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Vegetation responses to the first 20 years of cattle grazing in an Australian desert

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Abstract. Existing theoretical frameworks suggest three predictions relevant to grazing effects in Australian aridlands: grazing has a negative but moderate effect on plant species richness; a separate "state" resulting from degradation caused by extreme grazing will be evident; some plant species will have a strong association with grazing relief refuges that have only ever been subject to light grazing. These predictions were examined in the dune swales of an Australian desert, with data on herbaceous species collected along transects up to 14 km from artificial water points between four and 33 years old. A cumulative grazing index was constructed utilizing both the spatial occupation patterns of cattle and the length of exposure. Despite restricting sampling to a narrow habitat, silt/clay content and soil pH influence floristic patterns independent of grazing. The analysis of quadrat data in relation to grazing revealed almost no patterns in plant cover, species richness (at two different scales), or abundance across plant life-form groups. Five species had an increasing response, and seven a decreasing response, while the only species restricted to areas of extremely low grazing pressure was sufficiently rare that it could have occurred there by chance. The dominant annual grass, the most common shrub, and a perennial tussock-forming sedge all decrease with high levels of grazing. Most species exhibit an ephemeral life strategy in response to unreliable rainfall, and this boom and bust strategy effectively doubles as an adaptation to grazing. After 20 years of exposure to managed grazing with domestic stock in Australian dune swales, patterns in species richness have not emerged in response to grazing pressure, the ecosystem has not been transformed to another degradation "state," and there is no evidence that grazing relief refuges provide havens for species highly sensitive to grazing.

Key words: aridlands; desert; grazing; Simpson Desert, Australia; state and transition models; water remoteness.

INTRODUCTION

The effects of disturbance on species richness are a product of colonization opportunities and extinction likelihood (Olff and Ritchie 1988). In productive grassland, colonization and persistence may be mediated with competitive exclusion by dominant perennial grasses, particularly where these species are palatable (Pacala and Crawley 1992). With the removal of grazing, the dominant perennial species occupy space that would otherwise be available for sub-dominant species, many of which are ephemeral. As grazing pressure intensifies, species richness declines because of the extinction of palatable species. This conceptual framework for grazing systems mirrors the more general "intermediate disturbance hypothesis" (Grime 1973, Connell 1978).

The generality of grazing responses in plant communities has been examined (Milchunas et al. 1988) and clarified by Cingolani et al. (2005), suggesting that where evolutionary exposure to grazing by large mammals has been short and resources are limited (such as in Australian arid lands), declines in diversity with heavy grazing will be more pronounced than in environments with a history of greater exposure. However, declines will still only be moderate under low rainfall because preadaptation of plant species to resource limitations also confers grazing resilience (Cingolani et al. 2005). Modal responses to grazing are not expected in arid lands because resource limitations preclude dominance by any species. Some studies (Stohlgren et al. 1999, Kohyani et al. 2008) have demonstrated that response patterns are scale-dependent and that the relationship between grazing and species richness is more prevalent at small spatial scales than at large spatial scales. In Australian arid lands the impact of grazing may be particularly acute where there are fertile areas that provide important sources of scarce nutrients within the general matrix of an ancient and highly weathered continent (Stafford Smith and Morton 1990), and there is a general presumption that exposure to grazing over evolutionary timescales has been relatively low (Milchunas and Lauenroth 1993, Morton et al. 1995, Diíaz et al. 2007).

State and transition models suggest that grazing responses may be expressed differently within separate

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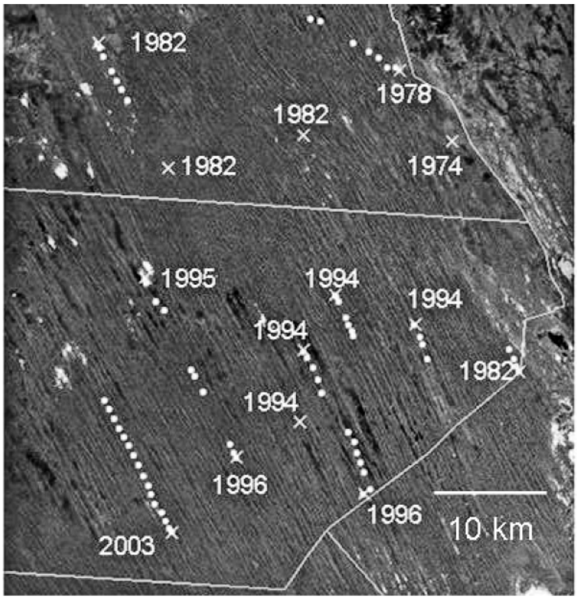

FIG. 1. Linear dunes in the eastern Simpson Desert, Australia, with locations of sites (circles), the locations of water-points (crosses), annotated with the year they were established, and property boundaries.

degradation "states" (Walker et al. 1981, Westoby et al. 1989). This framework predicts that ecosystems can be driven over the thresholds defining states such that return to the original state cannot be reversed by the short-term removal of herbivores. The diagnosis of states and thresholds is not a simple task (Bestelmeyer et al. 2003), but evidence can include abrupt changes in community composition (Sasaki et al. 2008), alteration of soil conditions (Elwell and Stocking 1976, van de Koppel et al. 1997), and the depletion of the soil seed bank (Sternberg et al. 2003, Kinloch and Friedel 2005). The transit to a new degradation state has been used to account for negligible differences in a study incorporating exclosures in arid environments with a long history of livestock grazing (Valone et al. 2002). Within a grazed ecosystem, a degradation state should become apparent in the immediate vicinity of stock watering points where intense grazing and other impacts of herbivores have been recorded to have profound effects on vegetation and soils (Friedel 1997, Turner 1998, Tongway et al. 2003, Smet and Ward 2006).

In many of the world's arid rangelands, grazing by domestic stock is limited by the availability of drinking water (James et al. 1999, Redfern et al. 2003, Smit et al. 2007, Fensham and Fairfax 2008). In this context "water-remoteness gradients" provide a valuable opportunity to study the effects of grazing on plant species composition (Andrew 1988, Fensham and Fairfax 2008). In arid Australia, where there has been a relatively light evolutionary history of grazing, only a short history of domestic stock grazing, and there are large areas that do not have natural water, it is proposed that water-remote areas act as grazing relief refuges that could provide havens for grazing-sensitive species (Landsberg et al. 2003). This framework predicts that there will be a suite of species with strong associations to areas subject to only light grazing.

There are logistic problems with employing water-remoteness gradients to examine species responses (Pringle and Landsberg 2004). In many arid-land environments the artificial water points are now so abundant that water-remoteness gradients more than 6 km do not exist (Fensham and Fairfax 2008). Other studies have been hampered by the confounding effects of ephemeral water (Friedel et al. 2003), a variety of soil types (Smit et al. 2007), the limited statistical power in studies without adequate sample size in a single location (Ludwig et al. 1999) or spread over a broad geographic range (Landsberg et al. 2003), and the effects of drought-tolerant native herbivores (Montague-Drake and Croft 2004). In addition there are substantial limitations on adequate identification of ephemeral flora, unless sampling can be timed to coincide with rare rainfall events. What is more, most studies have not considered the grazing impacts related to the age of watering points, which has been shown to be an important predictor of sheep track density in Australian rangeland (Pringle and Landsberg 2004), although Hunt (2001) has described the cumulative effects on some key species over short gradients. The limitations are overcome here by examining species responses and patterns in diversity and richness within a framework of multiple water-remoteness gradients, within a single selectively grazed land type, incorporating both spatial impacts and grazing history. The gradients represent a spectrum including heavy grazing around water points, but extend to areas subject to negligible grazing pressure.

It may be possible to refine generalizations about grazing responses, but this will require carefully controlled studies within clearly defined positions along rainfall–productivity, evolutionary history of grazing, and other gradients (Vesk et al. 2004). The current study combines spatial and temporal measures of grazing impact in the arid environment of the Simpson Desert, Australia, in fertile habitats within a matrix of infertile habitat, where the evolutionary history of grazing is light and intensive grazing relatively recent. The study specifically addresses three predictions that arise from the emerging theoretical frameworks that apply to grazing impacts on arid vegetation: (1) plant species richness will exhibit a negative but moderate decrease with grazing; (2) there will be evidence of a separate degradation state within the impact zone of water points; and (3) a suite of plant species will be restricted to grazing relief refuges.

METHODS

Study area

The study was conducted on two large pastoral properties (23°20′ S, 138°30′ E) in the eastern Simpson

Desert in western Queensland, Australia (Fig. 1). Mean annual rainfall in this area is 130–150 mm per annum, although only eight times per century is rainfall more than double the average (Bureau of Meteorology, *unpublished data*). Parallel linear sand dunes rise to 5–20 m height, with ~400–2000 m distance between dune crests, and with flat dune swales forming the majority of the land area. Sampling was conducted within dune swales that have not been buried by wind-blown sand (indicated by the absence of the spinifex grass *Triodia basedowii*), where gidgee (*Acacia georginae*) formed a very open woodland, and where rock cover was <3% (see Appendix A for photographs of the habitat). These areas are characterized by a very low proportion of coarse sand (<0.18 mm) and have higher fertility than the dunes (Crocker 1946, Buckley 1982*b*). The dune swales targeted for sampling compose ~50% of the dune fields and are favored by cattle, acting as fertile islands within the broad infertile landscape. As such they should be particularly vulnerable to degradation by grazing (Stafford Smith and Morton 1990).

Large marsupial herbivores only occur at low density, and rabbits have never occurred in sufficiently high numbers to have had a major impact (Letnic and Dickman 2006). Feral camels are present but have densities <0.03 camels/km^2 (Short et al. 1988). Grazing by domestic cattle only occurred sporadically when stray animals walked long distances during the brief periods when there was ephemeral water. Thus the study area was subject to only light and intermittent grazing prior to intensive managed cattle grazing facilitated by the sinking of bores in the 1980s (Fig. 1) and the establishment of fenced paddocks that only include the dune fields. When pastures have been exhausted during protracted dry periods, stocking rates are reduced. One of the properties tended to use the water points sequentially, exhausting forage around a group of water points before utilizing pastures around another set of water points. The other property tended to use the water points all at once until the lack of forage resource forced destocking. The maximum time that any bore had not provided water for cattle was two years.

Field sampling

Sampling was conducted during March 2007, when the area had received more than 300–430 mm of rain during the preceding three months and conditions for sampling the herbaceous flora were optimum. Gradients were selected to represent a range of distances within the first kilometer of watering points, were spaced roughly every 1 km thereafter, and always included the maximum accessible distance within the habitat for any particular water point (Fig. 1). Site selection was constrained by the availability of target habitat because many swales did not meet the habitat criteria of gidgee present, spinifex grass absent, and low rock cover. Sixty-eight sites were located away from tree crowns on 10 distance-to-water gradients with maximum distances of 2.2, 3.3, 3.4, 4.2, 4.3, 5.9, 6.0, 9.2, 9.6, and 13.9 km (Fig. 1).

Site sampling was conducted along a 31-m tape line that provided for the location of regular sampling points and formed the central axis of a 2 m wide quadrat. Species present in the first 1 × 2 m section of this larger quadrat were assigned an abundance of five, additional species present in the next 2 × 2 m section were assigned an abundance of four, the next 4 × 2 m section three, the next 8 × 2 m section two, and the final 16 × 2 m section one, and if a species was absent it was assigned an abundance of zero. This method, involving unrepeated scoring of species presence, has been demonstrated to provide the best return (robust measure of species density) for effort (no more time than presence/absence recording), thereby allowing for a relatively large quadrat size (Morrison et al. 1995). Voucher specimens of all species have been lodged at the Queensland Herbarium (Mt. Coot-tha, Queensland, Australia), and nomenclature follows Bostock and Holland (2007). *Abutilon fraseri* and *A. otocarpum* and *Boerhavia pubescens* and *B. repleta* were not consistently distinguished, and these congenerics were combined for the analysis.

Grass and forb cover was the mean of visual estimates from four 50 × 50 cm frames evenly spaced along the 31-m tape, assuming cover as solid convex polygons over the vegetative extremities of the plants. Soil was collected from 1–5 cm depth at each of those four sampling points, bulked, and then sampled for each site. Particle size of the samples was determined in three categories: coarse sand (>250 μm), fine sand (38–250 μm), and silt/clay (<38 μm). Surface soil pH was determined using a TPS WP-81 pH meter (TPS, Brisbane, Queensland, Australia) with a 1:5 solution. A penetration measure was determined at each of the four sampling points by dropping a sharpened probe from a standard height and scoring the depth of penetration. These measures were averaged for each site to provide a relative value for soil penetration. Cattle dung pats (>8 cm diameter) were counted in quadrats, centered on the tape but of variable size (124–620 m^2), depending on dung density.

Modeling grazing intensity

Dung counts have been correlated with herbivore activity (Landsberg and Stol 1996). To accommodate for patchiness in dung density, sites were grouped into 0.4-km segments along the distance-to-water gradient, and density was averaged within these segments. The averaged dung density (10 dung pats/m^2) values were modeled against the midpoint of the segments (i.e., 0.2, 0.6, 1.0, . . . km). A model using a Poisson-link function of the form $\ln(\text{dung density} + 1) \sim -0.8647 \times \ln(\text{distance to water} + 1) + 2.2318$ (multiple $R^2 = 0.576$) adequately described the dung data in relation to distance to water, except for the first 0.4 km, where it provides a substantial underestimate (Fig. 2). However, it is reasoned that cattle are spending most of their time in this zone

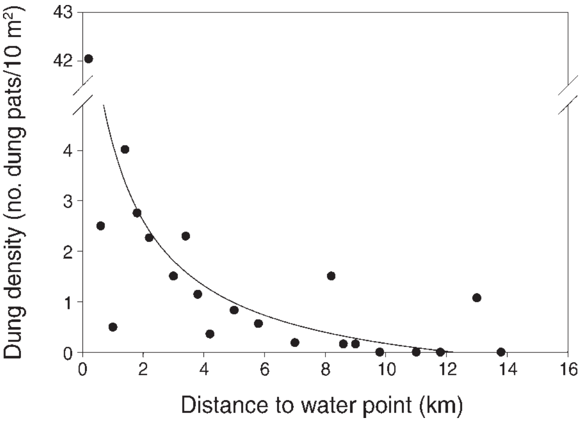

FIG. 2. The function modeling distance to water point vs. cattle dung density of the form $\ln(\text{dung density} + 1) \simeq -0.8647 \times \ln(\text{distance to water} + 1) + 2.2318$ (multiple $R^2 = 0.576$). Data points are the mean dung density for the 0.4-m segments. The modeled dung density values are used to provide a spatial grazing score.

drinking or resting rather than grazing, and the function was not adjusted for these sites that were included in the analysis. The sites closest to water points on each water-remoteness gradient are not floristically distinct from many other sites beyond 0.4 km distance (Fig. 3), and soil characteristics do not seem to have been dramatically transformed (see *Results*).

This function was applied to the distance from water for every site, providing a spatial grazing score. This score was multiplied by the number of years that the relevant water points have been used as foci for commercial grazing and were summed for all water points that are influencing grazing at a site. Thus if a site was 1 km from a water point (see Fig. 2) that had been subject to eight years of grazing (4.12 × 8) and 6 km from another water point subject to 28 years of grazing (0.73 × 28), these values were summed to provide the cumulative grazing index (CGI).

Multivariate analysis and statistical modeling

The site–species abundance data were ordinated by nonmetric multidimensional scaling after exploratory analysis suggested that a two-dimensional solution most accurately represented the data and the environmental variables. Vector fitting with 99 Monte Carlo tests was used to determine the direction, strength, and significance of the environmental variables through the ordination space. The relationship between the vectors was explored using Spearman's rank correlation coefficient.

A nonlinear relationship or break in slope between ordination scores and grazing index has been used to indicate a "spatial threshold," or preliminary evidence of an abrupt change in degradation state (Sasaki et al. 2008). We followed this methodology by plotting actual CGI scores against the ordination scores along the vector for CGI scores. The latter define the dimension of the two-dimensional ordination space that is best aligned with the CGI and the alignment of the sites along this vector provides a measure of the floristic dissimilarity in relation to the CGI.

Silt/clay, cumulative grazing index, and soil pH were highly significant vectors through the ordination space. For the 35 species with a frequency greater than nine, we modeled responses of richness, Shannon diversity, and abundance (by summing abundance scores) in total and according to individual life-form groups (Table 1); we also modeled rare species richness (richness of species with frequency less than 10). In addition to the large scale (62 m^2), total, annual, and perennial plant species richness were also modeled at the small scale (2 m^2). Responses were modeled against the explanatory variables silt/clay content, cumulative grazing index, and soil pH, both as main effects and in two-way interactions using the statistics program R (version 2.7.1; R Foundation for Statistical Computing, Vienna, Austria). Silt/clay values were positively skewed and were log-transformed.

Grass cover (as a percentage), forb cover (as a percentage), and diversity were modeled using multiple linear regression. The cover models displayed considerable heteroscedasticity (model residuals increasing with increasing fitted values) and were improved most effectively by square-root transformation (grass cover) and log transformation (forb cover). Richness and the life-form abundance data were examined for zero inflation (Warton 2005) and modeled initially using generalized linear models (GLMs) with Poisson errors and a log-link function. If the ratio of residual deviance over residual degrees of freedom was larger than 1.5, then the model was considered to be over-dispersed and the quasi-Poisson error structure was employed.

Species abundance data were examined using ordinal response regression models. Model fit and assumptions

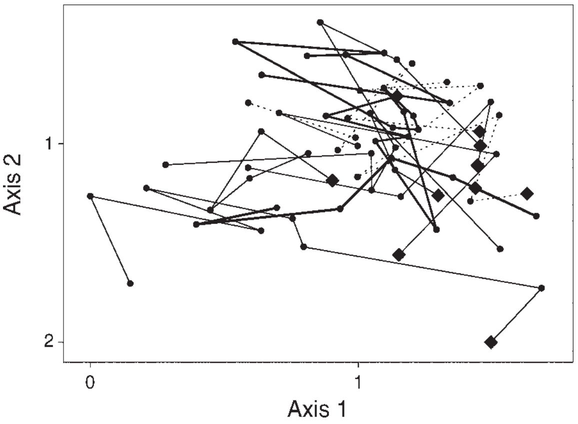

FIG. 3. Two-dimensional ordination of floristic data representing the 68 sites on 10 transects. Sites nearest to the water point on each gradient (<0.4 km) are represented by the large diamonds. The different line patterns only serve to distinguish individual transects.

Table 1. Frequency of plant species in all 68 sites in the dune swales of the eastern Simpson Desert, Australia, number of species occurring in more than nine sites, and species richness (mean ± SE) at large (62-m^2) and small (2-m^2) scales, by life-form group.

Life-form	Frequency of species: Total no. in all sites	Frequency of species: No. in >9 sites	Species richness: Large scale	Species richness: Small scale
Annual grass	22	10	5.1 ± 0.2	2.65 ± 0.14
Annual forb	44	16	8.6 ± 0.4	3.71 ± 0.22
Perennial grass	7	1	0.5 ± 0.1	0.09 ± 0.04
Perennial forb	25	7	2.9 ± 0.2	0.76 ± 0.10
Shrub	3	1	0.8 ± 0.1	0.15 ± 0.04
Tree	1	0	0.1 ± 0.0	0.01 ± 0.01
Total	102	35	18.0 ± 0.3	7.37 ± 0.30

were checked graphically following Guisan and Harrell (2000) and in almost all cases the assumption of ordinality was not verified. For the less common species this is due to excessive zero inflation, but for more common species is due mainly to the U-shaped distribution of the abundance data, with most records either in the zero or five categories. Consequently species abundance classes were converted to presence/absence data and modeled using logistic regression.

Models were simplified by deletion of the predictor variables one at a time from the full model, starting with interactions. Each smaller model was then compared with the full model using an F test on model variance/deviance (linear regressions, generalized linear models with quasi-Poisson errors) or a chi-squared test on the scaled change in model deviance (generalized linear models with Poisson errors, logistic regression). If an interaction was retained, then both main terms present in that interaction were included in the final model. Diagnostic plots of model residuals were inspected to check for violations of model assumptions. For logistic regression, this involved binning residuals into 10 groups (approximately seven residuals per group) and taking mean values per group. A "percentage of improvement" diagnostic statistic was also calculated for logistic models as the proportion of observations for which fitted model values were greater or less than 0.5 and in contradiction to the observed value (1 or 0) (Gelman and Hill 2007), e.g., a fitted value of 0.2 where the observed value was 1 would be regarded as erroneous. The statistic yields an approximate percentage improvement over the null model, which itself is simply the probability of occurrence given the observed values. Models of species occurrences that had low percentage improvement consistently exhibited obvious departure from model assumptions in diagnostic plots. Response variables (life-form variables or species presence/absence variables) that had acceptable model diagnostics included grass cover, forb cover, total species diversity, annual species diversity, perennial species diversity, total species richness, annual species richness, perennial species richness, annual grass richness, annual grass abundance, perennial forb abundance, rare species richness, total species richness (small-scale), *Amaranthus mitchellii*, *Aristida contorta*, *Eragrostis dielsii*, *Eremophila obovata*, *Fimbristylis dichotoma*, *Heliotropium tanythrix*, *Portulaca intraterranea*, *Ptilotus polystachyus*, *Salsola tragus*, *Tragus australianus*, and *Triraphis mollis*. For the remaining variables we conducted nonparametric Kendall's tau rank correlation tests. This test can only be used to test one explanatory variable at a time and thus is not appropriate for testing interactions between explanatory variables. For Kendall's tau correlation tests on species variables we used species abundance scores.

The response of all species was graphically prepared and assessed to search for a response that would be consistent with association with grazing relief refuges. The cumulative grazing index was ordered and then the sites were assigned to four equal segments ($n = 17$). Analysis of variance was performed on species richness and diversity with Tukey's test to determine significant differences between individual means of each cumulative grazing index segment.

RESULTS

The data was composed of 102 species from 68 sites, and there was a range in species richness from 11 to 38 (62 species/m^2), with a mean value of 18. *Pennsisetum ciliaris* was the only exotic species present (one quadrat). Sixty-five percent of the species sampled have an annual life-form (Table 1).

The plots that are within 400 m of the water points tend to be clustered at one end of the ordination diagram, although they are not obviously distinct from other plots (Fig. 3). The lack of consistent direction in the water-remoteness gradients is expected, given that transects have varying length and periods of exposure to intensive cattle grazing. The three strongest vectors through a two-dimensional ordination space are silt content (range = 0.21%–4.90%), cumulative grazing index (range = 0–206), and soil pH (range = 6.09–8.42) (Fig. 4). Of these three variables, cumulative grazing index and soil pH were the only two significantly cocorrelated ($P < 0.001$) because of low soil pH with low cumulative grazing index (Appendix B). Soil penetration index (Fig. 4) is significantly and negatively correlated

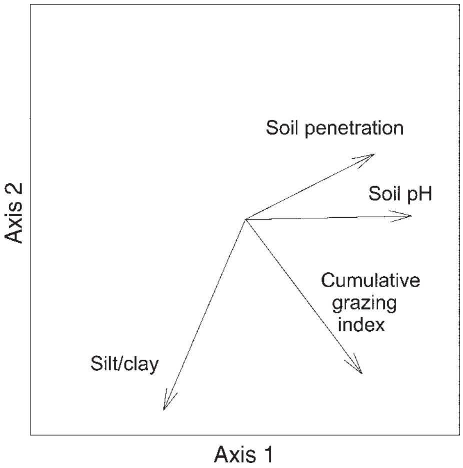

FIG. 4. Two-dimensional ordination with the direction and strength (indicated by the length) of environmental vectors. All vectors have P values greater than 0.001 with maximum R values as follows: silt/clay, $R = 0.684$; cumulative grazing index, $R = 0.624$; soil pH, $R = 0.524$; soil penetration, $R = 0.467$. Cumulative grazing index combines the spatial intensity of grazing with the length of grazing history.

with silt content ($P < 0.001$), positively correlated with cumulative grazing ($P < 0.01$), and positively correlated with soil pH ($P < 0.001$).

The relationship between cumulative grazing index and cumulative grazing index vector scores reveals no evidence of nonlinearity or a break in slope (Fig. 5) as would be expected if one degradation state was separated from another by a threshold.

Grass cover, annual grass abundance, and many of the diversity and richness measures were positively related to silt/clay content, while forb cover was negatively related to silt/clay content (Table 2). The only life-form measures related to the cumulative grazing index were perennial species richness and diversity, which had a weakly positive response (Table 2). Rare species richness was not related to the cumulative grazing index and of the 35 species with a frequency greater than nine, seven demonstrated a decreaser response and five an increaser response (Table 2, Fig. 6). For *Amaranthus mitchellii* and *Eragrostis dielsii* there was an interaction between cumulative grazing index and silt/clay content, whereby the likelihood of occurrence with increasing grazing is exaggerated by increasing silt/clay content (Appendix D). The abundance pattern of species significantly responding to the cumulative grazing index appears to be linear, although the interpretation of response shape can be marred by zero abundance values across a wide spectrum of cumulative grazing index values (Fig. 6). Examination of individual species responses revealed little evidence of a negative exponential response shape, with the herbaceous legume *Swainsona microphylla* being the only species with a frequency greater than four that was restricted to sites (on two transects) within the low 25th percentile of the cumulative grazing index (Appendix E).

When species richness variables (Table 2) were assigned to four segments of the cumulative grazing index (Fig. 7), a weak modal response pattern was revealed for total species richness and annual species richness at both large and small spatial scales, although there was no significant difference between any of the categories ($P > 0.05$). A modal response was not evident for perennial species and all patterns for species richness were mirrored for species diversity.

DISCUSSION

This study sought to minimize the influence of the physical environment by limiting sampling to a narrowly defined and seemingly homogeneous habitat type. However, the proportion of silt/clay in the soil, which was always less than 5% of total soil mass, was more strongly correlated with trends in species composition than the cumulative grazing index (Fig. 4, Table 2). The fine soil fraction has been correlated with nitrogen and carbon over broader gradients (from swales to dune crests) in Simpson Desert dune fields (Buckley 1982*b*) and also with the abundance of individual species (Buckley 1982*a*). The importance of soil factors for affecting plant composition is also emphasized by the independent effect of soil pH on species composition (Fig. 4). The importance of soil characteristics in determining species composition has been highlighted in other studies (Stohlgren et al. 1999, Friedel et al. 2003, Kohyani et al. 2008), but this study identifies that extremely subtle differences in soil characteristics can have a more substantial influence on floristic composition than grazing in arid environments.

There were almost no trends between grazing intensity and species abundance, richness, and diversity at either small or large spatial scales. A recent meta-analysis

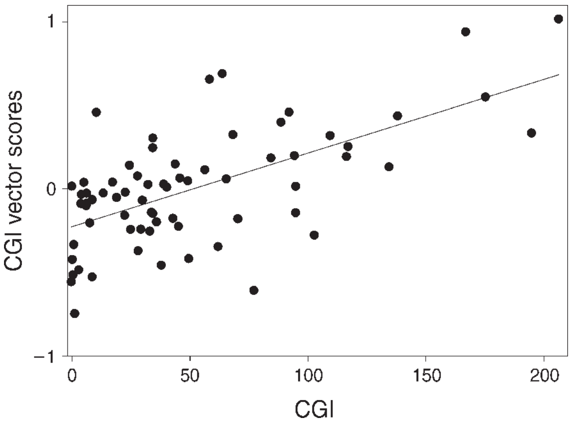

FIG. 5. Relationship and line of best fit between the cumulative grazing index (CGI) and the species CGI vector scores (a measure of the floristic dissimilarity in relation to CGI) within the ordination space. There is no evidence of a break in slope identifying a threshold where species composition represents two separate "degradation states."

Table 2. Significant positive (+) and negative (−) relationships from statistical models and Kendall's tau correlation tests.

Response variable† (life-form, frequency for species)	Silt/clay	CGI	Soil pH	Silt/clay × grazing	Silt/clay × soil pH	CGI × soil pH
Grass cover	int.		int.		−***	
Forb cover	−***		+***			
Total species diversity	+*					
Annual species diversity	+**					
Perennial species diversity		+*	−*			
Total species richness	+*					
Annual species richness	+*	int.	int.			−*
Perennial species richness		+*				
Annual grass richness	+*					
Annual grass abundance	+***					
Perennial grass abundance (small-scale)	+*			NA	NA	NA
Perennial forb abundance		+*				
Rare species richness	+**		−*			
Total species richness (small-scale)	+*					
Tribulus eichlerianus (AF, 57)	−*		+***	NA	NA	NA
Dactyloctenium radulans (AG, 56)	+***			NA	NA	NA
Aristida contorta (AG, 54)		−***	−***			
Eragrostis dielsii (AG, 53)	int.	int.		+**		
Tragus australianus (AG, 22)	+**	+**				
Triraphis mollis (AG, 44)	−***	−***	+**			
Ptilotus polystachyus (AF, 49)	−**	−**				
Indigofera colutea (AF, 40)	−*	+**	+**	NA	NA	NA
Amaranthus mitchellii (AF, 33)	int.	int.		+**		
Heliotropium tanythrix (AF, 33)	+*					
Portulaca intraterranea (AF, 32)	+**		+**			
Portulaca oleracea (AF, 30)	−*	−*		NA	NA	NA
Fimbristylis dichotoma (PF, 26)	+**	−*	−*			
Eremophila obovata (Shrub, 46)	−**	−***	−*			
Ipomoea polymorpha (AF, 14)	−*			NA	NA	NA
Eragrostis sororia (AG, 13)	+**			NA	NA	NA
Paspalidium rarum (AG, 13)	+***	−*	−**	NA	NA	NA
Sporobolus australasicus (AG, 13)		+*		NA	NA	NA
Sida cunninghamii (PF, 11)	−*		+*	NA	NA	NA
Vigna sp. (McDonald Downs Station RA Perry 3416) (AF, 11)	+**			NA	NA	NA

Notes: The abbreviation "int." indicates that the variable was present in the significant model interaction. Species that exhibited no significant relationship with any explanatory variables are listed in Appendix C. "NA" indicates that the interactions do not apply because the response variable was examined with the nonparametric Kendall's tau test. Empty cells in correlation columns indicate that the relationship is nonsignificant. CGI stands for cumulative grazing index. Life-form abbreviations are: AG, annual grass; AF, annual forb; PG, perennial grass; PF, perennial forb.

† For individual species as response variables, life-form and frequency are given in parentheses.

* $P < 0.05$; ** $0.05 < P < 0.01$; *** $0.01 < P < 0.001$.

(Díaz et al. 2007) showed a pattern of increase in abundance of annual plants with grazing in arid environments with an evolutionary history of relatively low exposure to grazing, but this trend was not evident in this study (Table 2). Perennial species richness and diversity had a weak positive response to grazing. A modal distribution pattern for total plant richness and annual plant richness at both small and large spatial scales cannot be interpreted as being consistent with the intermediate-disturbance hypothesis because the lower values where grazing is minimal do not correspond with higher abundance, richness, or diversity of perennial species as would be expected if the perennial species were excluding annual species through competition. These results are generally consistent with other analyses from arid grasslands (Friedel 1997, Adler et al. 2005, Lewis et al. 2008), but contrasts with patterns described for more mesic grassland where species richness and diversity does respond to grazing (Collins and Barber 1985, Fensham et al. 1999, Frank 2005). Highly variable and low rainfall does not allow for sufficient dominance by perennial species to limit the growth of ephemeral species on the soils in the dune swales. The results do not support the prediction for a modest negative effect of grazing on species and diversity in Australian aridlands (Cingolani et al. 2005) and suggest that any sensitivity of the Australian flora because of a light evolutionary exposure to grazing is offset by the limitations imposed by the low productivity of the environment and consequent spatial and temporal patterns of grazing activity.

The swales in the Simpson Desert dune fields seem to be an example of managed herbivore populations in "disequilibrium" with their plant resources (Illiuss and O'Connor 1999). During the rare periods after rain, moisture in forage and surface waters reduce the reliance of stock on artificial bore water. In these times of abundance, ephemeral species are able to complete their life cycle before herbaceous fodder has declined to the extent at which there is selective pressure on palatable

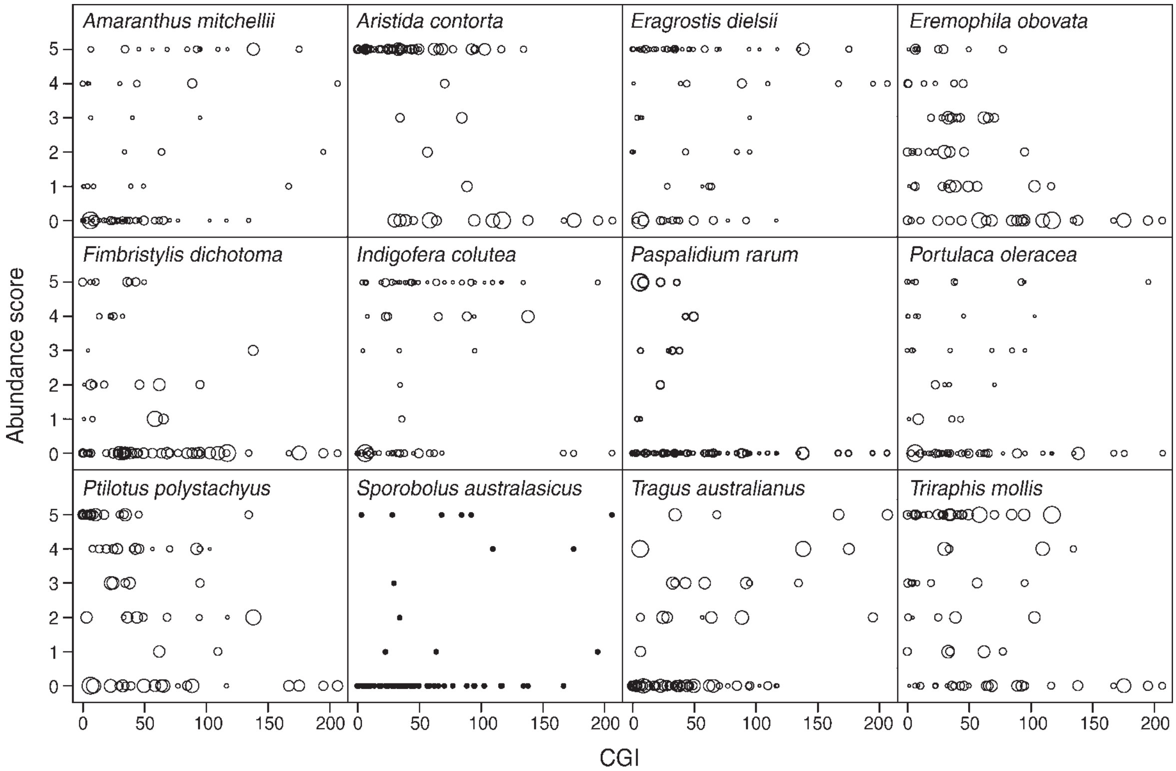

FIG. 6. Abundance data for the species exhibiting a significant response to the cumulative grazing index (CGI). Circle sizes are proportional to the value of other variables that either have an interactive effect (*Amaranthus mitchellii* and *Eragrostis dielsii*) on the response or have an independent effect on the response. The secondary variable is soil pH for *Aristida contorta* and silt/clay for other species. No secondary variable was significant for *Sporobolus australasicus*. Abundance data are derived from unrepeated scoring of species presence in increasing quadrat sizes (see *Methods*).

species. Adaptations for surviving boom and bust rainfall also act as adaptations to grazing in these arid environments. The understories of the dune swales are dramatically ephemeral, being reduced to bare ground during typical conditions and regenerating as a sparse herbaceous cover after rain. All of the common perennial forbs (Table 2), with the possible exception of *Fimbristylis dichotoma*, have an ephemeral growth strategy and germinate en masse after substantial rain (R. J. Fensham, *personal observation*).

Despite the importance of edaphic conditions, grazing seems to be having a largely independent effect on floristic composition in the Simpson Desert dune swales. Grazing and soil pH were significantly related in this study but the effect seems to result from the chance occurrence of low pH sites at water-remote locations rather than high soil pH around water points (Appendix B), as would be expected if long-term grazing disturbance resulting from the deposition of urea in urine and manure was raising alkalinity (Turner 1998, Smet and Ward 2006). The soils have not been compacted around the water points, and there was no evidence of exacerbated erosion. There is also no evidence of discontinuity in the composition of the floristic data (Fig. 5), as was apparent in a similarly designed study from Mongolian arid grassland (Sasaki et al. 2008). Grass cover and forb cover had no significant relationships with the cumulative grazing index. There are no perennial species that respond negatively to grazing that would seem to have an important role in stabilizing soils. The most likely candidate is the perennial sedge *Fimbristylis dichotoma*, which forms a small tussock, but the significance of its response pattern can only be tentatively suggested because, while it was only present in high abundance at lightly grazed sites, it was also frequently absent in these circumstances (Fig. 6). In any case, *Fimbristylis dichotoma* rarely forms sufficient cover to reduce erosion. The annual grasses *Aristida contorta* and *Triraphis mollis* and the annual forb *Ptilotus polystachyus* exhibit a decreasing trend with cumulative grazing and thus do seem to be preferentially grazed. The response of *T. mollis* and *P. polystachyus* is mostly a product of their absence where cumulative grazing pressure is high (Fig. 6), such as within 500 m of water points. Areas subject to this level of grazing pressure are only a miniscule proportion of the broader landscape in the Simpson Desert (Fig. 1). *Aristida contorta*, the most dominant grass, is also eliminated at high grazing pressure, but shows a more continual pattern of decline. All three species are currently common in the landscape

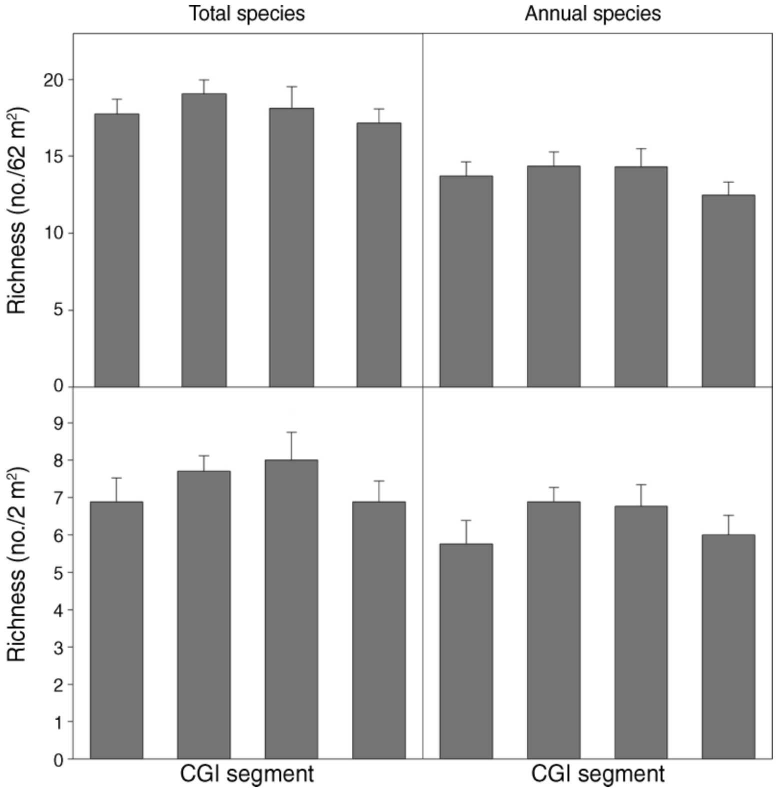

FIG. 7. Total species richness and species richness of annuals (mean + SE) at two spatial scales according to segments of the cumulative grazing index (CGI). Sites were ordered by CGI and then divided into four equal segments (4 × 17 sites). These groups are presented because they exhibit a weak modal pattern. There are no statistically significant differences between any of the four categories ($P > 0.05$). CGI increases from left to right.

and can persist where grazing pressure is moderate. All three have wind-dispersed seed, and with an annual life strategy it seems likely their populations would recover with the relaxing of grazing pressure. While it seems unlikely that degradation states have formed around water points the ultimate test will be the capacity of these areas to recover the plant composition represented in the lightly grazed parts of the landscape.

Swainsona microphylla was the only species with a frequency greater than four was restricted to sites with low exposure to grazing (Appendix E), and this distribution could easily be expected by chance. The lack of species that that can be identified as reliant on grazing relief refuges in the gidgee swales of the Simpson Desert seems to contrast with the findings of Landsberg et al. (2003). The sites in that study had a longer history of grazing than the Simpson Desert swales but also had a less rigorous analysis based on far fewer sampling stations across a broad range of environments. Landsberg et al. (2002) suggested that palatable, drought-hardy perennial species may be most susceptible to grazing on water-remoteness gradients. In this study the richness of perennial species and the abundance of perennial forbs showed a positive relationship with cumulative grazing. However, the results also reinforce that some perennial species can be sensitive to grazing in arid systems. Of the five relatively common perennial species, *Eremophila obovata* and *Fimbristylis dichotoma* are examples of perennial species that declined with grazing. The response of the low shrub *Eremophila obovata* is mostly a product of absence at heavily grazed sites (Fig. 6). However, further declines in *Eremophila obovata* would be expected if the adult plants are able to survive with moderate grazing, but recruitment is inhibited, as has been predicted for other palatable shrubs in Australian rangelands (Andrew and Lange 1986, Hunt 2001). For another palatable *Eremophila* with a similar life-form to *Eremophila obovata*, long-term monitoring data suggest that while grazing does cause adult mortality it does not inhibit recruitment (Watson et al. 1997), suggesting that as long as seed production can continue some grazing-sensitive perennial shrubs can persist in arid areas subject to moderate grazing pressure. *Eremophila obovata* was flowering and fruiting abundantly wherever they occurred during this study.

These findings may have relevance to Australian deserts at large. Of 16 species in common with other Australian grazing studies from aridlands (Table 3), one consistently increases with grazing, another consistently decreases with grazing, three have a consistent neutral response, and the other 11 have variable responses.

TABLE 3. Response to grazing of plant species from Australian grazing studies in arid environments.

Common species	Current study	Landsberg et al. (2003)	Read (1999)	Rogers and Stride (1997)	Letnic (2004)
Eragrostis dielsii	neutral and increaser	increaser and decreaser	neutral	increaser	
Tragus australianus	increaser			increaser	
Aristida contorta	decreaser		neutral	neutral	
Lepidium phlebopetalum		mixed			
Abutilon fraseri/*A. otocarpum*	neutral	decreaser			
Enneapogon polyphyllus	neutral	decreaser			
Salsola tragus	neutral	decreaser	increaser		
Dactyloctenium radulans	neutral		neutral	increaser	
Enneapogon avenaceus			decreaser		
Goodenia lunata			increaser		
Senna artemisioides			increaser		
Tribulus eichlerianus†	neutral		neutral		
Enneapogon cylindricus			neutral		
Sclerolaena diacantha	neutral		neutral		
Chenopodium cristatum		increaser			
Ptilotus polystachyus	decreaser				decreaser

Notes: Species are only included from Landsberg et al. (2003) if they were sufficiently abundant at more than one site to be classified. A mixed species response refers to a species that has an increaser response at one site and a decreaser response at another. Landsberg et al. (2003) conducted a study across a broad range of habitat types; Read (1999) conducted a study in linear sand dunes including both dune and swale; Rogers and Stride (1997) conducted a study in *Acacia aneura* shrubland on sand sheets; and Letnic (2004) conducted a study in linear dunes.

† Probably *T. terrestris* in Read (1999).

Comparisons can only be cautiously interpreted and may have more to do with statistical power associated with infrequent species than contrary responses. Furthermore, some studies represent recovery from a history of grazing, while others such as ours compare hardly grazed with more heavily grazed areas. This study has demonstrated that the responsiveness of some plant species to grazing is dependent upon relatively subtle changes in soil texture (Appendix D), so it is not surprising that species can exhibit a range of responses to grazing across their geographic range (Vesk and Westoby 2001).

The predictions that a modest decrease in species richness in response to grazing, that the impact zone in the immediate vicinity of the water points will exhibit characteristics of an alternative degradation state, and that there will be plant species reliant on grazing relief refuges are not supported by these results. It is possible that the relative short exposure to managed grazing in the Simpson Desert dune swales (mostly less than 20 years) has not been sufficient to have expressed full impact, but the results suggest that these environments are resilient to the early impacts of sustained livestock grazing at least. The findings do not demonstrate high susceptibility to managed grazing despite the study habitat satisfying the criteria of: (1) soil fertility within an infertile matrix and (2) from a continent with limited exposure to grazing over evolutionary timescales (Stafford Smith and Morton 1990, Morton et al. 1995).

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APPENDIX A

Photographs of Simpson Desert dune swale habitat (*Ecological Archives* E091-050-A1).

APPENDIX B

Relationship between the cumulative grazing index (CGI) and soil pH (*Ecological Archives* E091-050-A2).

APPENDIX C

Nonsignificant relationships from statistical models and Kendall's tau correlation tests (*Ecological Archives* E091-050-A3).

APPENDIX D

Modeled probability of occurrence of *Amaranthus mitchellii* and *Eragrostis dielsii*, having interactions between the cumulative grazing index (CGI) and percentage of silt/clay (*Ecological Archives* E091-050-A4).

APPENDIX E

Abundance of *Swainsona microphylla* (present at five sites) in relation to the cumulative grazing index (CGI) (*Ecological Archives* E091-050-A5).