegetation within a 1-km spatial extent. From this, we identified a critical threshold of ~30% retained vegetation in the landscape, above which the model predicted buffel grass was not likely to occur in a woodland fragment. Other explanatory variables in the model were site based, and included litter cover and long-term rainfall. Given the paucity of information on the effect of buffel grass upon biodiversity values, we undertook exploratory analyses to determine whether buffel grass cover influenced the distribution of grass, forb and reptile species. We detected some trends; hierarchical partitioning revealed that buffel grass cover was the most important explanatory variable describing habitat preferences of four reptile species. However, establishing causal links – particularly between native grass and forb species and buffel grass – was problematic owing to possible confounding with grazing pressure. We conclude with a set of management recommendations aimed at reducing the spread of buffel grass into remnant woodlands.

Additional keywords: clearing, fragmentation, grassy woodlands, invasive grass, thresholds.

Introduction

Frequent droughts during the early 1900s in northern Australia, Africa and North and South America compelled a worldwide search for a grass that could produce good forage for livestock with limited precipitation (Cox *et al*. 1988). The search ended with the discovery of several native grass species of southern Asia and East Africa, buffel grass [*Pennisetum ciliare* (L.) Link] being one of them. Buffel grass was subsequently introduced in northern Australia during the 1920s, and Texas (USA) and northern Mexico in the 1930s (Mayeaux and Hamilton 1983; Cox *et al*. 1988; Arriaga *et al*. 2004). In Queensland, buffel grass was first sown in Cloncurry in 1926, and then in the Rockhampton district in 1928 (Humphreys 1967). By the early 1930s experimental sowing of buffel grass were made in several Queensland districts, and seed from several cultivars have since been introduced to increase adaptability (Paull and Lee 1978).

The adaptive capacity of buffel grass in the arid and semi-arid tropics is unequivocal. Buffel grass produces large quantities of light, bristled viable seeds asexually, which are effectively dispersed via wind, water and animals. Aggressive expansion of rhizomes, effectively forming dense swards, also assists colonisation (Humphries *et al*. 1991). Since its introduction to the Sonoran Desert, Mexico, buffel grasslands now extend throughout an estimated 12% of the area (Búrquez-Montijo *et al*. 2002). This largely reflects the deliberate conversion of desert native vegetation to buffel grass pasture land, the area of which has effectively doubled approximately every 10 years since 1973 in the region (Franklin *et al*. 2006). However, buffel grass tends to occupy non-target ecosystems adjacent to pasturelands in this region (Búrquez-Montijo *et al*. 2002). In Texas, through sowing and natural dispersion, buffel grass occupied ~90% of rangelands within 40 years (Mayeaux and Hamilton 1983). On O'ahu, Hawaii, 33% of the native grasslands have been transformed to buffel grasslands within a 30-year period (Daehler and Carino 1998). In central Australia, quantitative long-term monitoring has shown an increase in buffel grass relative abundance from 5% to

more than 80% in less than 30 years (Clarke *et al.* 2005), and drainage systems and alluvial flats appear to be most at risk (Griffin 1993). Although buffel grass has now been recorded throughout much of arid and semi-arid Australia (Low 1999), the current extent of buffel grassland in Australia is unknown. However, ~68% of the country is predicted to be potentially suitable for buffel grass establishment (Lawson *et al.* 2004).

The ecology, and invasive capacity, of buffel grass has been studied in relation to rainfall variability and drought (Fitzgerald 1955; Sheriff and Ludlow 1984; Clarke *et al.* 2005), competition with established native vegetation (McIvor 2003; Clarke *et al.* 2005; Jackson 2005), tree canopy interactions (Christie 1975*a*), edaphic characteristics (Cox *et al.* 1988; Griffin 1993; Ibarra *et al.* 1995; Arriaga *et al.* 2004; Lawson *et al.* 2004), fire (Mannetje *et al.* 1983; Butler and Fairfax 2003) and grazing disturbance (Hodgkinson *et al.* 1989). These studies profile buffel grass as an extremely competitive species, with a high resistance to fire, drought and heavy grazing, particularly in arid and semi-arid regions. Consequently, buffel grass is a valued pasture improvement species, and continues to be the most widely sown pasture grass in Queensland (Cavaye 1991; McIvor 2003).

Conversely, buffel grass is also identified as one of the most widespread non-native plant species potentially posing a threat to rangeland biodiversity (Humphries *et al.* 1991; Grice 2004, 2006; Martin *et al.* 2006). However, there have been few studies that have quantified the impact of buffel grass establishment upon biodiversity in Australia. Most studies report a negative relationship between buffel grass biomass or cover and plant species richness and/or individual plant species cover (McIvor 1998; Fairfax and Fensham 2000; Franks 2002; Butler and Fairfax 2003; Clarke *et al.* 2005; Jackson 2005; Kaur *et al.* 2006; Smyth *et al.* 2009). The impacts upon fauna species are largely unknown, although it is generally surmised to be extremely detrimental (Low 1997). Of the few quantitative studies, Ludwig *et al.* (2000) report mammal and reptile species' decline with increased buffel grass cover in central Queensland. For bird species, a mixed response has been reported, with some species being negatively associated and others being positively associated with buffel grass extent (Hannah *et al.* 2007). In Arid Australia, ground dwelling bird species were found to be negatively associated with increased buffel grass cover, possibly through limiting foraging prospects (Smyth *et al.* 2009). There is some evidence to suggest that the 'hot climate specialist' functional group of ants are also adversely affected by encroachment of buffel grass (Smyth *et al.* 2009).

The study presented in this paper was conducted in the Maranoa region of south-west Queensland, one of three main buffel grass areas in Queensland (Paull and Lee 1978). In this region, it was estimated in 1991 that at least 1 million ha had been actively sown to buffel, resulting in pure buffel swards or mixtures with native grasses (Cavaye 1991). This constitutes a 50% increase from estimates made in the mid 1970s (Paull and Lee 1978; Cavaye 1991). We focussed our study in the remnant grassy poplar box (*Eucalyptus populnea* F.Muell.) woodlands, which in general are utilised for grazing but have not been subjected to the deliberate seeding of buffel grass. No previous study has yet endeavoured to detect thresholds for management of invasive risk of buffel grass into remnant vegetation. As such, the aim of this study was to: (i) identify the relationship between buffel grass and local- and landscape-scale environmental, habitat and disturbance variables; and (ii) identify vegetation clearing thresholds beyond which buffel grass is likely to invade remnant vegetation.

Inconsistent responses of various species to disturbances such as grazing pressure is known to occur at the continental, and even regional, scale (Vesk and Westoby 2001; McIntyre *et al.* 2003). A similar species response may be observed with the introduction or invasion of buffel grass, especially since invasion generally occurs in combination with other disturbances such as increased grazing pressure and native vegetation clearing. Given the concern regarding buffel grass spread and impact in Australia has been relatively recent, information is limited for meta-analysis of native species' response to buffel grass throughout Australia. As such, a third aim of this paper was to identify any trends in relationships between native ground layer plant species cover abundance or reptile species occupancy and buffel grass cover abundance in remnant vegetation.

Materials and methods

Study area and site selection

The study area incorporates 4.5 million ha of the Maranoa district within the Brigalow Bioregion of south-west Queensland (Fig. 1). The annual average rainfall is between 500 and 750 mm across the study region, the majority (>70%) of which occurs during October–March. State forests and conservation reserves occupy ~5 and 1% of the study area, respectively. The principal land use in the study region is agriculture, predominantly cattle and sheep grazing with opportunistic cropping in favourable seasons. Prior to the cessation of broadscale clearing in Queensland through amendment of the *Vegetation Management Act 1999*, ~70% of the original vegetation was cleared and is now grazed native pasture and non-remnant (regrowth) woodland. The establishment of buffel grass pasture through aerial or on-ground sowing accompanied the majority of vegetation clearing in the region (Cavaye 1991; Fairfax and Fensham 2000).

Of the total study area, 32% is covered by remnant forest and woodland, of which ~40% is mapped as poplar box dominant or co-dominant woodland (EPA 2003). The poplar box woodlands were the ecosystem type targeted by this study. We wanted to assess the potential of buffel grass to occur in remnant woodland in fragmented landscapes. Poplar box dominant remnants were mapped in the study region using 1:100 000 remnant regional ecosystems mapping (EPA 2003), and potential sites were located on candidate properties and access permissions sought. We used native woody cover derived by the Statewide Land and Tree Study (SLATS; NRM 2003) to identify levels of fragmentation in the landscape of each potential site, where a landscape was defined as a 5-km circular spatial extent radiating from the centre of the site. The extent of native woody cover in each landscape was then calculated using Geographical Information System software ArcGIS (Version 9.1; ESRI 2005). Botanical nomenclature according to Bostock and Holland (2007) is used throughout this paper.

Sites were selected to sample poplar box remnants in five broad landscape treatments typical of the region. These were; small fragments (<50 ha) in relictual landscapes (<15% retained vegetation in the landscape); small fragments in fragmented
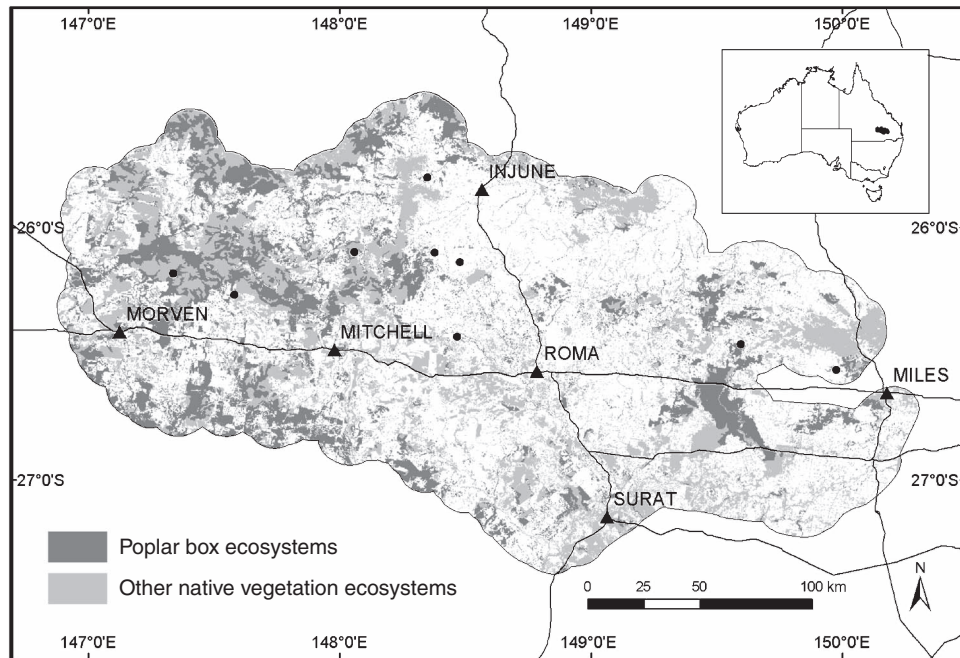
Fig. 1. The study area and location of survey sites.

landscapes (15 to 70% retained vegetation in the landscape); medium fragments (50–200 ha) in fragmented landscapes; large fragments (>200 ha) in fragmented landscapes; and large fragments in intact landscapes (>70% retained vegetation in the landscape).

Twelve replicates were sampled for each landscape-scale treatment type, resulting in a total of 60 sites (Fig. 1). In the field, sites were ground truthed for suitability. Suitable sites were located at least 2 km apart to avoid issues of spatial autocorrelation, and 500 m away from artificial water points. Riparian areas were avoided, and sites were located within the remnant at least 100 m from the edge where possible.

Local-scale variables

Several vegetation structure and environmental variables thought to influence occupancy of remnant vegetation by buffel grass were measured within a 100×10 m plot at each site between March and November 2003 (Table 1). Twenty soil cores (0–100 mm) were collected and bulked at each site and sampled for nitrogen. Litter cover was visually assessed by recording the percent cover of each within ten 1×1 m quadrats located along the central 100 m transect and averaged for the site. Projected foliage cover was measured as the percentage of ground area occupied by the vertical projection of foliage and branches of live tallest and mid-strata stems. The vertical interception of

Table 1.   Description of environmental variables recorded for each site

Variable code	Description
	Local-scale variables
SoilN	Total nitrogen of soil sample (%)
Precip	Mean annual rainfall averaged over 30 years data (mm)
PFC	Percentage of ground area occupied by the vertical projection of live foliage and branches of mid and tallest strata (%)
CWD	Volume of coarse woody debris >10 cm diameter, derived using the formula by Van Wagner (1968) (m^3 ha^{-1})
Litter	Percentage of ground area occupied by fine to coarse fallen organic litter such as leaves, twigs and branches <10 cm diameter (%)
Fire	0, no fire; 1, cool burn, scorch height up to 1 m on trees, tree canopy not scorched; 2, hot burn, tree canopy scorched
Graze	Categorised as 1, nil to light grazing, typical in national parks and state forests, swards intact and history of little or infrequent grazing; 2, moderate grazing, typical in grazed paddocks and stock routes, selective grazing obvious and history of moderate grazing; and 3, heavy grazing, typical in grazed paddocks, bare ground and/or closely cropped areas apparent, decreaser native pasture species such as *Themeda triandra* absent
	Landscape-scale variables
Veg1k	Extent of native vegetation retained within 1-km spatial extent (%)
Buffel landtype	Extent of brigalow-belah and softwood vine scrub landtypes cleared and sown to buffel within a 1-km spatial extent (%)
Near neighbour	Mean shortest straight-line distance between the focal vegetation patch and the nearest neighbour vegetation patch (m)
IJI	Interspersion and juxtaposition index of the extent to which all vegetation patches in the landscape are equally adjacent to each other

foliage was recorded at 1-m intervals along the 100 m transect using a gimbal ring sighting tube. The volume of coarse woody debris (CWD) at each site was estimated using the line-intersect methodology described by Van Wagner (1968). The diameter of fallen branches and trees >10 cm and >0.5 m in length that intercepted a 100 m transect centred on the plot was recorded and applied to the formula:

$$V = [(\pi)^2 / 8\,L] \times \Sigma(d)^2 \qquad (1)$$

where L was the transect length (100 m) and d was the diameter of the CWD in m.

Data on annual precipitation over the past years (1975–2003) were obtained for each site from the SILO national interpolated climate surfaces (Jeffrey *et al*. 2001), and averaged to give one value per site. Grazing pressure was rated from 1 (light grazing) through to 3 (heavy grazing) as estimated from landholder questionnaires on stocking history and visual observations. Fire intensity was also assessed from landholder surveys and measured evidence of burning at each site (Table 1).

Landscape-scale variables

A core set of four uncorrelated landscape-scale candidate variables were generated for the modelling procedure (Table 1). Each survey site was buffered in ArcGIS (ESRI 2005) using a 1-km radius from the centre of the site to create a circular spatial extent encompassing ~314 ha. This spatial extent was then intersected with the SLATS woody vegetation cover to derive data on the proportion of vegetation retained.

We also intersected the 1-km spatial extent with land types highly suitable for buffel grass establishment post-clearing. These land types have been identified as Brigalow Belah Scrub and Softwood Vine Scrub, which were preferentially sown to buffel following clearing in southern Queensland (Chilcott *et al*. 2004). We made the cleared, buffel land types spatial by matching them to regional ecosystem types, and then using the pre-clear 1 : 100 000 regional ecosystem mapping (EPA 2003) to derive their original extent in hectares. This original extent, minus the remnant extent of the regional ecosystems, provided an estimate of the area of land types preferentially sown to buffel grass within a 1-km radius of our sites.

Landscape metrics were generated for each site using FRAGSTATS version 3.3 (McGarigal *et al*. 2002) and the remnant regional ecosystem and SLATS mapping. FRAGSTATS produced a large number of metrics, many of which were difficult to interpret for management purposes. Others, such as patch area and patch shape, were highly correlated with each other and with the proportion of vegetation retained in the landscape. We, therefore, opted to retain only two FRAGSTAT metrics, the interspersion and juxtaposition index and nearest neighbour (Table 1).

Ground cover and reptile survey

Data on ground cover plant species and reptile species were obtained for each of the 60 sites between November 2002 and January 2004. The percentage cover of buffel grass and other ground cover species were visually assessed once from ten 1×1 m quadrats which were aligned 10 m apart along the centre transect. The percentage cover values were averaged across the 10 quadrats to give one percentage cover value for each species per site. For each site, four active searches for reptiles were conducted within a 200×50 m area, incorporating one morning and one afternoon search within adjacent 100×50 m areas during summer–autumn and repeated during a second visit period in spring–summer. These data were pooled to give a presence or absence value for each species per site.

Statistical analyses

One-way analysis of variance (ANOVA) was used to investigate any significant difference in the mean cover of buffel grass between sites on the various land tenures (freehold, leasehold, travelling stock routes and national parks and state forests combined) and the three categories of grazing pressure. One-way ANOVA was also used to test for mean differences in number of native ground cover species and reptile species among classes of buffel grass cover. Since the averaged estimates of buffel grass cover per site were quite low, we selected three cover classes to reflect this; zero cover; 0.1–5% cover and; >5% cover. Tukey's pairwise comparison tests were performed when significant differences were found. Prior to the analyses, the dependent variables were normalised using a log-transformation.

An information-theoretic approach (Burnham and Anderson 2002) was used to test the hypothesis that local- and landscape-scale variables influence buffel grass occupancy in poplar box woodlands. The information-theoretic approach allows comparison of fit between a suite of competing models using Akaike's information criterion (AIC). Models can then be ranked in order of decreasing AIC values, indicating increased model fit. Thus, we developed a set of models to evaluate the hypothesis that local-scale and landscape-scale variables influence buffel grass occupancy in poplar box woodlands. As this study had a small sample size, we evaluated the information content of the models using the second order AIC, AIC_c, which balances the fit of a maximum-likelihood least-squares model [$\log(L)$] against the number of estimable parameters in the model (K). Level of support for each model was evaluated using the difference between the AIC_c of a given model and the AIC_c of the model with the smallest AIC_c (Δ_i). Additionally, Akaike weights (w_i) were calculated for each model, as:

$$w_i = \exp(-0.5\Delta_i) / \Sigma[\exp(-0.5\Delta_i)] \qquad (2)$$

To reduce bias and increase precision, we used multi-model inference or model averaging where we were unable to determine a model that best fit the data (i.e. $\Delta_i < 2$ or $w_i > 0.1$) (Burnham and Anderson 2002). Hierarchical partitioning was used to identify the explanatory variables that explained the most variance independently of the others in the final model.

Logistic regression with a logit-transformation, a form of generalised linear model (McCullagh and Nelder 1989) was used to estimate the response between the presence or absence of buffel grass and the candidate set of local- and landscape-scale variables. The logistic regression model fits an S-shaped curve to binary data and follows the form:

$$\text{Logit}(p) = \log(p/1 - p) = \beta_0 + \beta_1 x_{i1} + \ldots \beta_p x_{ip} \qquad (3)$$

where the response variable p is constrained between 0 (absence) and 1 (presence), thus, the error structure is specified by the

binomial distribution (Hosmer and Lemeshow 2000). Models were developed and model AIC determined using the R statistical package (version 2.6.0; R Development Core Team 2007). Model-averaging of model combinations of the most plausible variables was conducted using the Bayesian model averaging (BMA) package in R (Raftery *et al.* 2006), and the hierarchical partitioning was undertaken using the hier.part package, also in R (Walsh and Mac Nally 2007).

Prior to the modelling procedure, the candidate variables were checked for normality, using normal probability plots. It is important to ensure no highly correlated explanatory variables exist with a model, as a lack of independence between the explanatory variables within a multivariate model violates an important assumption of regression analysis, and can lead to unreliable selection of the most appropriate explanatory variables (Mac Nally 2000). Hierarchical partitioning provides a mechanism to identify those explanatory variables that explain most variance independently of the others, thus overcoming issues of multi-collinearity between explanatory variables (Mac Nally 2002).

Model performance was assessed using the receiver operating characteristic (ROC) curve, where sensitivity values (the proportion of observations where the model correctly predicts presence) are plotted against false positive values (1 – the proportion of observations where the model correctly predicts absence) (Metz 1978; Zweig and Campbell 1993). The ROC curve provides a graphical approach to the assessment of model discrimination capacity, where perfect discrimination is represented when the curve follows the left hand and top axes of the graph area, and the area under the ROC curve (AUC) equals 1 (Zweig and Campbell 1993). When there is no discrimination capacity, the AUC will be equal to 0.5, and the curve will coincide with the diagonal. A model with an AUC > 0.7 is considered to have reasonable discrimination capacity and practical utility (Hosmer and Lemeshow 2000). To obtain a single index of the discrimination capacity of the final model, the area under the curve and the standard error was calculated using the software predictions by MedCalc (2006), which uses the maximum likelihood approach. MedCalc (2006) also provides the 95% confidence intervals (CI) for the area. This was used to test the hypothesis that the theoretical area is 0.5, or that the model has no discrimination capacity. If the confidence interval did not include 0.5, then it can be concluded that the model has the ability to distinguish between presence and absence of buffel grass (Hanley and McNeil 1982).

There are various documented ways of determining quantitative probability thresholds from logistic models. For example, Austin *et al.* (1990) arbitrarily defined a species qualitative environmental realised niche, where the probability of finding the species is $P > 0.1$, and the qualitative optimal niche at $P > 0.7$. Wintle *et al.* (2005) recommend avoiding the use of arbitrary thresholds altogether unless the model is well calibrated, or the management costs of false-negative and false-positive prediction errors are evaluated. For this study, we followed an approach similar to Guénette and Villard (2005), and used the ROC, which assesses model performance for all possible probability thresholds. To indicate the point at which buffel grass was likely to be present in a patch of poplar box woodland, we selected the maximum accuracy threshold, at which both the false

positive rate (proportion of sites where buffel grass was predicted as present but was observed as absent) and false negative rate (proportion of sites where buffel grass was predicted as absent but was observed as present) were minimised simultaneously.

Spearman rank coefficients were used to explore the relationship between percent cover of buffel grass and percent cover of native perennial grass and forb species recorded at more than six of the 60 sites. To explore the potential impact of buffel grass cover on reptile species, we used BMA to predict the probability of species occurrence using logistic regression and based on the local- and landscape-scale variables (Table 1). The analysis was conducted for reptile species detected at more than six sites. The BMA package accounts for uncertainty in model selection by combining the predictions from multiple models as weighted averages based on the Bayesian information criterion (BIC), which is analogous to the AIC. Consequently, estimates of uncertainty of model predictions are not reliant upon a single model (Raftery and Zheng 2003; Wintle *et al.* 2003). Bayesian inference allows the incorporation of a posterior probability, or prior belief, if knowledge or data is available. By averaging over the best models, BMA calculates a posterior probability distribution that a variable is included in the most plausible model (Raftery *et al.* 2006). Thus, we were able to ascertain whether buffel grass cover was an important predictor in determining reptile presence or absence if it was selected as an explanatory variable in one or more of the top five models. The estimate was averaged over the best models so that we could identify whether the relationship between species occurrence and buffel grass cover was positive or negative. We used hierarchical partitioning to identify the explained variance in reptile species presence or absence attributable to the univariate correlation with the local- and landscape-scale variables. This provided a measure of the independent contribution accounted for by the buffel grass cover variable for each reptile species.

Results

Buffel grass was recorded at 26 sites, eight of which were assessed with more than 5% buffel grass cover (Fig. 2). The mean cover of buffel grass varied significantly between sites on different tenure types ($F_{3,56} = 7.68$, $P < 0.001$) and grazing pressure categories ($F_{2,57} = 7.83$, $P < 0.001$), but not fire intensity ($F_{2,57} = 1.132$, $P > 0.05$). Stock routes contained the highest mean cover of buffel grass, whereas it was not detected at the sites within national park and state forest (Fig. 3a). Tukey's pairwise comparison tests revealed significant differences in buffel grass cover on heavily grazed sites as compared with lightly grazed sites (Fig. 3b). Buffel grass was recorded across both burnt and unburnt sites, and cover was quite variable at sites with cool and hot burns, as can be seen by the high standard errors associated with the mean (Fig. 3c).

Buffel grass in the landscape

Two buffel grass occupancy models were generated with a $\Delta_i < 2$ and a $w_i > 0.1$ (models 1 and 2; Table 2). Together, both models included percent native vegetation retained within a 1-km spatial extent, litter cover, volume of coarse woody debris and long-term mean annual rainfall as the explanatory variables influencing the probability of buffel occurring in a patch of poplar box woodland. Given there was no 'best' model, model averaging was conducted
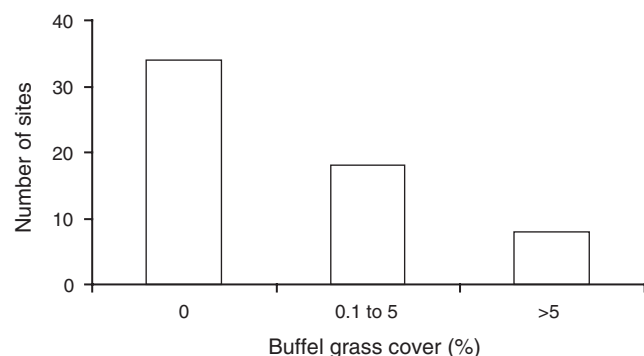
Fig. 2. Buffel grass cover per site ($n = 60$).

for the entire set of models incorporating these variables (Table 3). The AUC was calculated as 0.88 ± 0.05 (CI = 0.78–0.95), suggesting the averaged-model had good discrimination capacity. The maximum accuracy threshold at which the false positive and the false negative rates were minimised was $p = 0.45$

The relationship between the probability of buffel grass occurrence and each of the explanatory variables was negative. Based on hierarchical partitioning, the main contributing factor was the amount of native vegetation retained in the landscape (47%). Using the maximum accuracy threshold, the response curve suggests that buffel grass is unlikely to occur in a patch of poplar box if native vegetation is retained at ~30% in the surrounding landscape (Fig. 4). The second highest contributing variable (25%) was litter cover. Coarse woody debris and long-term precipitation contributed 14.6% and 13%, respectively. It is important to note that the 95% confidence intervals around the model-averaged estimate of coarse woody debris contained zero, suggesting that with the given data, this variable had no effect.

Native grass and forb species and buffel grass

There was a significant difference in number of native grass and forb species among the three buffel grass cover classes ($F_{2,57} = 4.43$, $P < 0.05$; Fig. 5a), with fewer species in the highest buffel cover class (>5%). There was no significant difference between the zero and 0.1 to 5% cover classes, with Tukey's tests showing that the significant difference was between the mean number of native ground species in the 0.1–5 and >5% classes.
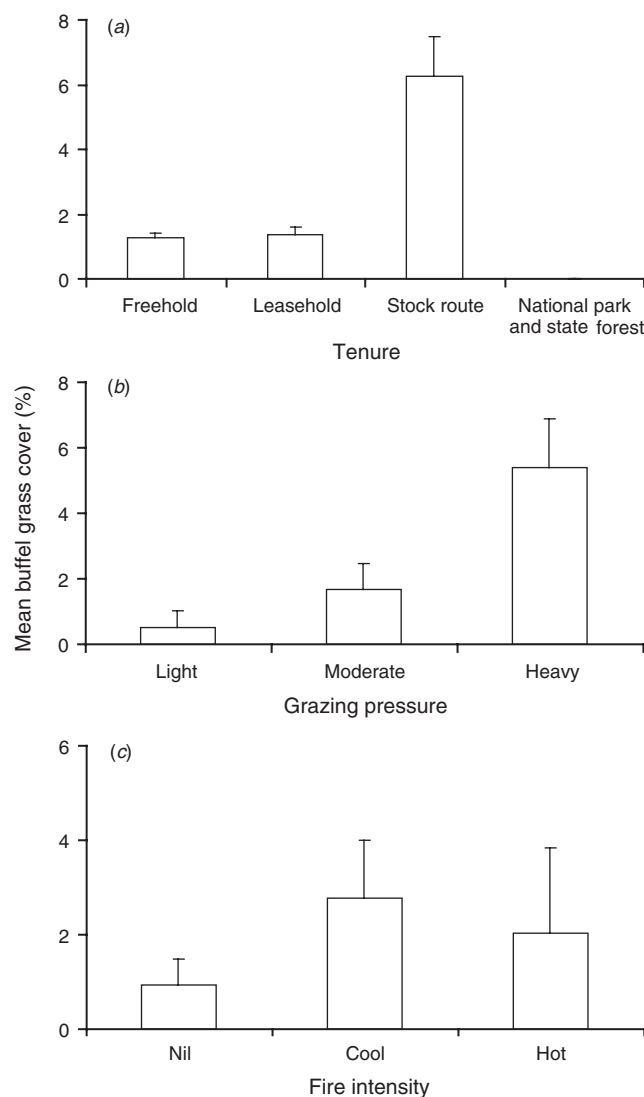

Fig. 3. Mean buffel grass cover by (*a*) tenure (freehold $n = 8$, leasehold $n = 24$, stock route $n = 19$, national park/state forest $n = 9$); (*b*) grazing pressure (light $n = 22$, moderate $n = 30$, heavy $n = 8$); and (*c*) fire intensity (light $n = 37$, moderate $n = 19$, high $n = 4$). Error bars show s.e.

Of the 30 more commonly encountered perennial grass and forb species, five had a significant correlation with buffel grass cover (Table 4). The cover of grasses *Aristida caput-medusae*,

Table 2. Results of the model selection analysis for probability of buffel grass occurrence in patches of poplar box

Values represent the maximised log-likelihood [Log(L)], number of parameters (K), Akaike information criterion corrected for small samples (AIC$_c$), AIC differences (Δ_i) and Akaike weights (w_i). Models are ranked in descending order relative to the AIC$_c$ of the model with the smallest AIC$_c$. The five highest ranked models are shown

Model	Model variables[A]	K	Log(L)	AIC$_c$	Δ_i	w_i
1	Veg1k, Litter, CWD, Precip	5	−19.002	49.114	0	0.237
2	Veg1k, Litter, Precip	4	−21.056	50.839	1.725	0.101
3	Veg1k, Litter, PFC, CWD, Precip	6	−19.164	51.913	2.798	0.058
4	Veg1k, Litter, CWD	4	−21.682	52.092	2.978	0.054
5	Veg1k, Litter, Precip, Fire	5	−20.629	52.370	3.256	0.047

[A]Variable codes and descriptions are provided in Table 1.

Table 3. Model averaged estimates, unconditional standard errors, confidence intervals and independent contribution for all explanatory variables in the buffel grass binomial model

Model variables[A]	Estimate	Unconditional SE	Upper CI	Lower CI	Contribution
Intercept	10.663	4.279	18.992	2.333	–
Veg1K	–4.821	1.560	–1.763	–7.878	47.42
Litter	–0.032	0.011	–0.010	–0.053	25.00
CWD	–0.033	0.035	0.035	–0.102	14.61
Precip	–0.014	0.005	–0.003	–0.024	12.97

[A]Variable codes and descriptions are provided in Table 1.
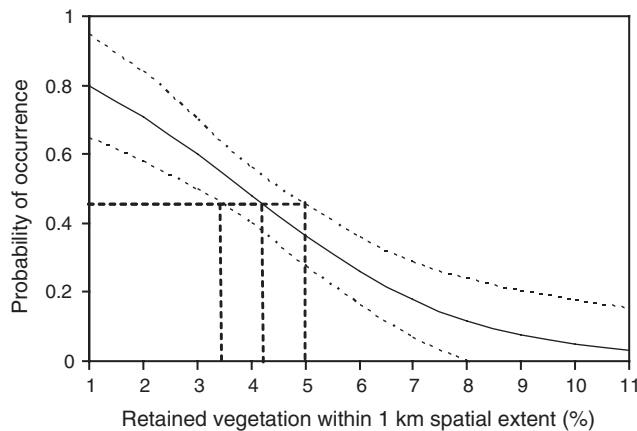
Fig. 4. Relationship between the probability of buffel grass occurrence and retained vegetation within a 1-km spatial extent. For the prediction, the other explanatory variables litter cover, precipitation and coarse woody debris were held constant at their mean. The threshold (where $p = 0.45$) is indicated. Dashed lines around the fitted response curve represent 95% confidence intervals.

Chloris divaricata and *Sporobulus caroli* each increased in cover with increased buffel grass cover. Of the forbs, *Cyperus gracilis* and *Rostellularia adscendens* had a negative response to increased buffel grass cover.
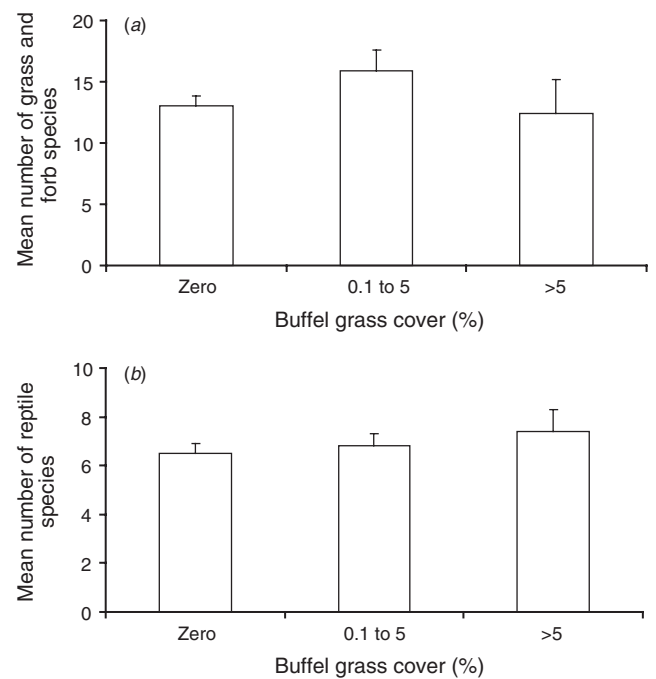
Reptile species and buffel grass

There was no difference in reptile species richness among the three buffel grass cover classes ($F_{2,57} = 1.46$, $P > 0.05$; Fig. 5b). However, of the 15 species that were detected at more than six sites, the top five most plausible models for two snakes *Demansia psammophis* and *Furina diadema*, one skink *Lerista punctatovittata*, and two geckos *Gehyra variegata* and *Oedura ocellata* included buffel grass cover as an explanatory variable (Table 5). The relationship between the probability of occurrence and buffel grass cover was positive for three species (*D. psammophis*, *F. diadema* and *G. variegata*) and negative for two species (*L. punctatovittata* and *O. ocellata*). Of the 10 local- and landscape-scale variables considered, buffel grass cover returned the highest independent contribution for *F. diadema*, *G. variegata*, *L. punctatovittata* and *O. ocellata* (Table 5).

Discussion

Buffel grass in the landscape

Buffel grass was recorded in more than 40% of the poplar box woodland patches sampled during this study, highlighting its

Fig. 5. Species richness for three buffel grass cover classes. (*a*) Mean number of native perennial grass and forb species; (*b*) Mean number of reptile species. Error bars show s.e.

capacity to invade retained woody vegetation. This substantiates earlier observations documenting the unintentional spread of buffel grass into retained woodlands of Queensland (Christie 1975a; Fairfax and Fensham 2000; Franks 2002; Ludwig and Tongway 2002; Butler and Fairfax 2003). Buffel grass occurrence in remnants was driven by landscape-scale and local-scale variables, the most influential being the amount of woody vegetation retained in the surrounding landscape. More vegetation in the landscape corresponded with a reduced likelihood of encountering buffel grass in a remnant. Presumably, two components were driving this relationship; propagule pressure and the competitive capacity of buffel grass.

Buffel grass invasiveness has predominantly been related to propagule pressure. Buffel grass has spread from sources where it has naturalised along drainage systems (Clarke *et al.* 2005), planted for erosion control (Daehler and Carino 1998) or accidental introductions from seed-contaminated soil (Dixon *et al.* 2002). However, sown pastures remain the most widely reported source of propagule pressure (Bishop *et al.* 1974; Mayeaux and Hamilton 1983; Franks 2002; Ludwig and

Table 4. Spearman rank order correlations between cover of commonly encountered native perennial grass and forb species and buffel grass cover

Probability levels are: **P < 0.05; **P < 0.01; ***P < 0.001*

Species	Spearman R	t(N–2)
Grasses		
Aristida caput-medusae	0.260	2.058*
Aristida jerichoensis var. *jerichoensis*	0.138	1.066
Aristida jerichoensis var. *subspinulifera*	–0.017	–0.137
Aristida personata	–0.058	–0.443
Aristida ramosa	–0.210	–1.636
Bothriochloa decipiens var. *decipiens*	0.001	0.007
Chloris divaricata	0.305	2.440*
Chloris ventricosa	–0.077	–0.594
Cymbopogon refractus	–0.084	–0.646
Enneapogon lindleyanus	–0.061	–0.465
Enteropogon acicularis	0.110	0.850
Eragrostis lacunaria	–0.100	–0.773
Panicum effusum	–0.097	–0.745
Paspalidium gracile	–0.046	–0.357
Sporobolus caroli	0.303	2.425*
Themeda triandra	–0.051	–0.389
Forbs		
Boerhavia dominii	0.159	1.234
Brunoniella australis	0.112	0.859
Chamaesyce dallachyana	–0.087	–0.672
Cheilanthes distans	0.018	0.140
Chrysocephalum apiculatum	–0.182	–1.415
Cyperus gracilis	–0.337	–2.727**
Desmodium varians	0.051	0.394
Einadia hastata	0.061	0.472
Einadia nutans subsp. *linifolia*	–0.126	–0.974
Evolvulus alsinoides	0.102	0.782
Glycine clandestina var. *sericea*	0.015	0.116
Lomandra multiflora subsp. *multiflora*	–0.155	–1.199
Phyllanthus virgatus	–0.060	–0.460
Rostellularia adscendens	–0.261	–2.006*

Table 5. Summary of logistic regression models describing presence or absence of reptile species where buffel grass cover was selected as an explanatory variable in the top five most credible models in Bayesian variable selection

Species	Model selection[A]	Estimate	s.e.	% I[B]
Carlia foliorum	NS	–	–	7.26
Carlia pectoralis	NS	–	–	3.24
Cryptoblepharus pannosus	NS	–	–	5.28
Demansia psammophis	S (1)	0.081	0.061	13.85
Egernia striolata	NS	–	–	2.29
Furina diadema	S (2)	0.122	0.064	23.51
Gehyra dubia	NS	–	–	1.68
Gehyra variegata	S (4)	0.129	0.065	16.16
Heteronotia binoei	NS	–	–	12.84
Lerista muelleri	NS	–	–	4.80
Lerista punctatovittata	S (2)	–0.087	0.051	14.20
Menetia greyii	NS	–	–	7.22
Menetia timlowi	NS	–	–	10.11
Morethia boulengeri	NS	–	–	5.00
Oedura ocellata	S (3)	–0.420	0.354	24.79

[A]Whether buffel grass cover was selected (S) or not selected (NS) is indicated. The number in parentheses indicates the number of models (of the top five models) buffel grass cover was included. Model-averaged estimates and standard error (s.e.) are given for species' models where buffel grass cover was selected.

[B]The percentage contribution of the buffel grass cover variable to the total explained variance for reptile species occupancy of poplar box patches that is attributable to independent effects (%I).

Tongway 2002; Butler and Fairfax 2003). In the study region, it is, thus, intuitive that increased retained native vegetation in the landscape meant less area of sown pasture from which buffel grass seed could spread and establish. This was particularly reflected in the narrow, linear strips of retained vegetation used as travelling stock routes, which contained the highest levels of buffel grass cover. Symptomatic of edge effects, increased biomass of invasive exotic grasses along edges as compared with core area of linear remnant woodlands has been well established (Milberg and Lamont 1995; Ash *et al.* 1997; Franks 2002).

Litter cover was another influential variable determining buffel grass occupancy in the study, where sites with increased litter cover had less incidence of buffel grass. Litter influences the suitability of conditions required for seedling emergence, underpinning variation in the structure and composition of plant communities through competition for resources (Facelli and Pickett 1991*a*, 1991*b*; Oswalt and Oswalt 2007). Similarly, the removal of litter in North American forests through harvesting activities has been implicated as a significant mechanism facilitating the expansion of an invasive, non-native C_4 grass (Oswalt and Oswalt 2007).

Other researchers have reported buffel grass exhibiting the capacity to colonise bare areas, but not densely vegetated areas (Cook and Dolby 1981; McIvor 2003), or areas with intact mid- or over-storey canopy cover (Franks 2002; Butler and Fairfax 2003). Under field conditions, litter has not specifically been implicated as having an effect on buffel grass spread. However, under experimental conditions, eucalypt litter cover has been shown to have a negative effect on buffel grass seedling emergence (Jackson 2004). The reasons for this remain unclear, although Jackson (2004) did identify increased pathogen activity typically associated with litter, as well as litter acting as a physical impediment to seedling growth, as reasonable explanations. Certainly, buffel grass seed predation by litter microfauna and pathogens has been observed in 16-year-old buffel grass siratro (*Macroptilium atropurpureum*) pastures, resulting in poor seedling emergence (Hacker 1989). Reduced contact with bare soil has also been implicated as a reason for poor buffel grass, and other exotic pasture species, seedling establishment in sown pastures (Cook and Dolby 1981; Cook *et al.* 1993). Jackson (2004) also found that buffel grass seedling emergence from bare soil was markedly faster than from under litter, and suggested that this would have a detrimental impact on its competitive capacity. If this is the case, then increased litter cover could reduce the capacity of buffel grass seeds to establish. This assumes that native grass species have a competitive advantage over buffel grass in littered environments, whereby they are not as hampered by increased levels of litter. Certain types of litter are known to depress germination and seedling establishment for certain species, including natives (Facelli and Pickett 1991*a*; Lenz *et al.*

2003; Maret and Wilson 2005). What we need to know is the relative capacity of buffel grass to establish in remnant woodlands with increased litter cover as compared with native grass species.

In semi-arid ecosystems the timing and amount of rainfall is a major driver of vegetative response (Friedel 1991; Clarke *et al*. 2005). Buffel grass belongs to the C_4 group of grasses which tend to respond best to summer rain. However, long-term monitoring data has shown that buffel grass responds to increases in both summer and winter rainfall, and this has allowed it to successfully compete with native herbaceous species (Clarke *et al*. 2005). Our long-term rainfall data was a coarse annual average based on calendar years rather than seasons, but it was still selected as an important variable explaining buffel grass occurrence. The averaged-model predicted a decrease in the incidence of buffel grass in poplar box fragments with increased long-term mean annual rain. This pattern is the reverse to that observed by Clarke *et al*. (2005), probably because the competitive capacity of buffel grass in the poplar box remnants was already compromised. The survival of buffel grass seedlings appear to be greatly affected by competition with established plants (McIvor 2003). The exception is during drought, when established native pasture species are weakened enough to allow successful colonisation by buffel grass, and its eventual establishment (Cavaye 1991). If so, then it would be only during times when rainfall was limited that buffel grass would get the opportunity to successfully colonise a poplar box remnant with established groundcover.

The model also predicted that coarse woody debris influenced the occupancy of buffel grass in poplar box, with more debris corresponding with a reduced probability of buffel grass occurring. However, the model confidence intervals revealed that the effect of this variable was ambiguous, and therefore this study cannot definitively demonstrate that coarse woody debris has any influence upon buffel grass occupancy. Intuitively, fire could have reduced the amount of woody debris and concurrently encouraged an increase in the distribution of buffel grass, suggesting no direct causal effect between woody debris and buffel grass occurrence but rather disparate responses by each variable to fire. However, we found no direct relationship between our fire index and buffel grass cover or with coarse woody debris volumes, suggesting either that at the time of the study fire had a minimal impact in the poplar box ecosystems or that our derived fire index was inappropriately derived. In cleared pastureland and degraded landscapes the presence of woody debris has been shown to aid colonisation of buffel grass (Bishop *et al*. 1974) and other vegetation (Ludwig and Tongway 1996) through mechanical effects such as seed, soil and moisture trapping. The mechanism that apparently benefits buffel grass establishment in an open paddock is likely to also assist native ground cover flora in a wooded ecosystem, further compromising the colonising capacity of buffel grass through competition. Indeed, in the poplar box woodlands in the study region, native grass and forb cover does appear to increase with more coarse woody debris (T. J. Eyre and J. Wang, unpubl. data).

Further, soil nitrogen did not appear to have a significant effect upon buffel grass presence in poplar box woodlands. Soil texture and fertility, in particular increased phosphorous and pH levels, have been identified as major factors influencing the efficacy of buffel grass spread into adjacent ecosystems (Christie 1975*b*; Christie and Moorby 1975; McIvor 1984; Cavaye 1991).

Phosphorous was not sampled during this study, and may contribute to reducing the unexplained variation in the model. It is recommended that future work investigating buffel grass spread incorporate more soil measures than were conducted by our study.

Native grass and forb species and buffel grass

We detected significant relationships between five plant species and buffel grass, and of these only two forb species displayed a negative response. Compared with other studies, the level of response between native species and buffel grass appears underwhelming, and this may reflect the fact that sampling occurred during a very low rainfall period. During our study buffel grass cover averaged 7% ($\pm$0.28 s.e.) of total cover at sites where it was recorded. This is relatively minor when compared with levels of cover recorded in highly fragmented poplar box woodlands to the west of our study area (average of 20% cover; Franks 2002) and in remnant gidgee (*Acacia cambagei*) and brigalow (*Acacia harpophylla*) woodland north of our study region, (average of 30% cover; Butler and Fairfax 2003). Therefore, it is possible that the levels of buffel grass cover were too low to have a discernible impact on most species.

Impacts of buffel grass establishment upon flora can be direct or indirect, influencing the structural, compositional and functional aspects of an ecosystem (Friedel *et al*. 2006). As a direct impact, the superior competitive capacity of established buffel grass for water and nutrients is one reason why the incidence of certain plant species decreases with increased buffel grass cover. Clarke *et al*. (2005) showed buffel grass directly influenced native grasses by reducing winter growth response as well as the summer growth response in forbs. Alleloepathy in buffel grass has also been implicated. Leachates from buffel grass leaves and roots have been shown to significantly reduce seed germination rates in some herbaceous species under experimental conditions (Cheam 1984*a*, 1984*b*; Nurdin and Fulbright 1990). Phytotoxicity appears to be particularly concentrated in the topmost layer in the soil profile (Cheam 1984*b*). This has particular ramifications for species whose seeds typically occur towards the soil surface.

Indirect impacts of buffel grass establishment, through alteration of functional components through changed fire and grazing regimes, have been more convincingly implicated by field studies as having a negative effect upon flora species (e.g. Franks 2002; Butler and Fairfax 2003). The two forb species that showed a decreaser response to buffel grass, *C. gracilis* and *R. adscendens*, were also shown by Fairfax and Fensham (2000) to be less abundant in pasture with more than 10% buffel grass cover compared with uncleared native pasture land. They appear to be species sensitive to disturbance, having been identified elsewhere as stock grazing decreasers (Fensham and Skull 1999; McIntyre *et al*. 2003), and in the case of *R. adscendens*, intolerant to soil disturbance and enrichment associated with exotic grass cultivation (McIntyre and Martin 2002). Similarly, the three grass species, *Aristida caput-medusae*, *Chloris divaricata* and *Sporobulus caroli* whose cover increased with buffel grass cover are each well known as grazing increasers (Henry *et al*. 1995). Therefore, our results probably reflect an ecological response to a gradient in grazing intensification, rather than any direct

competitive association, such as allelopathy, with buffel grass. Our study was not specifically designed to address the impact of increasing buffel grass cover upon floristic species composition, and this type of study is urgently required to provide more conclusive outcomes regarding the potential impact of buffel grass on native species in remnant woodlands.

Reptile species and buffel grass

There is an extreme paucity of research identifying impacts of buffel grass on reptiles, or fauna in general. The only other published paper relating buffel grass cover to reptile species suggested increased buffel grass cover was detrimental for one species, *Cryptoblepharus pannosus* (syn. *C. carnabyi*) (Ludwig *et al*. 2000). Although we found no response for this particular species, our results did show that buffel grass influenced several other reptile species, suggesting a potential shift in composition and abundance of reptiles with the spread of buffel grass into remnant poplar box patches.

Of the set of variables investigated, buffel grass cover was the most influential variable for four of the more common species, with *F. diadema* and *G. variegata* each exhibiting an 'increaser' response, and *L. punctatovittata* and *O. ocellata* each displaying a 'decreaser' response. With the exceptions of *G. variegata* and *L. punctatovittata*, little is known of the ecology and habitat specialisation of these species. It is therefore difficult to ascertain the ecological reasons why these species displayed variable responses.

Gehyra variegata is a generalist arboreal gecko species, although it is also widely known to forage and utilise ground habitat (Moritz 1987; Henle 1990). It is also highly territorial, and capable of colonising vacant and highly disturbed habitat (Moritz 1987; Kitchener *et al*. 1988; Sarre *et al*. 1995). We therefore reason that an increase in ground habitat cover provided by buffel grass tussocks may provide an advantage for an opportunistic species such as *G. variegata*. The small elapid snake *F. diadema* is likewise considered to have broad habitat requirements; even tolerating suburbia in some situations (Wilson 2005). It may, thus, be responding to the structural aspects of the tussocks of buffel grass, particularly where coarse woody debris is also present (T. J. Eyre and M. F. Venz, unpubl. data).

Consequently, more specialised species occupying similar habitat niches, such as the arboreal gecko *O. ocellata*, may become displaced. Parallel increaser and decreaser effects were seen in *G. variegata* and *O. ocellata* congener *O. reticulata* in remnant woodlands of the Western Australian wheatbelt (Sarre *et al*. 1995). Sarre *et al*. (1995) found that habitat quality (measured by the number of large eucalypts) influenced ability of *O. reticulata* to persist in the remnants it shared with *G. variegata*. If a decline in habitat quality is similarly significant for *O. ocellata* in the present study, it is difficult to explain how buffel grass could be a direct agent. Decreasing numbers of *O. ocellata* here are more likely to be attributable to competitive interactions with *G. variegata*, or correlated with other changes in habitat quality that allow buffel grass to proliferate, such as increasing habitat fragmentation.

The fossorial skink *L. punctatovittata* prefers sandy to loamy soils but can exist on heavier soils where there is a thick mat of leaf litter under the base of trees and shrubs (Wilson and Knowles

1988; Wilson 2005). One of the few ecological studies on this species identified microhabitat and food to be the most important determinants for niche partitioning (Henle 1989). Buffel grass may influence the microhabitat quality of *L. punctatovittata* via physical means (i.e. thick root mats) or via soil nutrient depletion (Ibarra-Flores *et al*. 1999) impacting on its primary food source of insect larvae (Henle 1989). However, owing to the dearth of information on reptile species habitat requirements means we are limited to speculation only. Similar to our conclusions regarding buffel grass and floristic species, more in-depth research on reptile community composition and distribution along a gradient of buffel grass cover is clearly required.

Management implications

This study demonstrated that an increase in grazing pressure corresponded with an increase in the cover of buffel grass, confirming the observations by Franks (2002) and Ludwig and Tongway (2002). The 'positive feedback' between buffel grass spread and hot fires described by Butler and Fairfax (2003) appears to be just as relevant to grazing in the poplar box remnants. Conversely, fire did not appear to have much influence on buffel grass establishment. This was not entirely unexpected, as in these ecosystems continuous grazing regimes coupled with highly variable rainfall and extended dry conditions, as experienced during the study, result in limited fuel loads (Hall *et al*. 1994). Indeed, in the region fire has been discouraged as a management tool in buffel grass pastures due to loss of pasture nutrients and consequent reduction in cattle production (Mannetje *et al*. 1983). However, the link between fire management, coarse woody debris and buffel grass is worthy of further investigation in the region.

The competitive capacity of buffel grass was enhanced in the more highly modified landscapes of our study area, with an increased presence of buffel in eucalypt woodland remnants with less than 30% woody vegetation retained in the landscape. Andrén (1994) advocated a theoretical threshold of between 10 and 30% retained habitat in the landscape, at which major ecological dysfunction occurs and species are lost from the landscape. In Australia, the 30% vegetation retention threshold has been used as a broad principle for sustainable grazing land management at the property scale (McIntyre *et al*. 2000; McAlpine *et al*. 2002). Others have provided empirical evidence that supports retention of >30% vegetation in the landscape for the maintenance of biodiversity (Radford *et al*. 2005) and productivity (Walpole 1999) values. Whether this threshold will hold for other vegetation communities, in particular those with edaphic features preferred by buffel grass e.g. brigalow, remains to be tested.

In the fragmented landscapes of semi-arid Queensland in the Brigalow Bioregion, the 30% woody vegetation retention threshold provides an indicative target for the restoration of cleared habitat, at least for eucalypt-dominated ecosystems. The threshold is particularly pertinent if grazing and fire are managed at levels that maintain sufficient litter cover and do not compromise the competitive advantage of native pasture species. Thus, the retention of regrowth native vegetation to obtain at least 30% native woody vegetation cover in the landscape, and reducing grazing pressure within remnants may be the most

effective approaches to minimising the spread of buffel grass into remnant poplar box vegetation in this region.

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