Abiotic effects predominate under prolonged livestock-induced disturbance

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Abstract Despite the widespread recognition that disturbance by livestock affects multiple indices of landscape health, few studies have examined their effects on both biotic and abiotic processes. We examined the effects of livestock disturbance on soil, vascular plants and reptiles across a disturbance gradient in a semi-arid Australian woodland. Our gradient ranged from long-ungrazed water remote sites, through intermediately grazed recovering sites, to currently grazed sites close to water. Our aim was to examine the nature of the effects of grazing-induced disturbance on biotic and abiotic processes along the gradient. We detected small biotic effects, but no abiotic effects, at low levels of disturbance (intermediate sites). We could not detect a consistent biotic effect on plants or reptiles along the gradient, except between the extreme disturbances. In contrast, we recorded substantial reductions in abiotic structure and function at the most disturbed sites. Structural changes included reductions in the cover of shrub hummocks and increases in bare soil, and reductions in cryptogamic soil crusts. Structural changes were associated with declines in function (soil stability and nutrient indices). Our data are consistent with the notion that abiotic effects predominate at high levels of disturbance in rangelands. Given the extent of abiotic modification at currently grazed sites, the cover of abiotic elements such as hummocks and soil surfaces would seem a better indicator of the long-term effect of grazing-induced disturbance than biotic components. The extent of disturbance at currently grazed sites across large areas of rangeland suggests that autogenic recovery will be protracted.

Key words: disturbance, grazing gradient, landscape function, overgrazing, plant diversity, reptiles.

INTRODUCTION

Over the past two decades substantial advances have been made in the theory of degradation processes in rangelands (e.g. Milton *et al.* 1994; Briske *et al.* 2003; Mayer & Rietkerk 2004). These developments have been accompanied by an improved understanding of the interconnections between both functional and structural, and biotic and abiotic components of ecosystems (King & Hobbs 2006). Functional semi-arid systems are characterized by tight controls over critical resources such as water, organic matter and nutrients (Noy-Meir 1979/80). These resources are concentrated within nutrient- and soil-rich patches that occur within a less fertile matrix (Tongway & Ludwig 1994). The patchy distribution of resources supports greater levels of plant growth and production and enhanced species diversity (Boeken & Shachak 1998), and is the basis for functioning dryland ecosystems.

Grazing-induced disturbance tends to alter the regulation of critical resources from biotic control to abiotic control (King & Hobbs 2006). Moderate grazing by domestic livestock reduces plant biomass and leads to a replacement of palatable by unpalatable plants, and sometimes, encroachment by woody plants (Jeltsch *et al.* 1997; Landsberg *et al.* 2003). These effects are largely biotic in nature. More persistent effects of livestock grazing are structural and functional changes to the abiotic environment. Grazing-induced trampling, for example, has been shown to increase soil compaction, reduce the resilience of surface soils to breakdown by wind and water, and ultimately reduce the structural complexity of surface soils (Jones 2000; Tongway *et al.* 2003). Feedback effects on plant and soil processes lead to reductions in litter cover and therefore its decomposition, reduced mineralization of organic matter and depleted soil nutrient pools (Golluscio *et al.* 2009).

There have been numerous studies of the effects of grazing-induced disturbance in arid and semi-arid ecosystems (Landsberg *et al.* 2003), and many have focused on grazing gradients out from livestock

Table 1. Characteristics of the three grazing treatments

Attribute	Long-ungrazed	Intermediate	Currently grazed
Proximity to water, grazing status	Remote, long-ungrazed	Close, recently ungrazed	Close, currently grazed
Grazing animals	Goats, kangaroos, rabbits	Goats, kangaroos, rabbits	Sheep, goats, kangaroos, rabbits
Distance to water (km)	3.14 (1.21)	3.3 (1.38)	1.7 (0.63)
Time since stock removal (years)	28.0 (0.00)	4.9 (3.33)	0
Expected condition response to grazing	Good	Intermediate	Poor

Data are mean (±SD).

watering points (see review by Fensham & Fairfax 2008). Disturbance is greatest close to watering points where animals tend to concentrate, and these effects tend to decline exponentially with increasing distance from water (Lange 1969; Fusco *et al.* 1995; Fensham & Fairfax 2008). Grazing gradients can be useful tools for studying not only degradation processes but the nature of the restoration of ecosystem function. The ecological framework for degradation and restoration presented by King and Hobbs (2006) predicts only small reductions in ecosystem functions with small increases in the intensity of disturbance in intact systems. Given the prediction that biotically driven processes predominate at lower levels of resource degradation, i.e. that resource regulation is controlled by biota at lower levels of degradation, we would expect only biotic changes in landscapes where the intensity of disturbance by livestock is low. Conversely, increased levels of disturbance in that part of the gradient that is subjected to more prolonged and greater levels of livestock grazing are predicted to result in substantial reductions in function i.e reductions in the capacity of the system to cycle nutrients, infiltrate water or resist deformation, which are largely abiotically driven (*sensu* Tongway & Ludwig 1996).

We used a grazing gradient approach to examine potential changes in structure and function associated with different levels of livestock grazing in a semi-arid *Casuarina pauper* woodland. Long-ungrazed sites in a National Park, which were generally remote from water, were compared with currently grazed sites relatively close to water and intermediately grazed sites with a short period of recovery. Our intermediate sites had been destocked within the past decade, and occurred at variable distances from water (Table 1). Our study is novel, because unlike many grazing gradient studies that consider only grazed and ungrazed sites, or those close to and far from water, we integrated both distance from water and time since destocking into a single measure of grazing-induced stress. Further, most grazing gradient studies have tended to concentrate on either biotic or abiotic changes, but rarely both. In our study we measured a range of compositional, structural and functional ele-

ments (plants and reptiles, biogeochemical indices, landscape elements) which together, are more likely to reflect long-term changes in woodland health rather than studies based on single attributes.

In comparison with the long-ungrazed National Park sites, we expected only small reductions in biotic components such as plant richness and cover at the recently reserved (intermediate) sites, and no substantial differences in abiotic structure or function. Conversely, we expected marked reductions in abiotic functions such as biogeochemical indices (infiltration, nutrient and stability functions) and abiotic structure such as the spatial arrangement of resource-concentrating patches, soil colonized by cryptogamic crusts, and cover of hummocks occupied by perennial shrubs, at the continuously grazed end of the gradient, in comparison with the long-ungrazed sites. Strong feedbacks between abiotic structure and function and biota mean that the most dysfunctional (continuously grazed) state would also have diminished biotic components i.e. reduced richness of plants and animals, but unknown changes in composition. The loss of abiotic structure from the severely disturbed sites with substantial accompanying resource loss, would therefore likely compromise ecosystem recovery.

METHODS

The study area

The study was conducted at 21 sites within a 30 km radius north-west of Buronga in south-western New South Wales, Australia (34°6′S, 142°6′E). The landscape is predominantly Quaternary sandy and clayey calcareous sediments occurring on level to slightly undulating plains with slopes to 1%, often interspersed by areas of aligned west-east trending dunes of low relief (<4 m). These calcareous sediments are a widespread geological formation of the Murray Basin, and contain large amounts of calcium carbonate (3–30%) in either the fine earth fraction or as soft and hard concretions. The soils are classified as Hypercalcic Calcarosols (Isbell 1996) and consist of a yellowish-red massive loamy sand to

loam grading to an earthy fine-sandy loam, with diffuse hard and soft carbonate nodules at 60 cm.

Landuse in the area is predominantly grazing of sheep on native pastures, although there is increasing pressure to clear woodland, particularly belah (*Casuarina pauper*)-rosewood (*Alectryon oleifolius*) communities, to establish winter cereal crops. Smaller areas are dedicated for nature conservation (e.g. Mallee Cliffs National Park, Mungo National Park). Mean annual rainfall for Buronga is 288 mm (Bureau of Meteorology 1988) of which 25% more rain falls in the six cooler months (March to August) compared with the warmer months. Average annual rainfall was below average in 2004 (173 mm) and about average in 2005 (277 mm). Mallee Cliffs was managed as a pastoral lease and gazetted as a national park in 1977. Stocking rates prior to gazettal varied according to vegetation community but were in the order of about 10 ha DSE^{-1} (dry sheep equivalent i.e. one non-lactating ewe) in the belah woodland (Department of Lands, unpubl. data, 2003). There have been few exceptionally 'wet periods' at Mallee Cliffs National Park apart from 495 mm in 1992. Significant drought years where the annual rainfall was <200 mm occurred in 1982, 1985, 1994, 2002 and 2004, and since 2000, annual rainfall has been below-average except for the year 2003. The vegetation at the sites is typical of the belah-rosewood vegetation association, dominated by belah, rosewood, sugarwood (*Myoporum platycarpum* ssp. *platycarpum*) and wilga (*Geijera parviflora*). The understorey supports a variable cover of sub-shrubs from the family Chenopodiaceae (*Atriplex*, *Maireana*, *Einadia*), *Dodonaea* spp. and *Senna* spp., perennial grasses *Austrostipa* spp. and *Austrodanthonia* spp., and a sparse cover of ephemeral forbs including *Sclerolaena* spp. The soils supported a rich community of lichens, mosses and liverworts (Eldridge 1998) which make up a cryptogamic crust with cover up to about 80%.

Site selection

The study was conducted over an area of about 2800 km². Its location was chosen because of the proximity of long-ungrazed and recently reserved sites within a matrix of currently grazed pastoral land within the belah woodland community type. The reserves were fenced, domestic livestock removed, and the watering points decommissioned to help reduce grazing pressure from goats and kangaroos. We selected seven reserve sites (termed 'Intermediate') from the 27 existing reserves on the basis of similar floristic association and vegetation structure, and a reasonable distance (~10 km) from long-ungrazed (National Park) and currently grazed sites. The seven long-ungrazed sites occurred within Mallee Cliffs National Park, and the seven currently grazed sites were from areas surrounding the Park that have been grazed continuously for the past 150 years (Table 1). We considered the National Park sites to be statistically independent as they were separated by distances of about 3–8 km. Rates of utilization for currently grazed sites were within the range of about 5–7 ha DSE^{-1}.

Sheep are known to graze about 3 km from water (Pringle & Landsberg 2004) so it is likely that the intermediate (reserve) sites have always been subjected to only light levels of grazing. All sites were selected on the basis that they were >1.5 km from a watering point, i.e. outside immediate heavily impacted zone of the piosphere (Lange 1969) but also close enough to water to be regarded as being grazed. In some cases an ephemeral ground tank was located close to the site, but only structures that held water for 12 months or more were considered. Sites were also selected to avoid any ecotonal (edge) effects between adjacent communities but had to be accessible by vehicle.

We used an Arc GIS platform incorporating Spot Imagery, Land System mapping and vegetation mapping in conjunction with Property Resource Plans to assist site selection and to calculate the minimum distance of each site from permanent water. As we were primarily interested in the grazing effects from sheep, cattle and feral goats, we did not consider water points that were closer, but where access was restricted because of stock-proof fencing. We acknowledge, however, that kangaroos and rabbits may also have grazed some areas of all treatments, but consider this to be minor in relation to the overriding effects of grazing by cattle and sheep. Although rabbit densities are relatively high in the region, they are not a major herbivore in the belah woodlands as the soils have higher clay contents than the more favoured adjacent sandy soils in open mallee areas. Additionally, since the spread of Rabbit Calicivirus Disease, rabbit numbers have been low in the region (0.06 rabbits km^{-2}; DECCW unpubl. data, 2010). Spotlight counts in Mallee Cliffs National Park indicate that kangaroo numbers are relatively low (0.17 km^{-2}) as the ground stratum tends to be dominated by chenopods rather than grasses. Goats are routinely taken from the Park and surrounding areas but their densities are very low. We used Lower Murray Darling Catchment Management Authority and Department of Lands databases to determine when grazing ceased on all sites. Currently grazed sites were assigned a value of zero for time since cessation of grazing.

Site measurements

Each sampling site consisted of two 0.1 ha (50 m by 20 m) plots, separated by about 300 m. Within each plot we centrally placed a smaller 20 m by 20 m plot that formed the basis for detailed assessment of groundstorey vegetation. Within the smaller plot we estimated the cover of all vascular plants (including trees and shrubs), as well as cover of litter, cryptogamic crust and bare soil. Within the larger plot we enumerated the number of hollows greater than 50 mm in diameter in all trees, and measured the total length of all logs >100 mm in diameter and 1 m long.

We placed a 50 m transect through the centre of the 50 m plot in order to characterize the different landscape units present at a site, and to assess the functional integrity of the site in terms of how resources such as runoff water, entrained sediment, seeds, nutrients and organic matter are either retained within various patches (see below) or 'leak' from the system (Landscape Function Analysis: LFA; Ludwig & Tongway 1995). Landscape Function Analysis has been used widely in arid and semi-arid systems and been shown to be highly correlated with plant and grasshopper diversity (Ludwig *et al.* 1999), the density of medium-sized mammals (Ludwig *et al.* 2004) and the abundance of small mammals, birds, reptiles and ants (Karfs & Fisher 2002). Further, landscape features such as the distribution of plant patches have been shown to be highly correlated with soil variables that are

Table 2. Percentage cover of the different landscape units at sites within the three treatments

Landscape units	Geomorphic origin	Long-ungrazed		Intermediate		Currently grazed	
		Mean	SE	Mean	SE	Mean	SE
Tree hummocks	Biotic, depositional	23.2	5.2	28.1	6.7	28.9	3.6
Shrub hummock	Biotic, depositional	8.4[a]	2.5	3.2[b]	1.5	0.0[b]	0
Mounds with litter	Biotic, depositional	11.6	2.5	10.5	0.9	6	2
Litter train	Biotic, depositional	0.7	0.5	1.9	1.8	1.6	1.2
Plains with cryptogams	Erosional	52.1[a]	5.3	47.5[a]	4.3	30.2[b]	5.5
Plains with litter	Erosional	0	0	0.2	0.2	1.1	0.7
Plains bare	Erosional	3.9[a]	1.6	8.3[a]	1.6	21.1[b]	4.8
Plains with windsheeting	Erosional	0	0	0.5	0.5	11	7.4

Different letters within rows indicate a significant difference in that landscape unit at $P < 0.05$. SE, standard error of the mean.

indicative of desertification processes (Maestre & Escudero 2009). Because LFA relies heavily on the type, cover and arrangement of physical structures in the landscape such as plant and tree hummocks and perennial grass patches, it is an ideal model for interpreting changes in the abiotic environment.

We recorded the total length of eight different landscape units along the transect in order to determine their relative differences across the gradient. Landscape units included permanent features of the landscape, delineated along the transect, such as tree and shrub hummocks and their interspaces (plains), which were characterized by different biotic and abiotic features such as cryptogams, litter or bare soil. We recorded the total number, length and width of permanent obstructions such as perennial grasses, shrubs and logs, as well as the length and number of the intervening spaces between them (fetches). This enabled us to derive three measures: (i) the number of obstructions per unit length of transect; (ii) the total width of obstructions per unit length of transect; and (iii) the average distance between obstructions (fetch length).

Detailed measurements of the morphology of the soil surface were made within the landscape units identified on each plot (Table 2) using simple, quadrat-based methods (Tongway 1995). Ten quadrats were assessed along each transect and stratified according to the relative cover of different landscape units on a plot. Thirteen soil surface features were recorded within each 0.5 m² quadrat. The features were: (i) crust coherence, which indicates the force required to dislocate surface particles, and the ability of the surface to respond to stress or reform following wetting (Tongway 1995); (ii) microtopography, which assesses the degree of surface roughness and therefore the potential for the surface to traps seeds and water; (iii) degree of surface cracking, which measures the proportion of the surface covered with cracks and relates to potential for soil to be displaced during an erosion event; (iv) crust stability, which measures, using the Emerson slake test (Emerson 1994) the degree to which the soil will breakdown because of slaking or dispersion when placed in water; (v) cryptogam cover, the cover of non-vascular plants (mosses, lichens, liverworts, cyanobacteria, etc.) on the surface; (vi) erosion amount, either wind or water, assessed by measuring erosional features such as rilling, sheeting, scalding, terracettes and pedestals; (vii) cover of deposited material resulting from deposition from

elsewhere; (viii) litter cover; (ix) litter origin, whether local litter or transported from elsewhere, and (x) degree of litter incorporation into the soil, i.e. how well the litter and soil are mixed together at the surface; (xi) plant foliage cover; (xii) plant basal cover; and (xiii) soil texture, which indicates how well the soil will receive and store water. A detailed description of this methodology is presented in Tongway (1995).

The 13 soil surface attributes described above were used to derive three biogeochemical indices of soil function that describe the extent to which the soil (i) cycles nutrients; (ii) conducts water; and (iii) resists erosion. These indicate the extent to which vital soil processes are maintained within an individual landscape unit, and the results can by scaled up to the site level. For a particular quadrat the value of each attribute was given a score, usually from 1–5, but sometimes from 1–4, such that a larger score equated with a healthier surface. Thus for example, the soil microtopography classes of <5 mm, 5–8 mm, 8–15 mm, 15–25 mm and >25 mm were assigned the scores of 1, 2, 3, 4 and 5, respectively. Thus a rougher surface implies a better soil condition and therefore receives a higher score. The quadrat's index of stability was derived as the sum of the seven scores for surface cracking, surface stability, crust coherence, degree of erosion, cover of cryptogamic crusts, foliage cover and litter cover expressed as a percentage of 40, the maximum possible score.

Four of the surface attributes described above (surface microtopography, cryptogam cover, basal plant cover, and a combined litter index derived from the product of its origin, cover and degree of incorporation) were used to derive a score for the nutrient status of the soil, based on its ability to cycle and retain nutrients. Finally, values for basal cover, litter cover-origin-incorporation, microtopography, slake test and soil texture were used to derive an index of infiltration; how well the soil accepts water.

Vertebrate pitfall trapping

In early February 2005, we established two 30 m pitfall lines adjacent to each LFA transect in order to assess reptile populations. Each pitfall line consisted of five plastic 20L bucket traps spaced at 5 m intervals along a 30 m fibreglass wire drift fence. Pitfall traps were left open for nine nights and checked every morning between 06:00 and 09:30 h. All

captured animals were identified, then marked on the ventral surface using a black felt pen in order to detect recaptures and then released. We report here only captures of reptiles as few mammals were captured.

Statistical analyses

We derived a value for each of the three biogeochemical indices (stability, infiltration, nutrients) for each site by adjusting for the relative proportion of the various landscape units at a given site. Prior to analyses, data were averaged over the two LFA transects or plots (plant, litter, bare soil, cryptogam cover, log cover, number of tree hollows, reptile abundance and diversity) at each site. We used one-way ANOVA to examine differences in the cover of landscape units, biogeochemical indices, landscape organization index (patch length as a proportion of total transect length), plant and soil cover, and plant and animal abundance and diversity among the grazing treatments after checking for homogeneity of variance using Levene's test (Minitab 2007). Data were transformed, where necessary (generally $\log_{10}$ or $\sqrt{x + 1}$), in order to normalize the residuals and/or to stabilize the variances. Data that could not be transformed were tested using the non-parametric Kruskal-Wallis test. *Post-hoc* Least Significant Difference (LSD) tests were used to examine differences in means. Simple regression analysis was used to examine the significance of relationships between landscape structure (e.g. geomorphic indices, cover of bare soil, litter cover, number and size of patches) and plant cover and richness.

Permutational multi-variate analysis of variance (PER-MANOVA, Anderson *et al*. 2008) was used to test whether the composition of vascular plants and reptiles varied significantly among the three grazing treatments. The relative positions of the 21 sites in terms of vascular plants, were then displayed with a Canonical Analysis of Principal Coordinates (CAP) biplot (Anderson *et al*. 2008). The degree of association between different vascular plant species and the three grazing treatments was evaluated with Indicator-Species Analysis using PC-ORD (McCune & Mefford 1999). Indicator values (IV) are maximal (100%) when all individuals of a given disturbance type are restricted, for example, to a particular vegetation community, or all samples from that community contain that disturbance type.

RESULTS

Landscape units

Eight landscape units were identified across the 21 sites (Table 2). Plains were typically expansive, level (<0.5% slope) environments with local microrelief to 2 cm, but generally <1 cm, and dominated by either cryptogamic crusts, bare soil, litter or an eroded surface. Cryptogamic surfaces were dominated by lichens and mosses. Plains sometimes had patches of sandy deposits up to 50 cm across (plains with wind-

sheeting), or were devoid of vascular or non-vascular vegetation. Tree and shrub hummocks were typically elevated (to 20 cm microrelief), reniform to semi-circular accumulations around the bases of individual trees and shrubs, groves of trees, and shrub patches. The surface often consisted of a variable cover of branches, leaves and detritus, sometimes with small patches of cryptogams. Tree hummocks generally showed evidence of soil disturbance by kangaroos (hip holes) and echidnas (foraging pits).

Mounds with litter were characterized by accumulations of coarse woody debris and organic material, generally associated with fallen timber and log mounds. The soils of these patch types were generally high in organic material and biological activity, with very sparse or non-existent cryptogam cover. Litter trains were characterized by arcs of organic depositional material perpendicular to the direction of slope, and resulting from the downslope movement by water or litter and entrained sediment. They were mostly found on more steeply sloping surfaces on wind-sheeted plains. Some litter trains showed evidence of colonization by termites and ants.

Plains with cryptogams, plains with bare soil and tree hummocks accounted for about 80% of the total area of the transects across the 21 sites. The cover of plains with cryptogams was significantly greater at intermediate and long-ungrazed sites than currently grazed sites ($F_{2,18} = 5.1$, $P = 0.018$). Conversely, cover of plains with bare soil was significantly greater at currently grazed sites than intermediate or long-ungrazed sites ($F_{2,18} = 8.1$, $P = 0.003$, on $\sqrt{}$–transformed data). Shrub hummocks were recorded only at intermediate and long-ungrazed sites (Kruskal-Wallis $H = 8.6$, d.f. = 2, $P = 0.017$).

Biogeochemistry and organization of landscape units

The average derived index of stability was greater at long-ungrazed (63.5%) and intermediate (64.9%) sites than currently grazed (56.5%) sites ($F_{2,18} = 15.9$, $P < 0.001$, Fig. 1). Nutrient index levels were marginally (but significantly) greater at long-ungrazed and intermediate (25.5%) sites than currently grazed (22.2%) sites ($F_{2,18} = 4.7$, $P < 0.023$ on $\log_{10}$ transformed data), but there were no significant differences in the infiltration index across the grazing gradient (29.2%, $P = 0.08$).

Predictably, the values of the three biogeochemical indices varied widely among the landscape units. Tree hummocks, litter mounds and litter trains generally had the highest values for nutrient and infiltration indices, while tree hummocks, litter mounds, litter trains and plains with cryptogams were the most stable. For all landscape units there were no significant

differences in any of the indices in relation to the grazing treatments ($P > 0.05$). Stable sites, i.e. those with a high score for the derived stability index, tended to have a greater plant cover ($F_{1,19} = 7.6$, $P = 0.013$, $R^2 = 0.25$), more extensive cryptogam cover ($F_{1,19} = 25.0$, $P < 0.001$, $R^2 = 0.55$) and a greater number of patches per unit length of transect ($F_{1,19} = 10.1$, $P = 0.005$, $R^2 = 0.31$). Similarly, sites that had high derived infiltration, stability and nutrient scores tended to have greater values of landscape organization ($F_{1,19} = 7.13$–8.68, $P < 0.015$, $R^2 = 0.24$–0.26).

There were significantly more permanent obstructions per 10 m length of transect at long-ungrazed sites than at either the intermediate or currently grazed sites ($F_{2,18} = 5.01$, $P = 0.019$, $R^2 = 0.29$ on $\log_{10}$-transformed data; Table 3). An increasing number of obstructions reflected the decline in average fetch length from long-ungrazed, through intermediate to currently grazed sites ($F_{2,18} = 4.57$, $P = 0.025$, $R^2 = 0.26$; √–transformed data). There were no differences in patch area (product of total obstruction 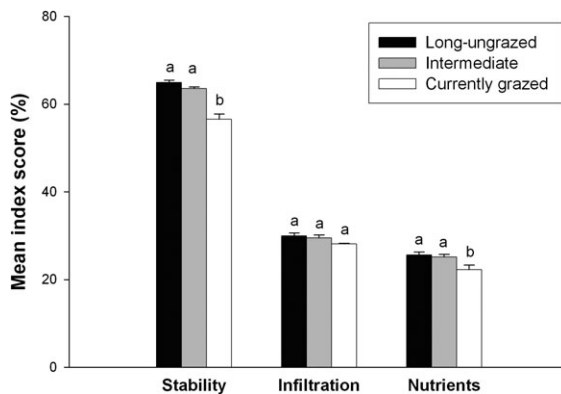width by length summed over the transect) or landscape orga-nization (total length of obstructions as a proportion of total transect length) across the gradient ($P > 0.11$). Sites with more permanent obstructions tended to have greater plant cover ($F_{1,19} = 24.3$, $P < 0.001$, $R^2 = 0.54$), but increasing distance between obstructions tended to be associated with greater plant species richness ($F_{1,19} = 14.5$, $P = 0.001$, $R^2 = 0.40$).

Plant diversity, cover and community structure

We recorded 65 vascular plant species across the 21 sites comprising seven tree species, three grasses, 17 shrubs and sub-shrubs, and 38 forbs (Table S1). There were significant differences in cover of five species (*Atriplex stipitata*, *Dodonaea viscosa* ssp. *angustissima*, *Chenopodium curvispicatum*, *Maireana appressa*, *Senna* form taxon '*filifolia*') among the three grazing treat-ments, with generally greater cover in the intermediate and/or long-ungrazed sites compared with currently grazed sites (Table 4). Three plant species (*Casuarina pauper*, *Atriplex stipitata*, *Olearia muelleri*) accounted for more than half of the total cover across all treat-ments (Table S1).

We recorded approximately 18% more plant species in the intermediate sites compared with long-ungrazed or currently grazed sites ($F_{2,18} = 6.08$, $P < 0.01$; Table 5). Margalef's richness was significantly lower in the long-ungrazed than the intermediate or currently grazed sites ($F_{2,18} = 4.75$, $P = 0.02$), but there was no significant difference in evenness ($P > 0.05$). Plant cover was 2.5-times greater at long-ungrazed and intermediate sites ($F_{2,18} = 4.67$, $P = 0.023$ on $\log_e$-transformed data), cover of litter ($F_{2,18} = 3.39$, $P = 0.056$) and bare soil ($F_{2,18} = 11.08$, $P = 0.001$) greater, and cover of cryptogamic crusts ($F_{2,18} = 13.1$, $P < 0.001$) less at currently grazed sites than the other sites. The cover of both native plants ($F_{2,18} = 3.92$, $P = 0.039$) and perennial plants ($F_{2,18} = 4.05$, $P = 0.035$ on $\log_{10}$-transformed data) was 1.6-times greater at long-ungrazed and intermediate sites

Fig. 1. Mean score for the three biogeochemical indices of soil health for the three disturbance treatments. Different letters within an index indicate a significant difference in treatments at $P < 0.05$. The mean values take into account the relative proportion of the various landscape units within the study area.

Table 3. Mean ($\pm$SE) values of landscapes function for long-ungrazed, intermediate and currently grazed sites

Attribute	Long-ungrazed		Intermediate		Currently–grazed	
	Mean	SE	Mean	SE	Mean	SE
No. of obstructions per 10 m	1.51[a]	0.25	0.85[b]	0.2	0.33[b]	0.1
Fetch length (m)	2.06[a]	0.14	2.92[b]	0.4	3.57[b]	0.48
Patch area[†]	0.87[a]	0.34	0.27[a]	0.1	0.27[a]	0.15
Landscape organization index[‡]	0.44[a]	0.04	0.42[a]	0.07	0.35[a]	0.05
Log length (m ha^{-1})	536[a]	87	556[a]	89.4	432[a]	79.6
Number of tree hollows (ha^{-1})	88.6[a]	16.6	89.3[a]	24.1	59.3[a]	15.3

Within an attribute, different letters indicate a significant difference at $P < 0.05$. [†]Sum of obstruction width by obstruction length. [‡]Total length of obstructions divided by total transect length. SE, standard error of the mean.

Table 4. Cover (%) of plant species by grazing treatment

Species	Long-ungrazed	Intermediate	Currently grazed
Atriplex stipitata	54.0[ab]	93.5[a]	5.0[b]
Chenopodium curvispicatum	17.5[ab]	29.0[a]	5.5[b]
Senna form taxon ' *filifolia*'	0.5[a]	11.5[b]	2.5[a]
Maireana appressa	2.5[a]	0.5[b]	0.0[b]
Dodonaea viscosa subsp. *angustissima*	2.0[a]	6.5[b]	0.5[a]

Different superscripts indicate a significant difference in cover between grazing factors at $P = 0.05$.

Table 5. Mean ($\pm$SE) indices of diversity and cover for the three treatments

	Long-ungrazed		Intermediate		Currently grazed	
Attribute	Mean	SE	Mean	SE	Mean	SE
No. of species	18.0[a]	0.95	22.6[b]	0.72	19.1[a]	1.15
No. of native species	17.0[a]	2.16	21.3[b]	1.8	17.4[a]	2.51
Margalef's richness	5.2[a]	0.26	6.3[b]	0.18	6.1[b]	0.36
Pielou's evenness	0.69[a]	0.02	0.71[a]	0.02	0.75[a]	0.05
Plant cover (%)	17.2[a]	5.5	18.2[a]	3	7.5[b]	1.2
Native plant cover (%)	56.1[a]	9.2	63.3[a]	6.4	37.6[b]	3.2
Perennial plant cover (%)	52.8[a]	9.1	58.3[a]	6.6	35.4[b]	3.1
Litter cover (%)	20.4[a]	2.5	17.2[a]	3.9	31.1[a]	4.4
Bare ground (%)	13.8[a]	2.4	15.9[a]	4.6	38.4[b]	4.8
Cryptogam cover (%)	48.6[a]	4.9	48.7[a]	4.1	23.1[b]	3.0

Values are averaged over the two transects at each site. For a given attribute, different letters indicate a significant difference at $P < 0.05$. SE, standard error of the mean.

(Table 5). There were no differences in the surface cover of logs or the number of tree hollows along the gradient ($P > 0.61$).

The currently grazed sites differed significantly in plant composition from long-ungrazed and intermediate sites, which were similar ($F_{2,18} = 1.84$, P(perm) = 0.011; Fig. 2). Increases in CAP axis 1 scores were associated with declining cover of *Atriplex stipitata*, *Dodonaea viscosa* ssp. *angustissima* and *Chenopodium curvispicatum*, while increases in the CAP axis 2 scores were associated with increasing cover of *Senna* form taxon '*filifolia*' and declining cover of *Maireana appressa* and *Olearia muelleri*. *Olearia muelleri* (Indicator Value = 53.2%, $P = 0.004$) was a good indicator of long-ungrazed sites, and *Atriplex stipitata* (IV = 56.9%, $P = 0.033$) and *Chenopodium curvispicatum* (IV = 55.8%, $P = 0.014$) good indicators of intermediate sites. *Salsola tragus* was a marginal (although significant) indicator of currently grazed sites (IV = 28.6%, $P = 0.033$).

Reptiles and small mammals

We trapped a total of 327 reptiles from 25 species. The reptile fauna was dominated by the Geckonidae (56%
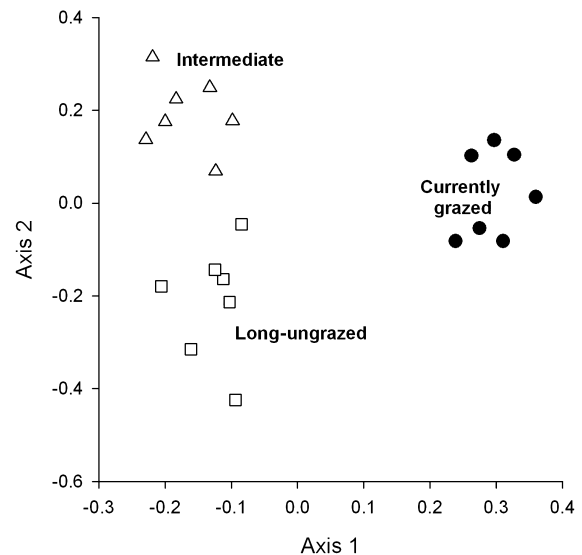

Fig. 2. Canonical Analysis of Principal Coordinates biplot of species data based on the cover of 65 vascular plant species across the averaged over the two transects at long-ungrazed, intermediate and currently grazed sites.

of captures) and the Scincidae (36%). The remainder comprised of three agamids, four elapids and one varanid (Table S2).

Some species were only found at the long-ungrazed (e.g. *Ctenotus brachyonyx*) or currently grazed sites (e.g. *Diplodactylus damaeus*), but low capture rates at many sites precluded us from making definitive statements about their distribution in relation to the gradient. There was no significant difference in the diversity ($P = 0.30$) nor composition ($F_{2,18} = 1.19$, P(perm) = 0.264) of the reptile community across the gradient. Skinks were slightly more abundant in long-ungrazed and intermediate than currently grazed sites (Kruskal-Wallis $H = 5.87$, $P = 0.053$), but there was no significant difference in abundance of geckos, nor any individual species across the grazing gradient ($P > 0.05$).

DISCUSSION

Our study examined the response of a range of biotic and abiotic attributes to grazing-induced disturbance in a *Casuarina pauper* woodland. Our aim was to understand more about disturbance processes using a gradient from long-ungrazed, water-remote National Park sites, to continuously grazed sites relatively close to water. The responses to grazing-induced disturbance were twofold. First, contrary to our prediction of a decline in biotic components under low levels of disturbance, we detected increases in vascular plant diversity and richness at the intermediate sites, and increased cover of some shrubs. Second, consistent with predictions, abiotic effects were most marked at the disturbed part of the gradient. We detected the largest reductions in structure (i.e. fewer perennial grass butts, reduced cover of shrub hummocks, more bare soil) at the most disturbed, continuously grazed part of the gradient. Furthermore, marked reductions in surface stability and nutrient cycling, measures of abiotic function, were apparent at the most disturbed part of the gradient. Overall our results suggest that sites close to water and subject to prolonged disturbance are likely to have a poorly functioning abiotic environment with depressed levels of ecosystem function; effects that are largely consistent with predictions under the King and Hobbs (2006) model.

Pronounced abiotic effects at higher levels of disturbance

A pronounced, abiotic effect of grazing in our study was the doubling of cover of bare soil at continuously grazed (38%) compared with the long-ungrazed (14%) sites and the concomitant halving of cryptogam cover (from 49 to 23%; Table 5). Although crypto-

gamic crusts are biotic in nature, the biotic component (lichen, moss, liverwort) cannot be considered in isolation from the underlying soil on which they are intimately attached, unlike vascular plants that can be removed without adversely affecting the abiotic environment. Cryptogamic crusts are important modulators of abiotic function in arid and semi-arid ecosystems. Crusts are hydrophobic (water repellent) and provide supplementary soil moisture sufficient to sustain the growth of perennial shrubs by redirecting interspace rainfall to the shrub hummocks (Bhark & Small 2003). Colonization of soil surfaces by cryptogamic crusts creates a roughened environment that is more resistant to physical breakdown under raindrop impact (Eldridge *et al.* 2002), and crust-resident cyanobacteria and cyanolichens fix nitrogen, which is used by vascular plants (Delgado-Baquerizo *et al.* 2010). Functionally therefore the crusted interspaces are relatively stable and productive, except under prolonged disturbance by livestock. Crust disturbance therefore impacts both upon biotic (crust organisms) and abiotic (underlying soil) structures. Field observations and studies of crust behaviour under simulated trampling (Eldridge 1998) suggest that moderately high levels of livestock trampling at the continuously grazed section of the gradient are responsible for extensive crust removal and considerable surface destabilization.

Prolonged disturbance of the crust in the interspaces has a potentially cascading effect on other abiotic components such as the shrub hummocks. Survival of hummocks and their attendant shrubs is compromised by changes in the condition of the crusted interspaces. Soil beneath shrub canopies contains higher levels of resources such as water, organic matter, seed and nutrients compared with soil from the interspaces (Schlesinger *et al.* 1996; Whitford 2002). This 'fertile island' effect of shrubs is reinforced by enhanced soil microbial and arthropod activity beneath the shrubs (Hibbard *et al.* 2001), promoting plant-soil feedbacks whereby the growth of shrubs and hummock-resident annual plants is promoted at the expense of plants in the interspaces. Destruction of soil crusts by livestock trampling not only starves the hummocks of supplementary water, but generates large volumes of sediment, ultimately leading to attrition of the hummocks (Offer *et al.* 1998; Eldridge *et al.* 2002). In our study many typical hummock-resident shrubs such as *Atriplex stipitata* and *Lepidium leptopetalum*, which are sensitive to overgrazing by domestic livestock (e.g. Graetz 1978), had diminished cover in the most disturbed section of the gradient. The loss of shrubs is a biotic process that precedes the loss of abiotic structure (the mounds), which is driven by livestock-induced trampling in the interspaces. Positive feedbacks on reduced water capture would accelerate erosion of the mounds and hasten surface destabilization. Reestablishment of

mounds and hummocks is protracted, and would take more than a century, even under destocking given projected accretion rates for hummocks and mounds on similar soils (Tongway & Ludwig 1996).

Biotic effects along the grazing gradient

Given the marked differences in abiotic effects within the most disturbed section of the gradient, we expected substantial negative flow-on effects on biota such as ground-dwelling reptiles, which prefer patchy environments with extensive surface cover (Mac Nally & Brown 2001) or perennial plants, which might require a stable soil surface. Changes in abiotic structure did not, however, produce consistent effects on all biota. Indeed, moderate disturbances have been shown to have variable effects on species diversity, with equi-probably chances of increases or decreases (Dumbrell *et al*. 2008). Total and native plant cover, and plant richness were greatest at the intermediate sites and least at the two extremes of the gradient, thus precluding a clearly defined grazing gradient effect. There were fewer shrubs at the most disturbed sites, but although we would have expected greatest shrub cover at the least disturbed sites, cover of woody species such as *Senna* spp*., Dodonaea viscosa* and *Atriplex stipitata* were greatest at intermediate sites. The trend was somewhat different for non-woody plants, with a very similar spectrum of species at intermediate and long-ungrazed sites; which were markedly different to that at the currently grazed sites (Fig. 2). Overall therefore the effects of disturbance on the structure of the biotic communities varied considerably depending on the taxa. The absence of a strong relationship between abiotic structure and biotic composition could be related to the generally undegraded status of the intermediate sites and thus their similarity to the long-ungrazed sites. Although all intermediate sites had been grazed prior to reservation, some were less disturbed than others, hence the higher cover of shrubs on the intermediate sites (Table 4), reflecting inherent site differences prior to reservation.

Reduced densities of obstructions such as grass butts would be expected to influence woodland biota by altering the quality of the habitat. In our study, the density of obstructions, most of which were grass butts and logs, declined from long-ungrazed (1.5 obstructions per 10 m) to currently grazed (0.33) sites (Table 3). Denser plant patches in grasslands, for example, have been shown to be positively correlated with abundances of invertebrates such as grasshoppers (Ludwig *et al*. 1999), although these relationships appear to be taxon-dependent (Abensperg-Traun *et al*. 1996). Similarly, reduced densities of web-forming spiders with increasing disturbance are thought to result from alterations in plant structure (Gibson *et al*.

1992), given that grazing reduces shrub shape and volume and is therefore likely to affect richness and abundance of spiders (Robinson 1981; Sanchez & Parmenter 2002). The greater abundance of reptiles at the long-ungrazed (49 species) compared with currently grazed (38 species) sites is consistent with studies of reduced reptile abundance under grazing (e.g. James 2003; Castellano & Valone 2006). The slight decline in abundance of skinks at the continuously grazed sites may reflect reductions in landscape structural elements such as shrub hummocks and grass butts, reduced litter (although we did not detect this at the site level) and increases in the cover of bare soil. Hummock-resident shrubs in arid areas provide habitat not only for arthropods (e.g. Whitehouse *et al*. 2003) but also their reptilian predators (Whitford 2002). Reptiles use shrubs and their hummocks as refugia from predation (Castellano & Valone 2006), but also as sites for foraging, basking and thermal regulation (Diaz 1992).

Large areas of bare soil and therefore sparse cryptogamic crust cover at the most disturbed end of the gradient would be expected to directly reduce populations of ground-active reptiles by creating high soil surface temperatures (James 2003). Conversely, increased cover of cryptogamic crusts might also improve habitat quality for reptiles, indirectly, by affecting the abundance of fossorial prey. Sites dominated by cryptogamic crusts are preferred habitat for some epigeic, fossorial spiders such as the Lycosidae and Gnaphosidae (Martin & Major 2001) which are preyed upon by goannas and some skinks. Spiders are probably responding more to the absence of litter, which enhances the ease of hunting, than to the presence of crusts *per se*. Cryptogamic crusts may provide a degree of structural stability to skink burrows as the thin cyanobacterial crust is harder than crust-free soils (Eldridge *et al*. 2002). In arid environments in the Negev Desert, burrows of geckos (*Stenodactylus*) and skinks (*Acanthodactylus*) occurred more frequently on soils with a cyanobacterial crust (Zaady & Bouskila 2002).

CONCLUSIONS

Our study demonstrates the marked effects of more than 150 years of disturbance by livestock grazing on the abiotic and biotic environment of a *Casuarina pauper* woodland. The effects of disturbance were apparent mainly in reduced cover of shrub hummocks, increased cover of bare soil and reduced cover of cryptogamic crusts. Overall, the study indicates that abiotic effects are pronounced within the most disturbed section of the grading gradient, consistent with the general theory of degradation processes and recovery in rangelands (King & Hobbs 2006). We were unable, however, to demonstrate a consistent biotic effect i.e.

changes in plant cover and diversity, and reptile composition, among the disturbance states, except between the extreme ends of the gradient i.e. currently grazed *vs.* long-ungrazed. Taken together, our results suggest that, given the extent of abiotic modification on currently grazed sites, the cover of abiotic elements such as hummocks and cryptogamic crusts would be a better indicator of the long-term effect of grazing-induced disturbance than biotic components. Further, and perhaps more importantly, autogenic recovery of the most disturbed sites is likely to be protracted, even after the disturbing processes have been removed.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Table S1. Cover of plant species by treatment and cumulative cover contributed by the species. *indicates exotic species. CG, currently grazed; I, intermediate; LU, long-ungrazed.

Table S2. Abundance of reptiles collected in pitfall traps in relation to the three grazing treatments. CG, currently grazed; I, intermediate; LU, long-ungrazed.