Managed livestock grazing is compatible with the maintenance of plant diversity in semidesert grasslands

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Abstract. Even when no baseline data are available, the impacts of 150 years of livestock grazing on natural grasslands can be assessed using a combined approach of grazing manipulation and regional-scale assessment of the flora. Here, we demonstrate the efficacy of this method across 18 sites in the semidesert Mitchell grasslands of northeastern Australia. Fifteen-year-old exclosures (ungrazed and macropod grazed) revealed that the dominant perennial grasses in the genus *Astrebla* do not respond negatively to grazing disturbance typical of commercial pastoralism. Neutral, positive, intermediate, and negative responses to grazing disturbance were recorded amongst plant species with no single life-form group associated with any response type. Only one exotic species, *Cenchrus ciliaris*, was recorded at low frequency. The strongest negative response was from a native annual grass, *Chionachne hubbardiana*, an example of a species that is highly sensitive to grazing disturbance. Herbarium records revealed only scant evidence that species with a negative response to grazing have declined through the period of commercial pastoralism. A regional analysis identified 14 from a total of 433 plant species in the regional flora that may be rare and potentially threatened by grazing disturbance. However, a targeted survey precluded grazing as a cause of decline for seven of these based on low palatability and positive responses to grazing and other disturbance. Our findings suggest that livestock grazing of semidesert grasslands with a short evolutionary history of ungulate grazing has altered plant composition, but has not caused declines in the dominant perennial grasses or in species richness as predicted by the preceding literature. The biggest impact of commercial pastoralism is the spread of woody leguminous trees that can transform grassland to thorny shrubland. The conservation of plant biodiversity is largely compatible with commercial pastoralism provided these woody weeds are controlled, but reserves strategically positioned within water remote areas are necessary to protect grazing-sensitive species. This study demonstrates that a combination of experimental studies and regional surveys can be used to understand anthropogenic impacts on natural ecosystems where reference habitat is not available.

Key words: *exclosures; grassland conservation; grazing disturbance; Mitchell grassland; resilience; semidesert grassland; species diversity.*

Introduction

Predictions that the biota of semiarid rangelands will be resilient to grazing (Brown and McDonald 1995) conflict with expectations that managed livestock grazing will have substantial impacts (Fleischner 1994). The former position is predicated on the assumption that grazing is part of the evolutionary history of rangelands, and that these ecosystems are in nonequilibrium with grazing pressure because of the variable climate (Ellis and Swift 1988, Briske et al. 2003). When rainfall is abundant, plant resources are sufficiently bountiful that impacts are minimal. This model

also proposes that the plant species are well adapted to drought and are more likely to survive than the animals that rely on their consumption.

The expectation of substantial impacts from livestock grazing is founded on the expectation that commercial livestock grazing is of much greater intensity than herbivory over evolutionary timescales. This is consistent with state-and-transition models recognizing thresholds between condition states that can be breached by the impacts of grazing (Friedel 1991, Laycock 1991). The processes causing the transitions from one state to another are not symmetrical; for example, intense grazing could eradicate the dominant perennial grasses in five years or other grazing-sensitive species, but they would not necessarily recover after five years reprieve.

The collation of global studies of grazing disturbance have generalized grazing impacts depending on site

productivity and the evolutionary exposure of the ecosystem to grazing disturbance (Milchunas et al. 1988, Cingolani et al. 2005). High-productivity ecosystems with a short evolutionary exposure to ungulate grazing are predicted to be susceptible to steep declines in the abundance of the dominant species. An initial increase in plant diversity with intermediate grazing disturbance has been proposed (Cingolani et al. 2005), followed by sharp decline, together with invasion by exotic species, as grazing intensifies such as might occur with commercial pastoralism. For low-productivity ecosystems with the same evolutionary history, plant diversity is predicted to decline even more steeply and is less reversible. In Australian ecosystems with limited exposure to grazing, it follows that there may be species that are poorly adapted to grazing under managed pastoralism (Lunt 1997), and grazing is listed as a threatening process for 36 out of 70 plant species identified as rare and threatened from grassy ecosystems (Leigh et al. 1984).

The systematic assessment of grazing impacts on biodiversity is difficult because of the large scale of the ecosystems involved and because reference areas subject to light grazing over the long term are rare (e.g., Rummell 1951). Long-term exclosures can provide important insights, but only generate statistical power for a small subset of the flora, and will not reveal the impact on the most grazing-sensitive elements of a flora that have already been eradicated with no capacity for recovery (Valone et al. 2002, Seymour et al. 2010, Fensham et al. 2011a). An approach that includes grazing manipulation in combination with regional-scale assessment may generate important insights.

The mid-latitude arid and semiarid environments represent some of the last relatively intact grassland, with much less conversion to intensive agriculture than temperate grassland (Hoekstra et al. 2005). These "semidesert grasslands" are mostly subject to rangeland pastoralism where densities of domestic livestock are substantially elevated compared to the evolutionary background. Mitchell grasslands are semidesert grasslands (Fig. 1) occupying vast fertile plains in semiarid and arid regions of northern Australia. These plains are intersected by ephemeral drainage lines and are remote from natural permanent water sources (Fig. 1). It can be assumed that they were subject to minimal mammalian grazing even prior to the Pleistocene megafauna extinctions (Johnson 2006). Since European settlement, thousands of artificial water sources including artesian bores and earth storage tanks have allowed for greatly amplified and expanded grazing pressure (James et al. 1999). Substantial negative impacts on plant diversity could be predicted in the Mitchell grasslands given they have not previously been subject to substantial mammalian grazing disturbance.

This study aimed to evaluate the following predictions for the consequences of livestock grazing on botanical diversity after 150 years of managed pastoralism in the Mitchell grasslands of northern Australia: (1) Changes in livestock grazing regimes will change plant community composition (Milchunas et al. 1988); (2) livestock grazing will favor annual species and disadvantage perennial species (Díaz et al. 2007); (3) dominant grass species will decline in abundance with increasing intensity of grazing disturbance, native herbivores, and livestock (Sutton and Morgan 2009); (4) exotic species will proliferate under livestock grazing because the native grasses will be less adapted to this newly imposed selected pressure, nutrient addition, and compacting of the soil by hard-hooved animals (Cingolani et al. 2005); (5) a substantial set of plant species, particularly those known to be palatable (Lunt et al. 2007), will show declines over time in herbarium records with the introduction of livestock grazing; and (6) rare species will have generally declined because of livestock grazing (Leigh et al. 1984).

These predictions are consistent with findings of local studies either from the Mitchell grasslands (Hall and Lee 1980, Orr and Phelps 1994) or from related grassland ecosystems on similar soils in more mesic climates (Fensham 1998, Fensham et al. 1999, Lewis et al. 2008).

A network of 15-year-old grazing exclosures that include exclusion of all large native and exotic herbivores, livestock exclusion, and grazing management typical of commercial pastoralism is employed to test predictions 1–4 above (Fig. 2). There are numerous examples where rangelands exhibit minimal recovery from a presumed degradation state after long periods of grazing protection (Laycock 1967). However, one of the few long-term studies with floristic baseline data did reveal substantial recovery after 15 years (Fuhlendorf and Smeins 1997). Exclosures may suggest that some species without adequate representation for statistical analysis are declining in the grazed landscape. Furthermore, rare species in the broad landscape may have declined because of grazing. Plant species in the first category are identified by developing geographical, morphological, and ecological characteristics consistent with grazing sensitivity (prediction 5). A similar analysis is then applied to the entire recorded flora of Mitchell grasslands to identify rare species that may be declining from grazing (prediction 6).

METHODS

Study area

The Mitchell grasslands, named after the dominant and endemic genus Mitchell grass (*Astrebla*), occupy 54 million ha in a discontinuous arc across eastern and northern Australia on clay- and silt-rich soils formed from fine-grained sediments and basalt or on alluvial plains, where mean annual rainfall is 200–550 mm (Fig. 1) falling mostly in summer. The soils are classified as vertosols because of their uniform profiles and tendency to self-mulch and crack on drying (Isbell 1996) and their high fertility (Orr 1975). Our study was conducted in the northeastern realm of the Mitchell grasslands in the
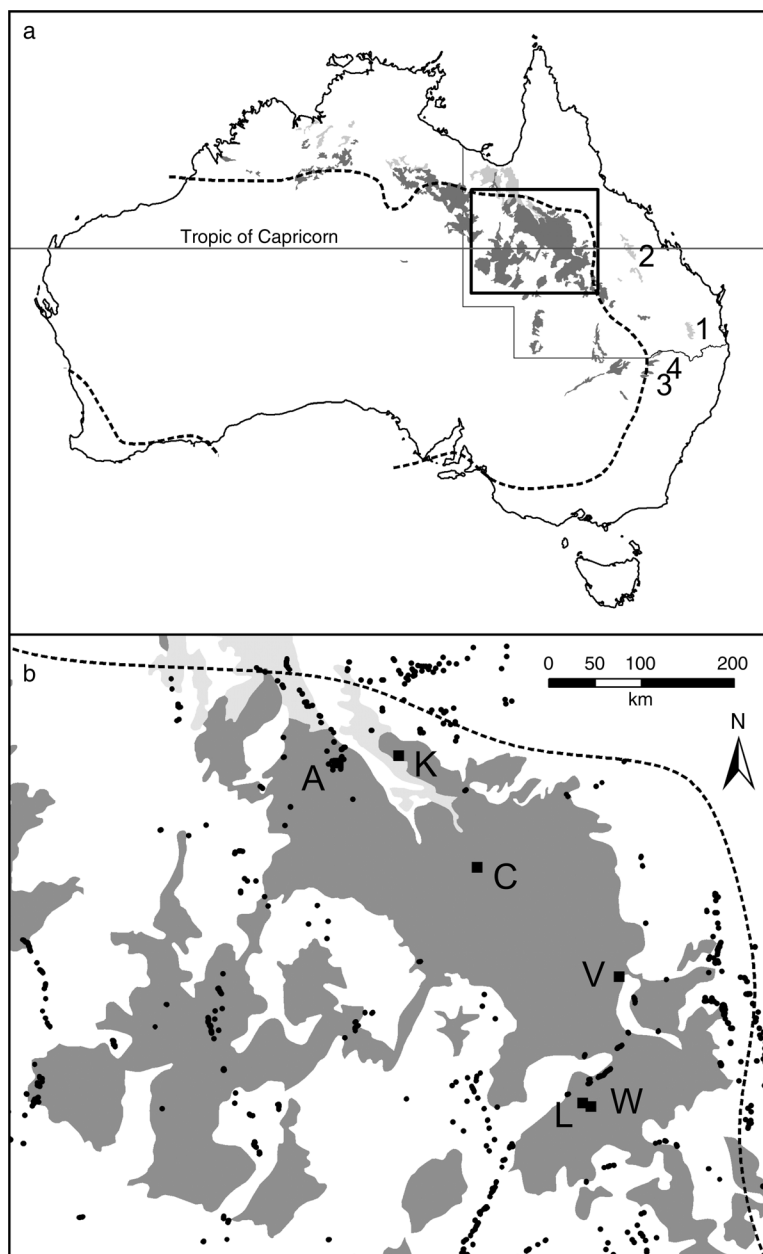
FIG. 1. (a) The distribution of *Astrebla*-dominated Mitchell grassland in Australia (dark gray) and *Dichanthium*-dominated blue grassland (light gray). The 500-mm rainfall isohyet is identified by the dashed line. Queensland is outlined by the thin black line. The location of other relevant studies are identified as: 1, Fensham (1998); 2, Fensham et al. (1999); 3, Lewis et al. (2008); and 4, Lewis et al. (2009). The broad survey by Fensham et al. (2000) encompassed the Mitchell grasslands within Queensland. The location of the detailed map (b) is also indicated by the box outlined with a bold black line. (b) Location of the six properties (black squares), each with three exclosures included in this study: A, Alva Downs; K, Kilterry; C, Cassilis; V, Verastan; L, Loongana, and W, Whitehill. The permanent natural waters are identified with black dots (after Fensham et al. 2011b).

state of Queensland, and we surveyed 18 sites all within separate paddocks (0.9–10.4 km apart) on six properties (Fig. 1). Mean annual rainfall as determined from modeled data (Jeffrey et al. 2001; SILO, data *available online*)[5] varies from 376 mm at Whitehill to 467 mm at

Kilterry, with 75% and 89% of the rainfall occurring in the wettest six months at the driest and wettest sites, respectively.

At each site there are two adjacent 45 × 45 m exclosures: a five-wire exclosure designed to exclude sheep and cattle but not kangaroos (hereafter the "macropod grazed") and a 2 m high netting fence (50-

Fig. 2. (a) Grazed Mitchell grassland after abundant summer rainfall dominated by *Astrebla*, demonstrating the low basal area and large inter-tussock spaces, and (b) open-grazed plot adjoining ungrazed exclosure at Verastan.

cm gauge) designed to exclude all mammalian herbivores greater than 200 g (hereafter the "ungrazed"). Areas outside the fences are designated as "open grazed." The exclosures were established between July and December 1994.

Grazing history was obtained through landholder interviews and indicates that some sites are grazed by cattle and others by sheep at a range of average intensities (Appendix A). Average stocking rates are difficult to estimate because all managers reported substantial variation, including periods of rest without stock, particularly during dry periods. However, the values reported, 0.07–0.12 cattle equivalents/ha, are typical of commercial pastoralism that is the dominant land use across the Mitchell grasslands (Scattini et al. 1988). Reported densities of kangaroos were low (~7 individuals/km^2) at the nine northern exclosures and medium to high at the southern exclosures (~18 individuals/km^2). Kangaroo densities are almost certainly higher at these sites with the addition of water and predator (dingo) control than they were in the pre-pastoral landscape (Newsome 1975). Using a conserva-

tive assumption that kangaroo densities were half those at present, and established equivalence conversions between kangaroo, cattle, and sheep (Appendix A), the combined kangaroo–livestock grazing intensity is currently between 21 and 88 times more intense than before pastoralism.

In order to describe the climatic conditions prior to sampling, modeled rainfall data was used to calculate the following: mean annual rainfall, rainfall seasonality (coefficient of variation of average monthly values), summer rainfall prior to sampling (October 2008–March 2009), and winter rainfall prior to sampling (April 2008–September 2008).

Grazing treatments

Sampling was conducted in April 2009 after substantial summer rainfall. Twelve plots were established within each of the two fenced treatments and in the open-grazed areas within 5 m of the perimeter of the exclosures. The plots were established at regular intervals, but the actual locations varied to ensure constancy of soil type and stone cover, to avoid trampled areas around the perimeter of the fences and areas where "tumbleweeds" had gathered along the fence lines.

The final data set comprised 648 plots (12 pseudo-replicates × 3 treatments × 18 sites). Species presence was recorded from within subplots of increasing size within a 7 × 2 m plot. Species present in the first 2 × 0.33 m subplot were assigned an abundance score of 4, species present in the next 2 × 0.67 m section were assigned an abundance score of 3, species present in the next 2 × 2 m section were assigned an abundance score of 2, and the final 2 × 4 m section an abundance score of 1. This method, involving unrepeated scoring of species presence, has been demonstrated to provide the best return (robust measure of species density) for effort, thereby allowing for a relatively large quadrat size (Morrison et al. 1995). The method does not accurately reflect abundance in terms of biomass, but discriminates abundance in terms of density unless a species density is consistently higher than one individual per smallest subplot (0.66 m^2). Plant nomenclature follows Bostock and Holland (2010). Infraspecific taxa were not recognized with the exception of *Dichanthium sericeum* var. *polystachyum* and *Dichanthium sericeum* var. *sericeum*, which are annual and perennial, respectively. *Iseilema fragile*, *I. macratherum*, and *I. vaginiflorum* were not distinguished. Voucher specimens of all species were lodged at the Queensland Herbarium (Brisbane, Australia).

Herbaceous biomass samples were collected from 12 25 × 25 cm frames positioned between the floristic plots. These samples mostly contained live material, but included a small fraction of dead litter. In order to allow for underlying soil influences that may be independent of grazing treatment, 12 surface (1–5 cm) soil cores were collected adjacent to each of the 12 plots,

bulk-sampled, and then subsampled to provide one sample for each site–treatment combination. Particle size analysis of soils was conducted using dispersion to separate coarse- and fine-sand fractions and the hydrometer method to quantify silt and clay content (Thorburn and Shaw 1987). Soil pH was determined following the method of Rayment and Higginson (1992).

Multivariate analysis

An ordination analysis was prepared to discriminate the relative magnitude of between-treatment effect and between-site effects on species composition. Replicated plots were grouped at the treatment scale, where species abundance was represented as a frequency of occurrence in the 12 2 × 7 m plots. These data were ordinated using non-metric multidimensional scaling in two dimensions with no transformation or standardisation of abundance data using the Bray-Curtis dissimilarity measure and other default settings in DECODA (Minchin 1991). ANOSIM was used to detect differences in species composition between grazing treatments.

Statistical modeling

Plot-level species richness (14 m^2), abundance (sum of abundance scores), and Shannon-weaver diversity were calculated overall and separately for each of four major life-form groups: annual grasses, annual herbs (excluding Poaceae), perennial grasses, and perennial herbs. To analyze the effects of the different grazing treatments on these diversity measures, we developed linear mixed-effects models (hereafter LMEMs) using R.2.13.2 and the R package nlme (Pinheiro et al. 2012).

Each biodiversity surrogate was modeled as a function of the three grazing treatments (fixed effect) with a nested random effects structure of (1) property, (2) site within property, and (3) plots within site within property. All response variables were approximately normally distributed, except perennial grass richness, which was square-root transformed. At the lowest level of the model, plot, we included a grouping factor to represent spatial relationships between plots within the exclosures and plots in the open that were located around the perimeters of the exclosures. To account for this spatial dependency among observations, we used the exponential correlation structure function, corExp, based on the Euclidean distance between x and y values (plot coordinates) with a range of 17 and a nugget of 0.7. In all cases, corExp improved model fits as assessed by comparing models fitted with restricted maximum likelihood with likelihood ratio tests and diagnostic plots (Pinheiro and Bates 2004). Wald F statistics were then used to assess the significance of the fixed effect within the LMEMs (Pinheiro and Bates 2004).

Species responses to grazing treatment were evaluated if they were present in at least 10 plots at more than two sites, and with a frequency greater than five at the site scale. Overall, 34 species (24% of species surveyed) met our criteria, allowing us to model their response to grazing treatments and environmental variables. We modeled changes in species abundance within the treatments using generalized linear mixed-effects models (GLMEMs) with a Poisson error distribution, which were fitted using maximum likelihood and the lme4 package within the R program (Bates and Maechler 2012).

As revealed by the ordination analyses, the importance of several environmental variables was evaluated as additional fixed effects, i.e., mean annual rainfall, previous six months of summer rainfall, previous six months of winter rainfall, rainfall seasonality, clay content, silt content, fine-sand content, coarse-sand content, total sand content, and soil pH. Environmental variables were standardized by subtracting mean values and dividing by standard deviations (except soil pH and rainfall seasonality). An information-theoretic model selection procedure was used to compare the predictive power of models with different fixed effects using ΔAIC_c, which is preferable over AIC for small sample sizes (Johnson and Omland 2004). Environmental variables were considered important predictors if inclusion led to a $\Delta AIC_c \geq -4$, as a conservative cutoff for identifying competing models (Burnham and Anderson 2002, Grueber et al. 2011). Multiple comparisons of means (Tukey contrasts) were made using the multcomp package, an algorithm for simultaneous inference tests for parametric models including LMEMs and GLMEMs (Hothorn et al. 2008).

Nonsignificant "decreaser" species

Some species in the Mitchell grasslands may have declined substantially with pastoral grazing, but remain relatively abundant. We assumed that these species could be exhibiting negative responses to grazing in the exclosures, although not necessarily at levels that are statistically significant. Potential candidates were identified as those species occurring at more than one site where the combined average abundance in the ungrazed and macropod-grazed treatment was greater than 140% of the average abundance in the open-grazed treatment. The potential sensitivity of species to grazing was based on seven morphological, geographical, population structure, and ecological characteristics (Table 1). Species that were determined to be sensitive to more than three of these characteristics were identified as grazing "decreaser" species.

Regional flora assessment

Another analysis was conducted to assess the Mitchell grassland flora, not represented in the exclosures, which may be threatened by livestock grazing. Botanical collection in Mitchell grasslands extends back to the first European explorer Major Thomas Mitchell (Barker and Barker 1990) and includes substantial effort prior to pastoral settlement and does not indicate any species that are extinct. Sites that have not been grazed extensively by livestock for use as reference areas are

TABLE 1. Assumptions pertaining to species characteristics regarding grazing sensitivity and the sections of this study to which they were applied.

Characteristic	Assumption regarding grazing sensitivity	Application
Life-form	perennial more than annual	assessment of decreaser species, regional assessment of flora
Geographic range	$<100\,000$ km^2 more than $>100\,000$ km^2	assessment of decreaser species
Occurrence in habitats outside Mitchell grassland	restricted to Mitchell grassland more than occurs in other habitats	assessment of decreaser species, regional assessment of flora
Frequency in 609 sites from a broad survey of Mitchell grasslands in Queensland (Fensham et al. 2000)	≤ 10 more than >10	assessment of decreaser species
Trends through time of herbarium collections (Appendix B)	flat trend more than steep trend relative to the trend through time in overall Australian collections	assessment of decreaser species
Grazing sensitivity from other studies (see Table 3)	decreasers more than other responses	assessment of decreaser species
Palatability as determined from literature (Cunningham et al. 1981, Milson 2000)	palatable more than non-palatable species	assessment of decreaser species
Population estimate (Appendix C)	$<100\,000$ more than $>100\,000$ individuals	regional assessment of flora
Palatability as determined by selective grazing from field observations	palatable more than non-palatable species	regional assessment of flora
Irruptive population dynamics (nonwoody species only; based on multiple visits to individual localities after rain)	non-irruptive more than irruptive populations dynamics	regional assessment of flora
Regenerating populations, at least 50% of population <50 cm tall (woody species only)	populations without more than populations with regeneration	regional assessment of flora
Positive response to disturbance (abundant on roadsides; where biomass has been substantially depleted by grazing	no evidence of disturbance response more than favoring disturbance	regional assessment of flora

difficult to find. Because there are no data regarding the pre-livestock grazing composition of our plots or the wider landscape, the 433 plant species known to Mitchell grasslands in Queensland were each assessed on their potential sensitivity to grazing using herbarium specimen notes, online herbaria, and expert knowledge and designated as: (1) known from >10 populations in Mitchell grasslands and other vegetation types subject to commercial rangeland pastoralism with an estimated total population size of >1 million (M) or (2) rare or poorly known species potentially threatened by grazing. We cannot assume that species in category 1 are not being reduced by grazing, but the arbitrary figure of 1 M is used to discriminate the species that may be under imminent threat of grazing. Random searches in Mitchell grasslands were conducted for these rare species at 345 locations, and population estimates derived on the number of plants located in the search area factored upwards for their area of occupancy in the Mitchell grassland (Appendix C). The searches also established evidence relating to the grazing sensitivity of the species based on morphological, population structure, and ecological characteristics (Table 1).

Following field survey, the rare or poorly known species were classified as grazing sensitive, not grazing sensitive, or data deficient. A woody species classified as "not grazing sensitive" has regenerating populations in the grazed landscape. A nonwoody species classified as "not grazing sensitive" has >1 M plants in the grazed landscape in more than five populations, is not selectively grazed, and may also have exhibited a positive response to disturbance. Species not meeting those criteria were classified as either "grazing sensitive" if, after substantial population surveys, these criteria could not be satisfied, or as data deficient if inadequate data ensued from the surveys.

RESULTS

Grazing treatments

After 15 years, herbaceous biomass ranged across treatments and sites from between 0.42 and 4.53 t/ha (1 t [metric ton] = 1 Mg). Differences between ungrazed treatments and macropod-grazed treatments were generally consistent with landholder interpretations of macropod densities, i.e., sites with high macropod densities had relatively low herbaceous biomass in macropod-grazed treatments compared to ungrazed treatments (Fig. 3). Herbaceous biomass was generally lower in open-grazed treatments (Fig. 3).

The data set from the exclosures consisted of 141 species (Appendix D for species list and frequency data), representing 33% of the Mitchell grassland flora in the state of Queensland, and included 21 annual grasses, 56 annual herbs, 17 perennial grasses, 43 perennial herbs, and four trees and shrubs. Mean annual rainfall, rainfall coefficient of variation, coarse sand, and clay content
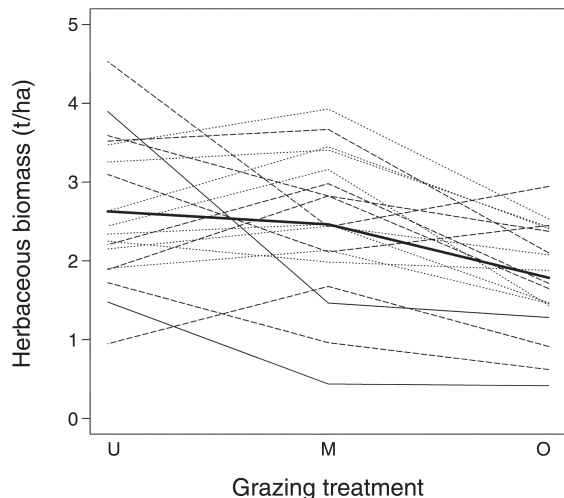
FIG. 3. Mean herbaceous dry biomass from 12 25 × 25 cm frames between grazing treatments (U, ungrazed; M, macropod grazed; O open grazed) for the 18 sites (1 t [metric ton] = 1 Mg). "Ungrazed" exclosures were designed to exclude all mammalian herbivores greater than 200 g; exclosures that excluded sheep and cattle, but not kangaroos, were termed "macropod grazed"; and areas outside the fences were designated "open grazed." Macropod densities from landholder interview (Appendix A) are assigned low (dotted lines), medium (dashed lines), and high (thin solid lines), and the mean value across all sites is indicated (bold solid line).

were much stronger correlates through a two-dimensional ordination space than grazing (Fig. 4), indicating that, in the year of sampling, these factors were more important determinants of species composition at the regional scale than grazing effects.

At all but three of the 18 sites, there were significant differences in species composition between the grazing treatments, and differences were significant ($P < 0.05$) between ungrazed and open-grazed treatments at all sites (Appendix E for ANOSIM results).

Total richness and diversity were not significantly different between any grazing treatments (see Appendix F for all LMEM results). Overall abundance was lower in the open-grazed treatment than the other treatments, but only marginally significant ($F_{2,52} = 3.00$, $P = 0.06$). Richness of annual grasses was lower in the ungrazed treatment than the others ($F_{2,52} = 3.41$, $P = 0.04$; Fig. 5), and abundance of annual grasses ($F_{2,52} = 3.98$, $P = 0.02$) was lower in the ungrazed treatment than the open-grazed treatment (Fig. 5). Perennial-herb abundance was significantly higher in the macropod-grazed treatment than the open-grazed treatment ($F_{2,52} = 5.06$, $P = 0.01$; Fig. 5), while annual-herb abundance was significantly lower in the open treatment than the other treatments ($F_{2,52} = 3.70$, $P = 0.04$; Fig. 5). We found no significant differences in abundance, richness, or diversity between grazing treatments for any of the other life-form groups.

Seven of the 34 most common species had statistically significant responses to the grazing treatments (Table 2). The annual grasses *Dactyloctenium radulans*, *Panicum laevinode*, and the annual herb *Streptoglossa odorata* had a positive response to grazing disturbance. The annual grass *Chionachne hubbardiana* and the perennial grass *Dichanthium sericeum* var. *sericeum* had a negative response. The annual grasses *Digitaria ctenantha* and *Eragrostis tenellula* and the perennial herb *Ipomoea*
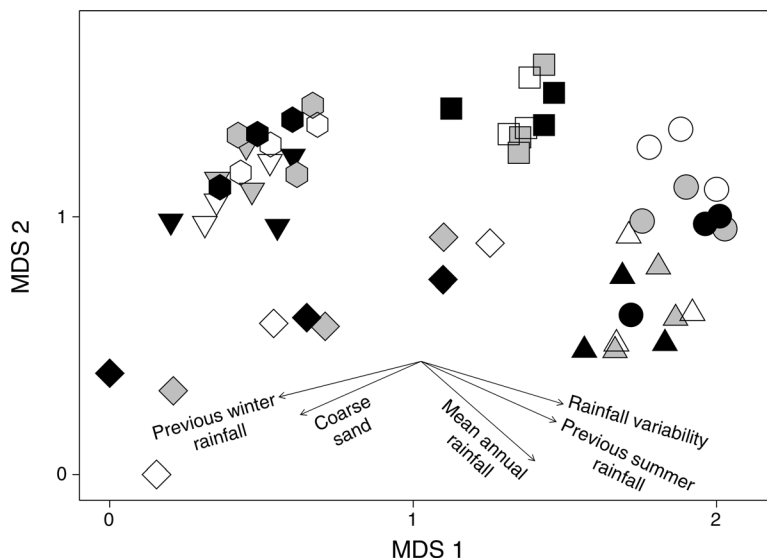

FIG. 4. Two-dimensional ordination diagram with properties identified by the shape of the symbols and annotated (multidimensional scaling; MDS). Grazed treatments are identified as ungrazed (black symbols), macropod grazed (gray symbol), and open grazed (white symbol). Individual sites are clustered, but cannot always be clearly determined because of overlap with other sites. The direction of the most significant vectors is indicated with their strength proportional to the length of the arrows. Only vectors with a maximum R value greater than 0.80 are indicated. Other factors that were not included with their maximum R values are: clay 0.69; silt 0.48, fine sand 0.68; soil pH 0.69; and grazing 0.11.
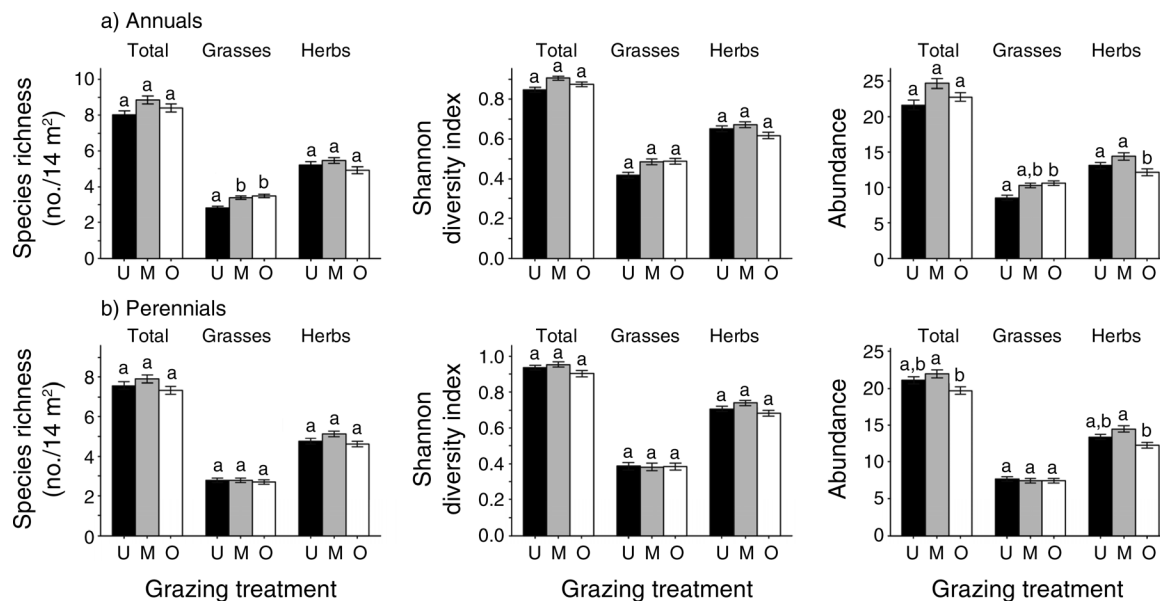
FIG. 5. Mean and standard error responses for species richness, Shannon diversity index, and abundance (sum of abundance scores for individual species; see *Methods*) according to life-form groups and grazing treatment (U, ungrazed; M, macropod grazed; O, open grazed) for (a) annual and (b) perennial totals, grasses, and herbs. Means that are significantly different as determined by multiple comparisons of means (Tukey contrasts) from linear mixed-effects models (LMEMs) are annotated with different letters.

lonchophylla had peak abundances in the macropod-grazed treatment.

The only exotic species in the data set was the perennial grass *Cenchrus ciliaris* and it occurred at six sites on the three most southerly properties (Fig. 1). Mean abundance score for this species in relation to grazing treatment was: ungrazed, 3.00; macropod grazed, 2.25; open grazed, 2.50.

Nonsignificant "decreaser" species

There were five species that were not sufficiently frequent for statistical modeling that met the criteria for potential decreasers. *Cyperus bifax*, *Flaveria australasica*, and *Trichodesma zeylanica* are generally unpalatable, are common with broad geographic ranges, and occur in habitats beyond Mitchell grassland (Table 3). *Peripleura hispidula* is widespread in other habitats and the collecting trend is higher than the null trend. The geophytic lily *Bulbine bulbosa* is palatable, was rarely recorded in the broad survey, has a flat collecting trend through time relative to the overall collecting effort, and is known to be a decreaser elsewhere (Table 3).

Of the four species that exhibited a decreasing trend with open grazing, *Chionachne hubbardiana* showed the most dramatic decline (more than a 40% reduction) and is regarded as palatable, restricted to grasslands, and shows a relatively flat trend in the collecting record (Table 3). *Dichanthium sericeum* var. *sericeum*, and *Panicum decompositum* are palatable, have a relatively flat trend in the collecting record, and both have ambiguous responses to grazing disturbance from other

studies (Table 3). These two species, together with *Aristida latifolia*, which is unpalatable, remain extremely frequent in Mitchell grasslands (Table 3).

Regional flora assessment

From a total of 433 species recorded from Mitchell grasslands in the state of Queensland (Appendix H), there were 12 species where pre-existing information could not confirm population size >100 000 plants. Surveys revealed that six of these species were likely to have populations greater than 1 M plants (Appendix I). The two tree species *Acacia crombiei* and *Acacia peuce* are classified as "not grazing sensitive" because seedlings were usually evident within grazed areas although some seedlings of both were browsed. Five herbaceous species were either not selectively grazed or were advantaged by disturbance, and total population sizes for all five are in excess of 1 M plants. Surveys after winter rain failed to locate *Iatosperma australiense* and *Spathia neurosa*, despite previous records suggesting this as the optimum time for sighting these annual species. Surveys within the geographic range of *Calotis suffruticosa* did not reveal characteristics of grazing sensitivity, but failed to locate a large population. *Picris barbarorum* was rare and observed to be grazed, but is known to be irruptive in other grasslands in higher rainfall environments. The shrub *Eremophila stenophylla* is more extensive in habitats outside Mitchell grassland, is selectively grazed, and is not regenerating in areas subject to commercial pastoralism.

TABLE 2. Mean (±SE) of the abundance scores and other predictor variables (identified by comparing for species with a significant response to grazing grouped according to their general response shape) of the most common species in the study.

Species	Life-form	Treatment			Other predictor variables
		Ungrazed	Macropod grazed	Open grazed	
Negative response					
Aristida latifolia	PG	0.57^A ± 0.37	0.51^A ± 0.37	0.22^B ± 0.37	
Chionachne hubbardiana	AG	1.26^A ± 1.0	1.11^A ± 0.3	0.55^B ± 0.07	+mean annual rainfall ΔAIC_c = −48, +rainfall seasonality ΔAIC_c = −40
Dichanthium sericeum var. *sericeum*	PG	0.36^A ± 0.20	0.29^{A,B} ± 0.20	0.19^B ± 0.20	
Panicum decompositum	PG	1.02^A ± 0.44	0.73^A ± 0.45	0.46^B ± 0.44	
Intermediate positive response (positive modal)					
Boerhavia dominii	PH	0.22^A ± 0.17	0.33^A ± 0.17	0.15^B ± 0.17	
Brachyachne convergens	AG	0.17^A ± 0.29	0.67^B ± 0.30	0.39^C ± 0.29	
Digitaria ctenantha	AG	0.98^A ± 0.40	1.47^B ± 0.40	1.06^A ± 0.40	
Gomphrena breviflora	AH	0.44^A ± 0.39	0.71^B ± 0.39	0.63^B ± 0.39	−coarse sand, ΔAIC_c = −40
Ipomoea lonchophylla	PH	1.88^A ± 0.8	2.06^A ± 0.6	0.92^B ± 0.8	−coarse sand, ΔAIC_c = −9
Iseilema membranaceum	AG	0.46^A ± 0.29	0.73^B ± 0.30	0.54^A ± 0.30	
Sida spinosa	AH	0.61^A ± 0.37	0.77^B ± 0.36	0.57^A ± 0.36	
Intermediate negative response (negative modal)					
Abelmoschus ficulneus	AH	0.73^A ± 0.36	0.50^B ± 0.37	0.76^A ± 0.36	+previous summer rain ΔAIC_c = −24, +previous winter rain ΔAIC_c = −28, +rainfall seasonality ΔAIC_c = −15
Alysicarpus muelleri	AH	0.75^A ± 0.44	0.41^A ± 0.44	0.84^B ± 0.45	
Hibiscus trionum	AH	0.39^A ± 0.22	0.21^A ± 0.21	0.32^B ± 0.22	
Phyllanthus maderaspatensis	AH	0.85^A ± 0.29	0.47^B ± 0.29	0.62^B ± 0.29	
Positive response					
Dactyloctenium radulans	AG	0.56^A ± 0.60	0.92^A ± 0.60	1.77^B ± 0.60	+coarse sand ΔAIC_c = −37
Eriochloa crebra	PG	0.64^A ± 0.42	0.94^B ± 0.43	0.97^B ± 0.42	
Panicum laevinode	AG	0.46^A ± 0.6	0.57^{A,B} ± 0.6	0.72^B ± 0.4	
Salsola kali	AH	0.70^A ± 0.45	0.78^A ± 0.45	0.95^B ± 0.45	−mean annual rainfall ΔAIC_c = −26
Streptoglossa odorata	AH	0.93^A ± 0.6	1.08^{A,B} ± 0.5	1.28^B ± 0.6	

Notes: The direction of the effect of the other predictor variables is indicated as positive or negative. Appendix G identified the response of 14 species with nonsignificant responses to grazing treatment. Life-form abbreviations are: AG, annual grass; AH, annual herb; PG, perennial grass; and PH, perennial herb. "Ungrazed" exclosures were designed to exclude all mammalian herbivores greater than 200 g; exclosures that excluded sheep and cattle, but not kangaroos, were termed "macropod grazed"; and areas outside the fences were designated "open grazed." Means that are significantly different as determined by multiple comparisons of means (Tukey contrasts) from generalized linear mixed-effects models (GLMEMs) are annotated with different superscript letters. Environmental variables were also added to the model one at a time and their explanatory power assessed using information criteria (IC) techniques (ΔAIC_c); we show results for predictors that resulted in $\Delta AIC_c \geq -4$.

DISCUSSION

Grazing treatments

With our combined experimental and regional assessment approach, we found that the effects of livestock grazing on the composition of the Mitchell grassland flora are subordinate to regional gradients in rainfall (annual average, seasonality, and recent rainfall history) and soil texture (Fig. 4). The dominant influence of rainfall gradients at regional scales (Fensham et al. 2000, Lewis et al. 2009), rainfall history (Foran 1986, O'Connor and Roux 1995), and soil patterns (Stohlgren et al. 1999, Fensham et al. 2000, Kohyani et al. 2008) have been shown to overwhelm management effects in other grasslands. The importance of rainfall history as a determinant of fluctuations in the dominant species in Mitchell grasslands has also been previously recognized

(Orr and Evenson 1984, Orr et al. 1988, Orr 1991). Despite these overarching influences, floristic composition varied modestly between grazing treatments at the scale of individual sites. There were roughly equal numbers of species with negative and positive responses to grazing treatments, and a larger group that responded positively to the intermediate grazing pressure of macropods.

We predicted that species composition would differ across the three grazing treatments, livestock grazing would favor annual over perennial species, and dominant species would decline in abundance with increasing intensity of grazing pressure. Contrary to our predictions, after 15 years of grazing exclusion compared with ongoing grazing typical of commercial rangeland pastoralism in Mitchell grasslands, there were few differences in plant diversity or abundance of any life-

TABLE 3. Attributes of potential decreaser species, including life-form, geographic range, diversity of habitat, frequency in the survey data set (Fensham et al. 2000), number of herbarium records, proportion of slope of collecting trend relative to the null trend (all Australian records), evidence of grazing sensitivity from other studies, and palatability.

Species	Life-form	Range (millions of km²)	Habitats outside Mitchell grassland	Frequency in data set ($n = 609$)	No. herbarium records (percentage of trend)†
Nonsignificant decreaser species					
Bulbine bulbosa	PH (geophyte)	2.57	other grassland, *Eucalyptus* woodland, *Acacia* woodland, floodplain	6	684 (0.68)
Cyperus bifax	PH (geophyte)	8.32	other grassland, floodplain	136	631 (0.83)
Flaveria australasica	AH	6.41	other grassland, *Acacia* woodland, cultivated grassland	14	475 (0.89)
Peripleura hispidula	AH	4.80	*Eucalyptus* woodland, *Acacia* shrubland	0	162 (1.21)
Trichodesma zeylanica	PH	8.23	*Eucalyptus* woodland	17	1597 (0.84)
Species identified as descreasers from exclosures					
Chionachne hubbardiana	AG	1.35	other grassland	23	103 (0.68)
Dichanthium sericeum	PG with some annual forms	9.04	other grassland, *Acacia* woodland, *Eucalyptus* woodland	271	2434 (0.53)
Panicum decompositum	PG	8.42	other grassland, *Eucalyptus* woodland, *Acacia* woodland	220	1446 (0.59)
Aristida latifolia	PG	5.39	other grassland, *Acacia* woodland	268	917 (0.64)

Notes: Life-form abbreviations are: AG, annual grass; AH, annual herb; PG, perennial grass; and PH, perennial herb. Evidence of grazing response was taken from the following studies: 1, Orr (1980); 2, Foran and Bastin (1984); 3, Orr and Evenson (1984); 4, Dorrough et al. (2011); 5, Fensham et al. (1999); 6, Fensham and Skull (1999); 7, Phelps and Bosch (2002); 8, McIntyre et al. (2003); and 9, Lewis et al. (2008). Palatability was taken from the following studies: 1, Cunningham et al. (1981); and 2, Milson (2000). Increasers are species favored by grazing, decreasers are species disfavored by grazing, intermediate refers to species with a preference for intermediate grazing disturbance, and neutral refers to species with no discernible preference for grazing.

† The values in parentheses show the percentage of trend in collections relative to all collections.

form group. In the northern hemisphere, grazing generally increases species diversity in high-productivity ecosystems, and reduces diversity in low-productivity ecosystems (Bakker et al. 2006). The neutral response of species to grazing in the Mitchell grasslands may be compatible with this pattern because they occur on fertile soils, but productivity is constrained by variable rainfall (Lewis et al. 2008). A very modest peak in diversity in the macropod-grazed plots is insufficient to implicate the intermediate disturbance hypothesis that predicts a decline in diversity when disturbance is removed because a few species with high biomass become dominant and suppress diversity through competition (Gough and Grace 1998, Cingolani et al. 2005, Sasaki et al. 2009). This response is evident in more productive grasslands where undisturbed tussock grasses exclude species of smaller stature that occupy the inter-tussock spaces (McIntyre et al. 2003, Fynn et al. 2004, Frank 2005). In the Mitchell grasslands, the vast majority of the inter-tussock flora are not suppressed by perennial *Astrebla* grasses even after long periods without grazing (Lewis et al. 2008). The small subset of species with a positive response in the macropod-grazed treatment, despite representing a diversity of life-form groups (Table 2), are mostly palatable plants of low stature (Cunningham et al. 1981, Milson 2000) likely disfavored by competition and grazing. There is also a small suite of rare species in the Mitchell grasslands that

prosper in disturbed environments with reduced competition (Appendix I).

There were no significant differences in the abundance of the perennial *Astrebla* grasses between the grazing treatments. *Astrebla* can be depleted with both extreme grazing pressure (Hall and Lee 1980, Orr et al. 1986, Orr and Phelps 1994) and severe drought (Orr and Phelps 1994), but has the capacity to rejuvenate through seedling establishment after adequate rainfall (Orr and Evenson 1991). The nonsignificant results for *Astrebla* abundance between grazing treatments lend no support to the notion that grazing enhances the germination and vigor of the dominant perennial grasses in Mitchell grassland (Everist 1964, Orr 1980). Similar conclusions have been drawn after livestock removal in both prairies (Willms et al. 2002) and other semidesert grassland (Brady et al. 1989).

All three of the perennial grasses identified as decreasers (*Aristida latifolia*, *Dichanthium sericeum* var. *sericuem*, and *Panicum decompositum*) are widespread and abundant in Mitchell grasslands (Table 3), but have probably diminished with livestock grazing. *Aristida latifolia* has previously been recognized to indicate the early stages of degradation (Phelps and Bosch 2002), but this perspective may reflect its perception as a pest with seeds that irritate sheep and taint wool (Lee et al. 1980). Substantial increases in the relative abundance of *Dichanthium sericeum* occur in the Mitchell grassland during periods of above average rainfall (Orr 1981, Orr

TABLE 3. Extended.

Evidence of grazing response from other studies (reference)	Palatability (reference)
decreaser (4)	moderately palatable (1)
increaser (5), neutral (9)	unpalatable (1)
	unpalatable (1, 2)
	unpalatable (1, 2)
	palatable (2)
intermediate (3, 9), decreaser (1, 5, 7), increaser (6, 8)	mostly palatable (1, 2)
decreaser (8, 9), intermediate (1, 5)	palatable (1, 2)
decreaser (1, 3), neutral (2)	unpalatable (1)

and Evenson 1984, Austin and Williams 1988, Orr et al. 1988).

The most dramatic decreaser with grazing was the annual grass *Chionachne hubbardiana*. While it is recognized as palatable, it has not previously been considered an important component of Mitchell grassland pastures (Phelps and Bosch 2002). The results of our study suggest it would have been ubiquitous before the advent of stock grazing north of the Tropic of Capricorn. In rangelands dominated by annual species it has been suggested that an ephemeral life-form may confer considerable grazing tolerance (Fensham et al. 2010, Silcock and Fensham 2013). However, this may not necessarily apply in grazing systems dominated by perennial grasses where grazing pressure can be maintained when annuals are in active growth immediately after rain. *Chionachne* is an example of an annual that is also grazing sensitive. Other grazing-sensitive plant species that were formerly dominant and have since been greatly reduced by pastoral management in northern Australia include the perennial grasses *Dichanthium queenslandicum* from subhumid grassland (Fensham et al. 2011a) and *Capillipedium parviflorum* from savanna woodland (Fensham and Skull 1999).

We predicted that under the wide-scale use of Mitchell grasslands for livestock grazing, a substantial number of plant species would have declined, particularly species already rare in the landscape. However, the species from the exclosures exhibiting negative responses to grazing and the nonsignificant but potentially declining species (Table 3) were all common, widespread, and secure, even if overall population numbers may have declined.

Of the nine species from the treatment data set identified as potential decreasers, only the geophytic lily, *Bulbine bulbosa*, showed consistent evidence suggesting that it may have declined over 100 years of pastoralism. However, this species responds rapidly after rain and occurs at high density, particularly in alluvial situations, over a large area of the Mitchell grasslands.

Regional flora assessment

Regional field surveys determined that 8 of the 12 species potentially threatened by grazing from the Mitchell grassland flora do not have characteristics suggesting grazing sensitivity (Appendix I). Four species were deemed data deficient. Field surveys failed to locate three poorly known plant species despite searching in suitable habitat within their geographic range. These species could be threatened by grazing, but it is also possible that they irrupt in response to specific seasonal cues consistent with an annual life cycle and winter germination. *Eremophila stenophylla* is the only species in the entire Mitchell grassland flora for which there is consistent evidence (rarity, selectively grazed, and lacking regeneration) of potential decline because of sensitivity to grazing.

The grazing treatment plots were not in positions to represent some exotic species that have proliferated in Mitchell grasslands. The only exotic species from the treatment data set was buffel grass (*Cenchrus ciliaris*), which exhibited no response in relation to grazing treatment. It is widespread through northern Australia, where it has negative effects on plant diversity (Fairfax and Fensham 2000), and does occur in Mitchell grasslands on particular combinations of soil and climate.

Other studies of grazing effects in semidesert environments have generated mixed results. For example, grazing relief elevated plant species diversity in Arizona (Brady et al. 1989) and decreased diversity in Colorado (Manier and Hobbs 2007). One of the most comprehensive studies, encompassing multiple exclosures from southwestern USA (Stohlgren et al. 1999), revealed remarkably similar findings to those presented here: environmental gradients were more important than grazing gradients, grazing had modest effects on composition, and there were no consistent trends in species diversity between grazing treatments.

The tolerance of the flora of the Mitchell grasslands and semidesert grasslands, even under the regime of commercial pastoralism, suggests a nonequilibrium ecosystem (Ellis and Swift 1988, Briske et al. 2003, Silcock and Fensham 2013). Sporadic rainfall events result in germination and growth of both perennial and annual species. In these periods of abundant forage, stocking rates of managed herbivores are rarely high enough to inhibit flowering and seed-set, even for most palatable species. In the long periods of low rainfall, grazing animals reduce herbaceous biomass across a broad spectrum of species, many of which are palatable

Fig. 6. Mitchell grassland converted to open shrubland after invasion by prickly acacia (*Acacia nilotica*) (Source: Department of Agriculture Forestry and Fisheries, Queensland, Australia).

and nutritious. In general, livestock are removed before the lack of forage would result in livestock mortality, ensuring the survival of the dominant grasses, albeit as stubble. At regional scales, the great majority of plant species persist in Mitchell grasslands under typical pastoral management.

Managed livestock grazing may be compatible with botanical conservation in semidesert grasslands. However, this sanguine conclusion should be tempered by several caveats: (1) Managed grazing does not result in the removal of the dominant perennial grasses. (2) Grazing-sensitive species form a minor component of semidesert grasslands. These will benefit from reserves where the impacts of domestic livestock are minimized. The achievement of grazing relief refuges must consider the preservation and enhancement of water-remote areas (James et al. 1999, Fensham and Fairfax 2008) both within and outside the reserve network. (3) There may be incremental decline in the populations of some decreaser plant species. (4) Exotic species may undermine biological integrity. Buffel grass (*Cenchrus ciliaris*) and Indian couch (*Bothriochloa pertusa*) have invaded some Mitchell grassland areas and will probably continue to expand as in other environments (Fensham et al. 2013). The former species is promoted by some pastoralists (Friedel et al. 2011). The invasive leguminous trees prickly acacia *Acacia nilotica* and mesquite *Prosopis pallida* have heavily infested >60 000 km^2 of the Mitchell grasslands (Fig. 6; Osmond 2003, Spies and March 2004). Cattle ingest the pods of both species and are a vector for the dispersal of seed (Brown and Carter 1998, Brown and Archer 1999). *Prosopis* is not advantaged by decreased grass biomass (Brown and Archer 1999), suggesting that dispersal rather than grazing impact may be the main advantage provided by livestock.

Anthropogenic pressures have been applied to natural ecosystems worldwide. In many of these ecosystems, it is

a challenge piecing together the full impacts of these disruptions because there are few, if any, pristine areas remaining to serve as reference areas. Our study demonstrates how a combined experimental and targeted survey directed towards the rare plants that may be the "canaries in the mine" can provide insights for vast ecosystems such as semidesert grasslands.

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SUPPLEMENTAL MATERIAL

Appendix A

Grazing history for exclosure sites as determined by landholder interview (*Ecological Archives* A024-029-A1).

Appendix B

Method for assessing herbarium collecting trends (*Ecological Archives* A024-029-A2).

Appendix C

Survey methodology for rare or poorly known species potentially threatened by grazing (*Ecological Archives* A024-029-A3).

Appendix D

Species list from the Mitchell grassland grazing treatments (*Ecological Archives* A024-029-A4).

Appendix E

Bray-Curtis dissimilarity measures from ANOSIM results from the grazing treatments (*Ecological Archives* A024-029-A5).

Appendix F

Results from ANOVAs conducted to assess the significance of the fixed effects from the grazing treatment analysis (*Ecological Archives* A024-029-A6).

Appendix G

Species that did not respond significantly to grazing treatment (*Ecological Archives* A024-029-A7).

Appendix H

Species list and life-form for Mitchell grasslands in Queensland (*Ecological Archives* A024-029-A8).

Appendix I

Species known from Mitchell grassland and prior to this study assessed as having insufficient evidence to be certain that there are greater than 100 000 plants in landscapes grazed by domestic livestock, as well as results of subsequent field survey in grazed Mitchell grasslands (*Ecological Archives* A024-029-A9).