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After the fence: vegetation and topsoil condition in grazed, fenced and benchmark eucalypt woodlands of fragmented agricultural landscapes

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Abstract. Emerging ecological theory predicts that vegetation changes caused by introduction of livestock grazing may be irreversible after livestock are removed, especially in regions such as Australia that have a short evolutionary exposure to ungulate grazing. Despite this, fencing to exclude livestock grazing is the major tool used to restore vegetation in Australian agricultural landscapes. To characterise site-scale benefits and limitations of livestock exclusion for enhancing biodiversity in forb-rich York gum (*Eucalyptus loxophleba* Benth. subsp. *loxophleba*)–jam (*Acacia acuminata* Benth.) woodlands, we compared 29 fenced woodlands with 29 adjacent grazed woodlands and 11 little-grazed 'benchmark' woodlands in the Western Australian wheatbelt. We explored the following two hypotheses: (1) fencing to exclude livestock facilitates recovery of grazed woodlands towards benchmark conditions, and (2) without additional interventions after fencing, complete recovery of grazed woodlands to benchmark conditions is constrained by ecological or other limits. Our first hypothesis was supported for vegetation parameters, with fenced woodlands being more similar to benchmark woodlands in tree recruitment, exotic plant cover, native plant cover, native plant richness and plant species composition than were grazed woodlands. Further, exotic cover decreased and frequency of jam increased with time-since-fencing (2–22 years). However, we found no evidence that fencing led to decline in topsoil nutrient concentrations towards concentrations at benchmark sites. Our second hypothesis was also supported, with higher topsoil nutrient concentrations and exotic plant cover, and lower native plant richness in fenced than in benchmark woodlands, and different plant species composition between fenced and benchmark woodlands. Regression analyses suggested that recovery of native species richness is constrained by exotic species that persist after fencing, which in turn are more persistent at higher topsoil nutrient concentrations. We conclude that fencing to exclude livestock grazing can be valuable for biodiversity conservation. However, consistent with ecological theory, additional interventions are likely to be necessary to achieve some conservation goals or to promote recovery at nutrient-enriched sites.

Introduction

Grazing by livestock and other ungulates strongly affects ecosystem structure and diversity, with ecosystem response known to depend on grazing intensity, ecosystem productivity and evolutionary exposure to grazing (Mack and Thompson 1982; Milchunas *et al*. 1988; Olff and Ritchie 1998). Further, emerging theory predicts that vegetation change associated with increasing grazing intensities is not necessarily reversible, especially in ecosystems with a short evolutionary exposure to grazing. Rather, subsequent reduction in grazing intensity can result in alternative vegetation trajectories that may not return to the initial vegetation state (Westoby *et al*. 1989; Cingolani *et al*. 2005). These alternative trajectories or states are often poorly characterised, despite their importance for recovery of ecosystems degraded by livestock grazing (Lunt *et al*. 2007*a*).

In Australia, the widespread introduction of livestock grazing has resulted in dramatic impacts on vegetation composition and ecosystem processes (Lunt *et al*. 2007*a*). Because these impacts have occurred relatively recently (within the past 200 years), they have been well characterised, perhaps to a greater extent than in any other region with a short evolutionary history of ungulate grazing (but see Milchunas and Noy Meir 2002). In eucalypt woodlands of the temperate zone where agriculture is intensive, key impacts include widespread replacement of dominant native grasses and shrubs by exotic annuals and secondary native grasses, decline of native forb and shrub species, and limited tree recruitment (Dorrough and Moxham 2005; Prober and Thiele 2005; Prober and Smith 2009). These outcomes can result directly from livestock grazing or indirectly through changes to soil condition, especially enrichment of available nitrogen or phosphorus in topsoils (Yates *et al*. 2000*a*; Prober *et al*. 2002;

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Standish *et al.* 2006; Dorrough and Scroggie 2008; Prober and Wiehl, in press). For over 20 years, fencing to exclude or reduce livestock grazing has been the major tool used in Australian agricultural landscapes for maintaining and restoring biodiversity in degraded vegetation, with over 70 000 ha of native vegetation fenced through the Natural Heritage Trust program in 2005–2006 alone (NHT 2007). These programs assume that fencing will result in positive biodiversity outcomes; however, this assumption is poorly substantiated and, for restoration goals, is challenged by theoretical predictions of irreversibility (Cingolani *et al.* 2005). In eucalypt woodlands of agricultural landscapes, several studies have shown improved tree recruitment, reduced weed abundance or increased native plant richness or cover in fenced woodlands. However, results have been variable and all studies have suggested that ecological thresholds limit the recovery of some or all woodland characteristics (Fox 2001; Pettit and Froend 2001; Duncan *et al.* 2007; Lunt *et al.* 2007*b*; Briggs *et al.* 2008; Spooner and Briggs 2008; Price *et al.* 2010).

Frameworks are emerging to facilitate prediction of the benefits and limitations of fencing for restoration. For Australian ecosystems, Lunt *et al.* (2007*b*) proposed a two-factor model, suggesting neutral to small positive outcomes of grazing exclusion in relatively intact ecosystems of low productivity, through to potentially negative impacts in degraded, productive sites. More broadly, for ecosystems with a short evolutionary exposure to grazing, Cingolani *et al.* (2005) proposed that beyond certain thresholds of grazing intensity, changes in plant diversity induced by grazing are irreversible and that alternative trajectories followed after grazing removal will depend on historical grazing levels and ecosystem productivity. Given the limited number of studies evaluating impacts of grazing exclusion on biodiversity and ecosystem processes, further data are needed to inform these frameworks. In particular, few studies have explicitly evaluated condition of fenced woodlands in the context of benchmark conditions or potential limits to recovery, and few studies have assessed recovery of topsoil condition (Duncan *et al.* 2007; Price *et al.* 2010).

Towards these goals, we evaluated whether fencing for up to 22 years has promoted recovery of degraded, low-productivity forb-rich York gum–jam woodlands. These were one of the most common ecological communities of the south-western Australian wheatbelt (Beard 1990); however, because they occur on some of the most profitable agricultural land, more than 90% have been cleared (Hobbs and Saunders 1993; Shepherd *et al.* 2002). The remainder is typically heavily affected by altered fire regimes, livestock grazing and nutrient enrichment (Prober and Smith 2009), commonly resulting in reduced tree recruitment, widespread invasion by exotic annuals and loss of native plant diversity (Prober and Smith 2009; Prober and Wiehl, in press). We used cross-fenceline contrasts of grazed and fenced woodlands, and explicit comparisons with nearby benchmark woodlands to explore the following two hypotheses regarding recovery of these attributes: (1) fencing facilitates recovery of degraded, low-productivity woodlands towards conditions of benchmark sites, and (2) without additional interventions after fencing, complete recovery of degraded woodlands to benchmark condition is constrained by ecological limits such as propagule availability, nutrient enrichment and weed invasion.

Materials and methods

Survey design

We sampled 40 patches of forb-rich York gum (*Eucalyptus loxophleba* subsp. *loxophleba*)–jam (*Acacia acuminata*) woodlands (hereafter York gum woodlands) across the range of this ecological community in the central wheatbelt, Western Australia (Fig. 1). The native understorey of these woodlands comprises a matrix of sparse to moderately dense tussock grasses (particularly *Austrostipa* spp., *Austrodanthonia* spp. and *Neurachne alopecuroidea*), interspersed with diverse annual and perennial forbs, patches of bare ground and scattered shrubs (by contrast with more arid *Eucalyptus loxophleba* woodlands where the understorey can be dominated by shrubs). Annual net primary productivity of native understorey is typically low (<200 g m^{-2}; S. Prober, unpubl. data; Cingolani *et al.* 2005). To infer topsoil and vegetation changes associated with fencing, we compared plots placed within 29 fenced York gum woodlands with plots placed in adjacent, grazed woodlands. This sampling strategy assumed similar starting conditions within each grazed and fenced pair. Our sample also included 11 little-grazed York gum woodlands across the same range (i.e. benchmark woodlands; Fig. 1).

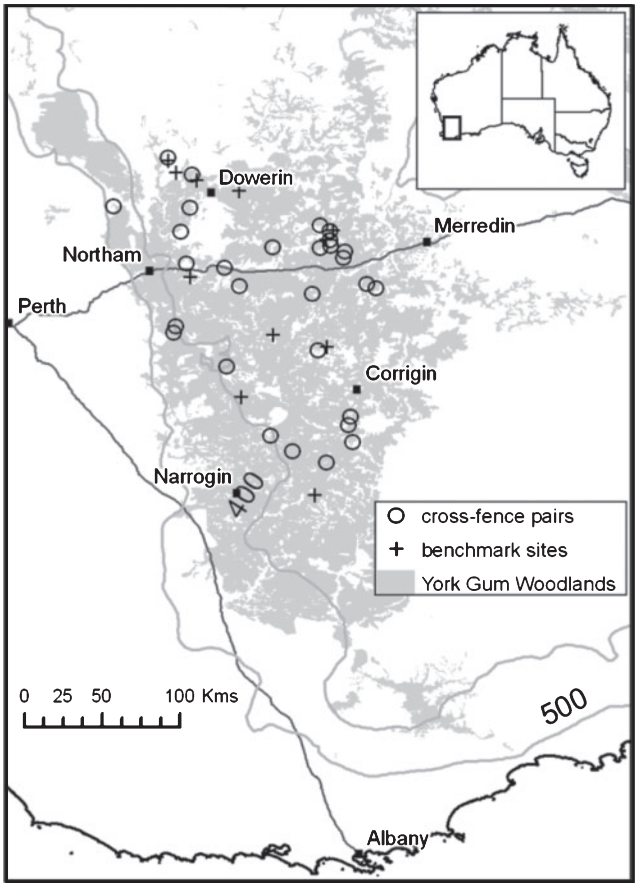

Fig. 1. Distribution of cross-fenceline pairs and benchmark (reference) sites sampled in the study, overlaid on the distribution of York gum woodlands (Shepherd *et al.* 2002).

To locate cross-fenceline pairs, we invited 150 managers of fenced York gum woodlands to participate in the project, and asked whether their sites met the following criteria: (1) the woodland contained York gum, (2) the fence passed through the woodland, leaving similar but grazed woodland on one side of the fence, (3) before fencing, woodlands now on different sides of the fence were similar, and (4) management of the grazed site since fencing was similar to that before fencing.

Then, we visited 134 woodlands on 61 farms and selected 29 cross-fenceline pairs that met the above criteria. They ranged from 1 to 511 ha (median 20 ha), and had been fenced for between 2 and 22 years (median 9 years). Sites extended across gradients in topographic position and vegetation condition, and spanned a rainfall gradient of 320–469 mm mean annual rainfall (median 358 mm). Mean annual temperature ranged from 15.9 to 17.7°C (median 17.1°C). Consistent with the distribution of York gum woodlands, most sites occurred on soils of relatively recent granitic or granitic gneiss origin, with occasional dolerite or sedimentary influence (consistent across pairs, Department of Industry and Resources 2001). Land managers provided information on grazing levels before and after fencing (scored on a subjective scale from 0 to 5, as follows: nil, very low, low, moderate, moderate–heavy, heavy–very heavy).

The 11 benchmark woodlands had no known history of cultivation or direct fertilisation, and a history of minimal livestock grazing. They included five woodlands on private land, four nature reserves and two town reserves. Although ungrazed for >50 years, most reserves were intermittently grazed by livestock early in the 20th century, so some legacy of livestock-grazing impacts cannot be excluded (Main 1992).

Monitoring

At each of the 29 cross-fenceline woodlands, we placed one 20 × 50 m plot on each side of the fence (at least 1 m from the fence and 10 m from woodland edges) and monitored the following variables in spring 2008 (September–November):

(1) Diameter at breast height (1.3 m, DBH) was measured for stems of all live and dead trees and tall shrubs. A nominal DBH of 0.5 cm was allocated to plants ≤1.4 m tall (defined as ‘recruits’). For multi-stemmed plants, an averaged DBH was calculated as the square root of the sum of squares of the DBH of each live or dead stem.

(2) Abundance of predefined native and exotic plant life-forms was estimated using a line-intercept technique (see Prober *et al*. 2005). An 8-mm dowel was placed vertically at each of 50 points spread evenly across each plot; the relative abundance for any life-form was the percentage of points at which any leaves, stems or inflorescences of species from that life-form intercepted the dowel. Groups that were present but did not intercept the dowel at any point were allocated a nominal abundance of 0.5% points. This technique provided an objective measure of abundance reflecting, but not equivalent to, projective cover, and is hereafter referred to as cover.

(3) Bare ground, native and exotic plant litter and abundance of logs were estimated using the same line-intercept technique. We also measured the cumulative length of all logs >5 cm in diameter as a measure of potential fauna habitat.

(4) All plant species occurring within a 10 × 10 m subplot nested within each 20 × 50 m plot were recorded, and abundances estimated as above. Subplots were selected to be representative of the larger plot and comparable to their cross-fence comparison in canopy cover. Nomenclature follows the Western Australian Herbarium (2010).

(5) Topsoil nutrient concentrations were measured by collecting 30 soil cores, each 2 cm in diameter, 10 cm deep, spread evenly across the 10 × 10 m subplots. Samples were stored at ~4°C and transported within 72 h to CSBP Limited (Bibra Lake, WA: http://www.csbp.com.au/Home-Corporate.aspx). Samples for each plot were mixed, air-dried at 40°C and ground to pass through a 2-mm sieve. Analyses were undertaken as follows (method numbers refer to Rayment and Higginson 1992): available phosphorus (Colwell method, bicarbonate-extractable phosphorus, 9B1), potassium (Colwell method, bicarbonate-extractable potassium, 18A1), ammonium and nitrate (measured simultaneously with Lachat Flow Injection Analyser (Lachat Instruments, Milwaukee, WI, US; soil : solution ratio of 1 : 5, 1 M KCl, indophenol blue (Searle 1984) and with copperised-cadmium column reduction), pH (1 : 5, soil : 0.01 M $CaCl_2$, 4B2), conductivity (1 : 5, soil : water extract, 3A1), organic carbon (Walkley and Black method, 6A1), extractable sulfur (40°C for 3 h, 0.25 M KCl, measured by inductively coupled plasma spectrometry, Blair *et al*. 1991) and total nitrogen (oxygen combustion, 950°C with Leco FP-428 Analyser, Leco Corporation, St. Joseph, MI, US).

(6) Topsoil physical properties were measured in the 10 × 10 m subplots. Soil-surface compaction was measured at 30 random positions by using a calibrated 0–5 MPa pocket penetrometer (6.4-mm needle diameter). Bulk density was estimated by weighing dried soil from each of five soil cores (55-mm diameter and 60-mm depth) per plot, and dividing by the volume of each core. Instantaneous volumetric soil water content to 7-cm depth was measured using a MPM406 soil moisture probe (Decagon Devices: Armidale, NSW, Australia), with 15 measurements averaged across each plot.

We also scored or calculated other environmental variables that might influence recovery of fenced sites, including topographic position (an ordinal variable from hill top to drainage lines), distance from the nearest crop paddock edge to the nearest plot edge, landscape integrity (%area of native vegetation within a 100-m and a 1000-m radius, calculated using remnant vegetation extent layers in ArcGIS; Shepherd *et al*. 2002) and mean annual rainfall and temperature (estimated by using BIOCLIM, a component of ANUCLIM version 5.1; Houlder *et al*. 2001).

In benchmark woodlands, we measured the same variables as described above, except for abundances at the 20 × 50 m scale (variables 2 and 3 above). Other studies have shown that soil properties in eucalypt woodlands vary beneath trees compared with gaps (e.g. Prober *et al*. 2002). To maximise the range in topsoil properties sampled in benchmark woodlands, we measured floristic composition and topsoil properties in each of two 10 × 10 m plots per benchmark woodland, one beneath York gum canopy and one in a gap.

Data analyses

Comparisons of fenced, grazed and benchmark plots

Univariate statistical analyses were conducted using GENSTAT 12.1 (VSN International Ltd 2009). Paired Student's *t*-tests were used to test for differences in average floristic and topsoil characteristics between fenced and grazed plots. Topsoil chemical and plant-cover variables required log-transformation ($\ln(x+1)$) to satisfy the assumptions of parametric analysis. We also used permutational tests (with 4999 random permutations) to obtain significance values. These gave results similar to those of parametric tests, so are presented only for analyses with more than 20% zeros. Means and standard errors for benchmark sites were also calculated, and were compared with fenced and grazed plots by using independent-groups Student's *t*-tests.

For dominant tree species, 'other trees' and 'other shrubs', we compared the frequency of all live individuals, dead individuals and live recruits in fenced, grazed and benchmark plots, using generalised linear regression with a Poisson distribution and log-link function. For mean DBH of dominant trees, we fitted similar models by using a normal distribution and identity-link function.

Which variables predict benefits of fencing?

We used general linear regression to elucidate determinants of the magnitude of within-pair differences (fenced *v.* grazed) in key response variables. The most informative explanatory variables were identified by including all relevant environmental and other variables in all-subsets regressions. Stepwise general linear regression was then applied to identify optimal combinations of these and selected interactions and quadratic terms. Model selection was based on maximum adjusted R^2. We also used this approach to investigate potential drivers of some explanatory variables.

Preliminary Student's *t*-tests suggested a small sampling bias, with grazed plots on average 42.6 m from crop edges compared with 48.8 m for fenced plots ($P = 0.045$). However, within-pair differences (fenced *v.* unfenced) in neither distance from crop edges nor landscape integrity contributed significantly to any models, suggesting that the bias did not unduly influence results.

Multivariate analyses

Ordinations were used to explore differences in topsoil and floristic properties of grazed, fenced and benchmark plots by using PC-ORD (McCune and Mefford 1999). For soil data, we applied principal components analysis (PCA), using the correlation matrix (data centred and standardised by standard deviation; Greig-Smith 1983) and Euclidean distance. For floristic data, we used non-metric multidimensional scaling (nMDS). Quantitative floristic data (excluding tree species) were square-root transformed (to reduce the influence of dominant species) and used to produce a distance matrix using the Bray–Curtis coefficient of dissimilarity (Faith *et al.* 1987).

Table 1. Means for topsoil properties in York gum woodlands

Comparisons are shown between benchmark (bmk), long-fenced (9–22 years), all fenced (2–22 years) and grazed plots. Significance: ***$P < 0.001$; **$P < 0.01$; *$P < 0.05$; n.s., not significant for comparisons as indicated; n.a., not available. Means are back-transformed for all nutrients, moisture, bare ground, litter, logs and cryptogams

Variable	Unit	Mean				Significance			
		Bmk ($n = 22$)	Long-fenced ($n = 16$)	Fenced ($n = 29$)	Grazed ($n = 29$)	Bmk *v.* long-fenced	Bmk*v.* fenced	Bmk *v.* grazed	Fenced *v.* grazed
Topsoil chemistry									
Ammonium	mg kg^{-1}	2.32	2.61	3.32	4.14	n.s.	n.s.	**	n.s.
Conductivity	dS m^{-1}	0.04	0.07	0.08	0.08	*	***	***	n.s.
Nitrate	mg kg^{-1}	3.19	6.33	5.92	5.95	**	**	**	n.s.
Organic carbon	%	1.13	1.61	1.83	1.76	***	***	***	n.s.
pH		5.12	5.36	5.22	5.26	n.s.	n.s.	n.s.	n.s.
Phosphorus	mg kg^{-1}	2.43	4.38	4.66	5.04	***	***	***	n.s.
Potassium	mg kg^{-1}	84.1	160.7	148.6	152.2	***	***	***	n.s.
Sulfur	mg kg^{-1}	3.78	4.23	5.06	5.11	n.s.	*	*	n.s.
Total nitrogen	%	0.08	0.12	0.15	0.14	***	***	***	n.s.
Topsoil physical and surface properties									
Bulk density	g cm^{-3}	1.32	1.23	1.21	1.31	n.s.	***	n.s.	***
Moisture	%Vol	n.a.		2.78	2.70				n.s.
Hardness	MPa	2.80	3.33	3.00	3.44	*	n.s.	*	n.s. ($P = 0.064$)
Bare ground	%Points	25.8	20.6	15.7	26.7	n.s.	**	n.s.	***
Native litter	%Points	47.9	29.8	34.4	30.2	***	**	***	n.s.
Weed litter	%Points	0.46	4.32	4.84	7.65	***	***	***	*
Length of logs	m	78.8	75.8	69.0	85.3	n.s.	n.s.	n.s.	*
Cryptogam crusts									
All[A]	%Points	n.a.	27.40	23.60	19.10				n.s.
Leafy lichens	%Points	n.a.	3.22	3.26	2.31				n.s. ($P = 0.076$)
Mosses	%Points	n.a.	6.70	4.16	2.88				n.s.
Other	%Points	n.a.	17.60	16.20	13.90				n.s.

[A] Cumulative score derived by summing %points of relevant subclasses.

Preliminary analyses were performed in one to four dimensions, with 10 random starts; these indicated that the three-dimensional solution was optimal, and the solution with the lowest stress (0.15) was selected.

Direct overlays and biplots were produced to examine relationships between the ordinations and environmental variables. We used the blocking procedure in PC-ORD (MRPP) to test the significance of topsoil and floristic differentiation between benchmark and other plots. To test for apparent recovery of floristic composition towards benchmark sites as a result of fencing, we calculated the vector best separating benchmark sites, by using the vector-fitting procedure of DECODA (Minchin 1989). Scores for the position of plots on this vector were extracted and further analysed using paired Student's *t*-tests as described above. Scores were also used to order sites and species in two-way tables indicating species contributing to the difference between benchmark and other plots.

Results

Sheep were the major livestock present before fencing at nearly all sites. Current grazing levels for grazed plots varied across sites, but were similar to (or sometimes lower than) levels before fencing of their adjacent pair, and had increased in only one case. Livestock grazing rarely occurred at fenced sites after fencing. Managers reported moderate to high levels of rabbit or kangaroo grazing for nine pairs of plots, two pairs had been burnt within the past 10 years and one had been flooded.

Topsoil attributes

On average, fenced pots and grazed plots had significantly higher concentrations of all measured topsoil nutrients than did benchmark plots (except for ammonium). There was little evidence for recovery of topsoil chemical properties associated with fencing, with no significant differences between means for fenced plots and those for grazed plots for any nutrients (Table 1). Topsoil pH did not differ among any plot types. Even for a subset of 16 plots that had been fenced for 9 years or longer ('long-fenced plots'), concentrations of most nutrients were, on average, higher in long-fenced than in benchmark plots (Table 1) and not significantly different from concentrations in grazed plots (not shown). Notwithstanding, the extent of differences between means was not particularly large, ranging between 1.3 and 1.9 times greater in fenced than in benchmark plots. Further investigation of the difference in topsoil nutrient concentrations between fenced and grazed plots in each pair revealed no significant linear or non-linear relationships with potential explanatory environmental variables, including the number of years plots had been fenced.

Some differences between means of fenced plots and grazed plots were evident in topsoil physical properties and surface conditions. Fenced plots had on average less bare ground, lower fallen-log length, less weed litter, lower topsoil bulk density and a tendency to lower surface hardness ($P = 0.064$, Table 1) than did grazed plots. Notably, the shift in bulk density and bare ground was away from rather than towards benchmark levels, which were more similar to grazed plots in these characteristics. There were no differences between fenced and grazed plots in instantaneous topsoil moisture content, native litter or cover of soil cryptogams, although there was a tendency towards a higher cover of foliose lichens in fenced plots ($P = 0.076$, Table 1).

Principal components analysis of topsoil properties showed a strong gradient along Axis 1, explaining 48% of the variance in the data (Fig. 2*a*). This was parallel to the maximum separation between benchmark and other plots (MRPP, $P < 0.001$), and was most strongly related to Colwell phosphorus, total nitrogen and organic carbon. Fenced plots showed no consistent shift from their grazed pair towards benchmark plots along this axis (Fig. 2*b*, $P = 0.86$), and there was no apparent relationship between the position of fenced plots on this axis and years since fencing. Axis 2 explained only 13% of the variance in the data and was unrelated to time-since-fencing.

Although fenced plots and grazed plots were on average nutrient enriched compared with benchmark plots, PCA indicated notable overlap between these groups. About 10 cross-fenceline pairs were comparable with benchmark plots in topsoil properties, and about five woodlands were within the range of benchmark topsoil conditions for their fenced but not grazed plots (Fig. 2).

Floristic diversity and composition

There was strong evidence that vegetation condition was better in fenced than in grazed plots (Table 2). In particular, mean native plant richness was on average four species greater in fenced plots, contributed mostly by annual and perennial forbs. Native shrub richness was generally very low, although

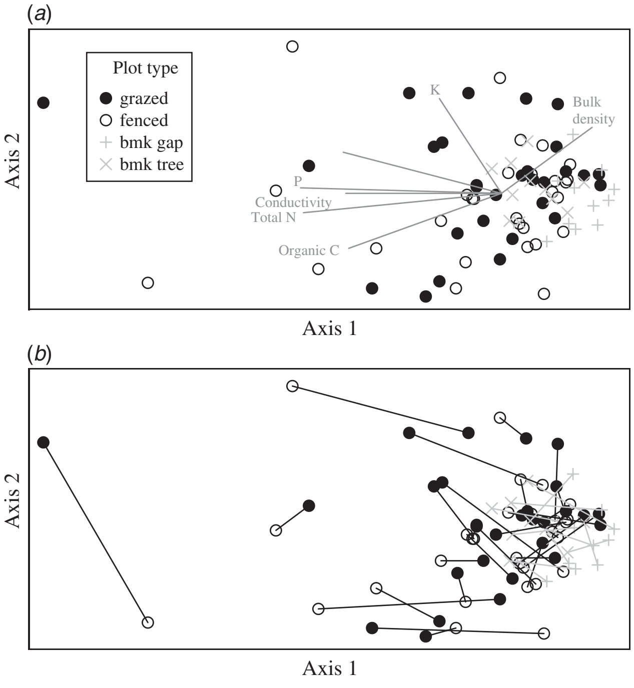

Fig. 2. Principal components analysis (PCA) of topsoil variables, showing separation among fenced, grazed and benchmark (bmk) plots, and (*a*) relationship with topsoil variables, (*b*) grazed *v.* fenced pairs (black lines) and pairs in gaps (bmk gap) *v.* beneath trees (bmk tree) for benchmark sites (grey lines).

Table 2. Means for floristic characteristics in York gum woodlands

Comparisons are shown for benchmark (bmk, averaged across canopy and gap plots), long-fenced (9–22 years), all fenced (2–22 years) and grazed plots. Significance: ***$P < 0.001$; **$P < 0.01$; *$P < 0.05$; n.s., not significant for paired comparisons as indicated; n.a., not available. Richness measured in 10 × 10 m plots; cover (%points) in 50 × 20 m plots, unless 10 × 10 m indicated. Means for cover are back-transformed

Variable	Mean				Significance			
	Bmk ($n=22$)	Long-fenced ($n=16$)	Fenced ($n=29$)	Grazed ($n=29$)	Bmk *v.* long-fenced	Bmk *v.* fenced	Bmk *v.* grazed	Fenced *v.* grazed
Native species cover								
Trees	n.a.	23.39	26.97	23.09				n.s.
Understorey[A] (50 × 20)	n.a.	40.72	43.66	34.73				*
Understorey[A] (10 × 10)	148.75	96.91	106.45	95.25	***	***	***	n.s. ($P=0.13$)
Shrubs	n.a.	1.33	1.36	0.95				n.s.
Ground layer[A]	n.a.	37.21	40.68	31.62				*
Grasses	n.a.	21.53	19.39	16.27				n.s.
Perennial forbs	n.a.	3.22	3.18	1.61				*
Annual forbs	n.a.	7.07	10.88	9.00				n.s.
Native species richness								
Total	28.23	21.81	22.41	18.28	***	***	***	***
Shrubs	1.50	1.19	1.10	0.69	n.s.	n.s.	**	n.s. ($P=0.077$)
Ground layer	24.95	18.88	19.38	15.97	***	***	***	***
Grasses	4.82	4.19	4.17	3.86	n.s.	n.s.	*	n.s.
Perennial forbs	7.68	5.81	5.86	4.24	n.s.	*	***	**
Annual forbs	12.45	8.88	9.34	7.86	***	***	***	**
Exotic species cover								
Total[A] (50 × 20)	n.a.	29.23	34.23	54.37				***
Total[A] (10 × 10)	12.61	38.02	41.69	53.49	***	***	***	n.s. ($P=0.078$)
Annuals[A] (50 × 20)	n.a.	25.84	31.79	50.52				***
Annuals[A] (10 × 10)	11.77	31.46	35.74	50.11	***	***	***	*
Annual grasses	n.a.	15.01	19.33	32.45				**
Annual forbs	n.a.	7.93	8.01	12.24				*
Perennial forbs	n.a.	1.75	1.10	1.16				n.s.
Exotic species richness								
Total	1.06	8.86	9.51	9.07	***	***	***	n.s.

[A] Cumulative score derived by summing %points of relevant subclasses.

it was marginally higher in fenced plots. Despite the better vegetation condition of fenced plots, native plant richness (especially for forbs) was still significantly lower than that in benchmark plots, by an average of six species. This difference remained for the subset of 16 sites fenced for 9 years or longer (Table 2). Cumulative cover of native understorey showed patterns similar to native plant richness (Table 2).

Cumulative cover of exotic species was 20% lower in fenced plots than grazed plots, whereas fenced plots had significantly higher average exotic cover than optimum levels (0%) or levels in benchmark plots (12%). This trend was consistent and significant for exotic species richness and cumulative cover of exotic annual grasses and exotic annual forbs, but not for exotic perennial forbs (Table 2).

The degree of difference in floristic characteristics between fenced and grazed plots in each pair varied significantly in relation to explanatory variables. For difference in native plant richness, the best-fit model ($R^2 = 46\%$) had three components. First, a quadratic relationship with richness of grazed plots suggested that high initial richness limited potential for increase (Fig. 3*a*), an intuitive result. Second, the model suggested that gains in richness decreased with increasing residual weed cover (Fig. 3*b*), explaining low gains at low initial richness. Third, richness decreased with decreasing landscape integrity (1000-m scale; Fig. 3*c*, Table 3). If landscape integrity was replaced with prior grazing levels, only slightly less variation was accounted for, consistent with a significant relationship between these two variables (Table 3). No significant relationships between native plant richness and time-since-fencing were detected.

For exotic annuals, the difference between fenced and grazed plots became more negative (suggesting a greater decline in exotics) with time-since-fencing, and the extent of the difference was dependent on topsoil total nitrogen (or, to a lesser extent, with the other variables related to ecosystem productivity, such as organic carbon or mean annual rainfall; Fig. 4, Table 3).

Similar to PCA of topsoil data, nMDS ordination of floristic data showed that benchmark plots clustered at one extreme of Axis 1, overlapping with some fenced plots and some grazed plots (Fig. 5*a*). These trends were strongly correlated with native plant richness and exotic species cover. They illustrated that, although benchmark plots were on average higher in native species richness, lower in weeds, and different in species composition, some sites were already in good condition before fencing. Several benchmark plots were 'outliers' on the ordination, falling closer to grazed and fenced plots. This could reflect historical degradation in these benchmark sites; hence, it is not possible to delineate exactly which sites match benchmark conditions. Nonetheless, few pairs were within the core range of benchmark floristic composition for their respective fenced plots but not grazed plots, suggesting that fencing had rarely led to full recovery of degraded woodlands. Despite this, fenced plots generally occurred significantly closer to benchmark plots on Axis 1 (the axis best distinguishing benchmark plots) than did their grazed pairs ($P = 0.035$; Fig. 5*b*).

Species contributing to trends along Axis 1 – reflecting condition in relation to benchmark sites – included a predominance of exotic annuals (e.g. *Hordeum leporinum*, *Erodium botrys*, *Bromus rubens*, *Avena barbata*) at the greatest distance from benchmark sites, and at the other extreme, a suite of native species most frequent in benchmark plots (Supplementary Table 1). These included the native annuals *Gilberta tenuifolia*, *Lawrencella rosea* and *Gnephosis tenuissima*, and the native perennial forbs *Thysanotus patersonii* and *Dampiera lavandulacea.* Many other native species were absent from the most species-poor plots, but occurred with increasing cover along Axis 1 (e.g. the native perennial grass *Neurachne alopecuroidea* and the native annuals *Waitzia acuminata* and *Trachymene cyanopetala*).

Axis 2 of the ordination correlated most strongly with mean annual rainfall and topsoil bulk density (which tended to increase with decreasing rainfall; Fig. 5*a*). Organic carbon and total nitrogen increased at higher rainfall and decreased towards benchmark sites, resulting in a diagonal trend on the ordination (Fig. 5*a*). There was no relationship between the position of fenced plots on the ordination and time-since-fencing.

Tree and shrub demography

Frequencies of live York gum, jam, tall shrubs and other trees (but not needle tree, *Hakea preissii*) were each significantly higher in fenced than in grazed plots (Fig. 6*a*). This included significantly more jam and York gum recruits in fenced plots, although there was little difference in recent recruitment of other species (Fig. 6*b*). Jam recruits were abundant and occurred in 72% of fenced plots, compared with 38% of grazed plots. York gum recruits were uncommon, and occurred in 28% of fenced plots compared with 10% of grazed plots. Most York gum recruits occurred in the three fenced plots that had been burnt or flooded within the past 10 years – 31 individuals, compared with six individuals across five other fenced sites.

Frequency of trees in fenced and unfenced plots was generally not distinguishable from that at reference sites. However, jam recruitment was higher in fenced than in benchmark plots, probably owing to past clearing in fenced but not in

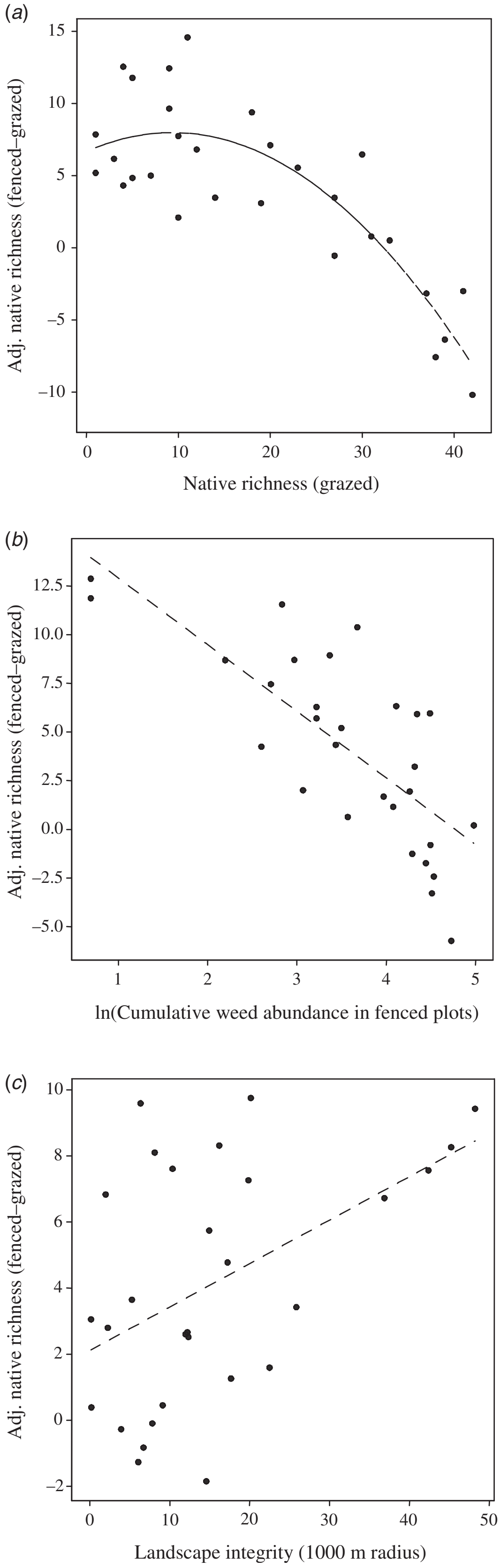

Fig. 3. Effects of (*a*) initial richness, (*b*) residual weed cover and (*c*) landscape integrity (%) on within-pair differences between fenced and grazed plots in native species richness, after adjustment for other model components. Note that the apparent decline in native species in some highly degraded sites would in reality be constrained by the low initial richness.

Table 3. Summary of regression models suggesting constraints to woodland recovery

Alternative variables and associated R^2 (*) are provided where relevant. No models were significant for topsoil nutrients (ammonium, organic carbon, phosphorus, potassium, nitrate, sulfur, total nitrogen), length of fallen logs, jam or York gum recruits, or York gum frequency. F, fenced; G, grazed; ln, natural log

Response variable	Form of response variable	*n*	Best model	Adjusted R^2 (%)
Native species richness	F–G	29	+Native species richness grazed – native species richness grazed^2 – exotic species cover fenced + landscape integrity 1000-m radius (*or –prior grazing)	46.0 (*or 45.3)
Exotic species annual cover	ln(F+1) –ln(G+1)	29	–Years fenced – ln(total N grazed) + years fenced × ln(total N grazed)	41.6
Jam frequency	ln(F+1) –ln(G+1)	29	–ln(Jam frequency grazed) + landscape integrity 1000 m radius + years fenced + ln(K grazed)	60.5
			Relationships among explanatory variables	
Landscape integrity (1000-m radius)	Untransformed	58	–Prior grazing level – lnS (*or –ln P) – surface compaction	57.5 (*or 53.8)
		58	–Topographic class – lnS – surface compaction + rock cover (constrained to exclude prior grazing level)	37.1
Total nitrogen	ln(*X*+1)	58	+ln(organic C) + ln(Colwell P)	69.5
		58	+ln(Colwell P) + rainfall + lnS (constrained to exclude organic C)	53.3

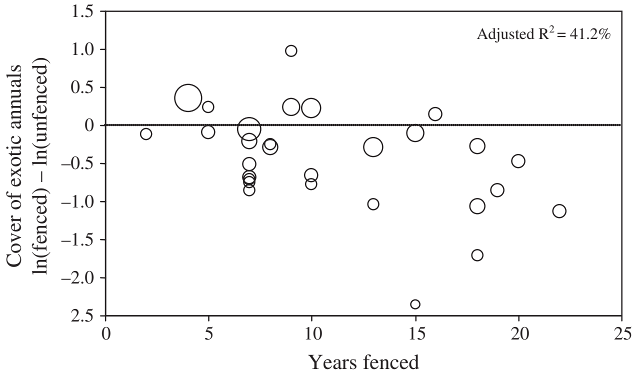

Fig. 4. Difference in cover of exotic annuals between fenced and grazed plots in relation to time-since-fencing and total nitrogen (0.08–0.32%, represented by the size of circles).

benchmark plots (Fig. 6*b*). We did not detect an effect of fencing on the mean DBH of any species except needle tree, which was larger in grazed than in benchmark plots (Fig. 6*c*). The frequency of standing dead jam, other trees and other tall shrubs was greater in fenced than in grazed plots (Fig. 6*d*), although there were more fallen logs in grazed than in fenced plots (Table 1).

Regressions suggested that jam frequency increased more in fenced plots that had fewer individuals than in respective grazed plots (implying a greater increase in jam frequency where there were fewer jam individuals to begin with). Once this had been accounted for, the difference between the fenced and grazed plots was weakly explained by a positive relationship with landscape integrity (within a 1000-m radius), time-since-fencing and topsoil potassium concentrations ($R^2 = 60.5\%$; Table 3). No models significantly explained the degree of increase in recent York gum or jam recruits or the frequency of York gum as a result of fencing.

Discussion

Benefits of fencing

Our results suggested that, if appropriately targeted, fencing can enhance understorey condition in York gum woodlands degraded by livestock grazing. Our first hypothesis, that fencing to exclude grazing facilitates recovery towards benchmark conditions, was supported for native species richness of most plant life-forms, native and exotic plant cover, and floristic composition. Given theoretical predictions for poor recovery in ecosystems with a short evolutionary exposure to grazing (Cingolani *et al.* 2005; Lunt *et al.* 2007*a*, 2007*b*), these results are encouraging. Other grazing-exclosure studies in temperate eucalypt woodlands have reported mixed results for these attributes, with declining weed abundance in three of six studies, enhanced native species cover in four of seven studies, and increased native species richness in two of three studies (Fox 2001; Pettit and Froend 2001; Duncan *et al.* 2007; Briggs *et al.* 2008; Spooner and Briggs 2008; Price *et al.* 2010). However, few studies have shown improvement in as many characteristics as we observed.

These positive outcomes may reflect several factors considered to predict recovery from grazing impacts (Cingolani *et al.* 2005; Lunt *et al.* 2007*a*, 2007*b*). First, the relatively low rainfall of our study system is likely to lessen the persistence of exotic annuals (McLendon and Redente 1991; Lenz and Facelli 2006) and preclude the need for disturbance to maintain native plant diversity (e.g. Morgan and Lunt 1999), consistent with predictions for better outcomes of grazing removal in low-productivity environments (Lunt *et al.* 2007*a*, 2007*b*). Second, our sample included fenced sites with low to moderate levels of (assumed) grazing impacts at fencing, which are predicted to recover better than highly grazed sites (Cingolani *et al.* 2005; Lunt *et al.* 2007*a*, 2007*b*).

Fenced York gum woodlands also had higher frequency and recruitment of York gum and jam than did grazed woodlands; however, this pattern was not observed for needle tree. Other

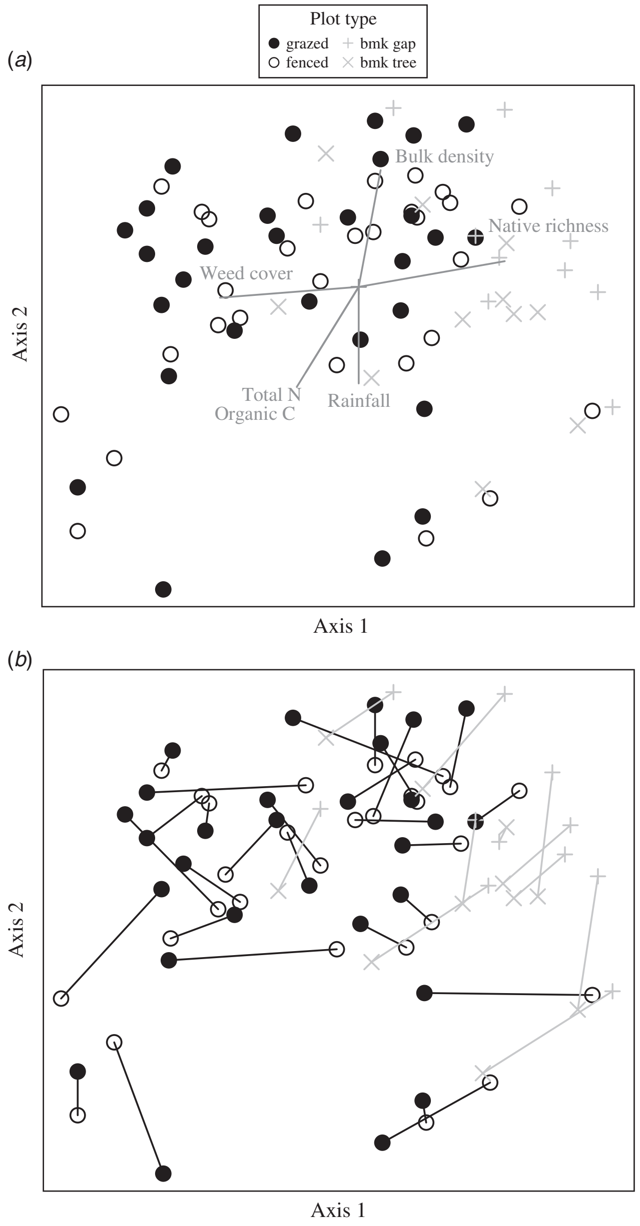

Fig. 5. Non-metric multi-dimensional scaling analysis of fenced, grazed and benchmark (bmk) plots on the basis of floristic data (rotated to best show differentiation between reference and other plots). (*a*) Relationship with variables correlating with these axes at $R^2 > 0.35$ (length of line indicates relative strength of correlation), (*b*) Grazed *v.* fenced pairs (black lines) and plots beneath trees (bmk tree) *v.* gaps (bmk gap) for benchmark sites (grey lines).

studies have similarly found that benefits of fencing for tree recruitment are species dependent (Pettit and Froend 2001; Duncan *et al*. 2007; Briggs *et al*. 2008; Spooner and Briggs 2008). As a palatable legume, it is not surprising that jam recruits are suppressed by livestock grazing, and with a long-lived soil seed store, can recover rapidly after grazing exclusion. Conversely, needle tree has pungent spines that defend against grazing and so appears unaffected by fencing. For York gum, recruitment was absent at most sites (81%, including benchmark sites); however, abundant recruitment in three fenced plots that were recently burnt or flooded supports a need for natural disturbance as well as fencing to promote York gum recruitment (Hobbs and Atkins 1991; Standish *et al*. 2006). Unlike Dorrough and Moxham (2005), we found no predictors of tree recruitment associated with vegetation condition or ecosystem productivity (except for a weak, unexplained effect of topsoil potassium on jam recruitment). However, increases in jam recruitment were greater at sites that we assumed had fewer trees at fencing, an intuitive result although counter to the concept of better recovery at less-degraded sites (noting that tree recruitment was not specifically addressed by Lunt *et al*. 2007*a*, or Cingolani *et al*. 2005).

Our first hypothesis was not supported for soil conditions, because we found no evidence for recovery of enriched woodland topsoils after fencing. Topsoil enrichment is a well established consequence of livestock grazing and adjacent cropping in vegetation of agricultural landscapes in southern Australia (Scougall *et al*. 1993; Yates *et al*. 2000*b*; Fox 2001; Prober *et al*. 2002), and our analyses confirmed that a proportion of fenced plots and grazed plots in our study were nutrient enriched. Few studies have directly evaluated recovery of topsoil chemical properties as a result of cessation of livestock grazing; however, a lack of recovery is consistent with Duncan *et al*. (2007) for Victorian woodlands and Standish *et al*. (2006) for two old-fields in York gum woodlands. Notwithstanding, the magnitude of differences between means for fenced and grazed plots was not large, probably because many woodlands selected for fencing are already in reasonable condition and/or have not had substantial fertiliser additions. Further, our capacity to detect differences between pairs may have been limited by the small size of our sampling plots.

Topsoil physical conditions did not follow expected patterns. Other Western Australian studies have suggested that soil bulk density and levels of bare ground increase with livestock grazing or cultivation (Yates *et al*. 2000*b*; Standish *et al*. 2006), whereas our grazed sites were similar to benchmark sites. Lower bulk density and bare ground associated with fencing might generally be seen as positive outcomes for plant growth and soil health; however, given the deviation from benchmark sites, it is difficult to interpret whether such outcomes are favourable for biodiversity conservation. Exotic annuals are also associated with lower topsoil bulk density and bare ground (Prober *et al*. 2002; Prober and Wiehl, in press), so our results could reflect an interaction between release from grazing and a greater cover of exotic annuals at fenced than at benchmark sites. Soil-surface hardness, however, followed more expected patterns, being lowest at benchmark sites and highest on grazed plots.

By measuring vegetation condition, our study indirectly addressed benefits of fencing for woodland fauna. Differences between fenced and grazed plots suggest that enhanced fauna habitat includes higher tree densities, greater structural diversity associated with higher tree recruitment and shrub frequency, and higher native ground cover and forb richness (Barrett *et al*. 2008; Montague-Drake *et al*. 2009). Fallen logs are often cited as an important element of fauna habitat (e.g. MacNally 2006); however, we recorded fewer fallen logs in fenced than in grazed plots. This was compensated by higher numbers of standing dead trees in fenced plots, suggesting that dead trees

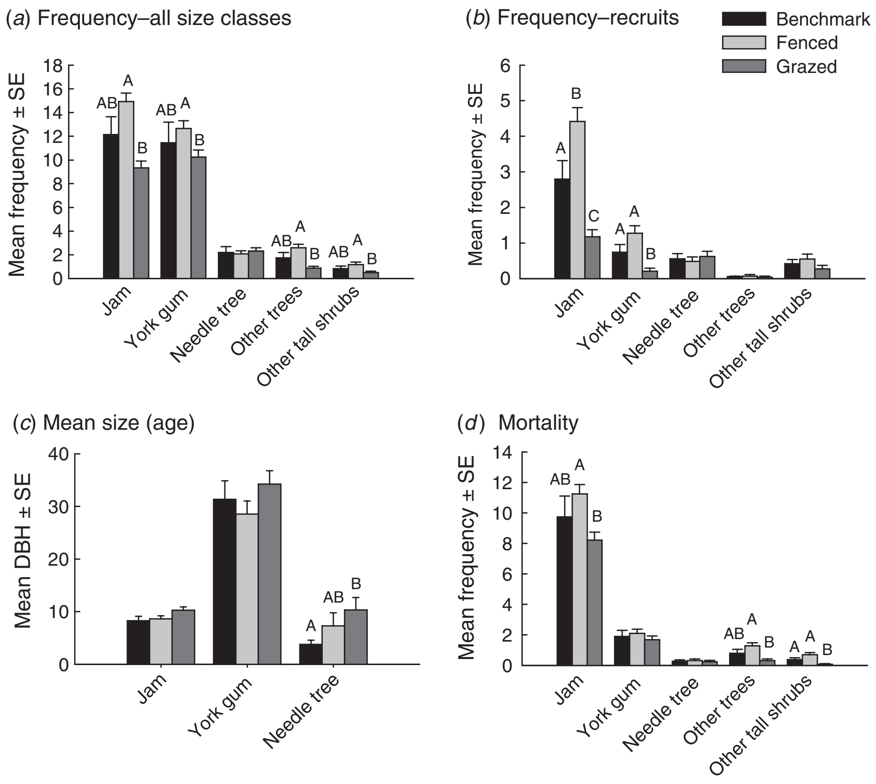

Fig. 6. Demography of trees and shrubs recorded in fenced, unfenced and benchmark plots: (*a*) frequency of live individuals (all size classes); (*b*) frequency of recruits (i.e. live plants with ≤0.5-cm DBH or <1.4 m tall); (*c*) mean size of three most frequent species; and (*d*) frequency of dead individuals (all size classes). Jam = *Acacia acuminata*, York gum = *Eucalyptus loxophleba* subsp. *loxophleba*, needle tree = *Hakea preissii*; other trees = *Allocasuarina campestris*, *A. huegeliana*, *Eucalyptus salmonophloia*, *E. wandoo*; other shrubs = *Acacia acuaria*, *A. microbotrya*, *Exocarpos aphyllus*, *Grevillea paniculata*, *Santalum spicatum*, *Senna artemisioides*. Frequencies are the mean number of individuals per 1000 m^2 predicted by the generalised linear models of frequency data; different letters indicate significant differences at $P = 0.05$ for each group of comparisons.

were more likely to have fallen over in grazed plots. Few data are available to evaluate outcomes of fencing for fauna in other eucalypt woodlands, although Briggs *et al*. (2008) concluded that recovery of fauna habitat is slow.

Limits to recovery

Our second hypothesis, that recovery of York gum woodlands to benchmark conditions is limited by ecological or other constraints, was supported for most condition measures. First, average soil and floristic conditions of fenced plots were significantly different from those of benchmark sites, owing to elevated topsoil nutrients, higher exotic species cover and lower native species richness. Second, soil and floristic ordinations suggested recovery to benchmark condition in only a small subset of cases. Pettit and Froend (2001) and Fox (2001), similarly, observed incomplete recovery to benchmark floristic composition in fenced eucalypt woodlands.

Third, several variables were significantly associated with differences between fenced and grazed plots, suggesting that these factors limit recovery. One constraint is likely to be lack of sufficient time, as supported by the significant association between some condition variables and time-since-fencing. Given this, it is not possible to infer whether our results indicate irreversible grazing impacts, as propsed by Cingolani *et al*. (2005) for ecosystems with a short evolutionary exposure to ungulate grazing, or whether recovery will eventually occur over longer timeframes.

In addition to time constraints, we hypothesised that limits to recovery would include lack of propagules, nutrient enrichment and weed invasion. Our data supported the latter, with higher exotic cover in fenced plots limiting the increase in native species richness in fenced compared with grazed plots. This is consistent with studies in other ecological communities that have indicated that exotic annuals limit recruitment and growth of native herbaceous species (Alvarez and Cushman 2002; Lenz and Facelli 2005; Prober *et al*. 2005; Smallbone *et al*. 2007; Standish *et al*. 2008).

Further, regression analyses pointed to elevated total nitrogen as a limit to recovery from exotic invasion. Models containing various combinations of the variables organic carbon, mean annual rainfall, sulfur and Colwell phosphorus explained nearly 70% of the variation in total nitrogen. Hence, we interpret our results more broadly as indicating that exotics are more persistent in high-productivity environments, consistent with Lunt *et al*. (2007*a*, 2007*b*), Lenz and Facelli (2006) and related studies that emphasise reduction of soil nutrient concentrations for restoration of temperate eucalypt woodlands (Prober and Thiele 2005; Dorrough *et al*. 2006; Prober *et al*. 2009; Standish *et al*. 2009). Our results contrast with those on many semiarid ecosystems, where recovery from overgrazing can be limited by 'leakage' of nutrients and water because of soil compaction and loss of micro-catchments on the soil surface (Ludwig *et al*. 1997; Yates *et al*. 2000*a*).

One other variable, landscape integrity at the 1000-m scale, provided a significant additional contribution to best models of change in native species richness and jam frequency. This variable was intended to reflect propagule availability; however, nearly 60% of the variation in landscape integrity could be explained by variables reflecting land-use and ecosystem productivity. Indeed, when we replaced landscape integrity with historical grazing levels in the regression for native species richness, total variance explained declined by <1%. By contrast, historical grazing levels did not significantly contribute to models for explaining change in the frequency of jam individuals. Jam naturally becomes a more prominent component of York gum woodlands in less productive parts of the landscape, providing an alternative explanation for a greater change in jam frequency in areas with greater native vegetation cover. Correlations between landscape integrity, ecosystem productivity and land-use are thus important to consider when analysing effects of landscape- and site-scale vegetation measures on biodiversity.

Finally, we emphasise that our study relied on the assumption that cross-fenceline pairs were similar before fencing, which could have led to a sampling bias (see also Briggs *et al*. 2008; Spooner and Briggs 2008). However, confidence in our conclusions is suggested by several factors, including significant regression models (these are independent of the above assumption) and lack of relationships between response variables and within-pair differences in factors such as distance from crop paddocks or topsoil nutrient concentrations (that might be attributed to edge effects or differing history). Further, comparisons of fenced sites with benchmark sites are free from these potential biases.

General models for biodiversity recovery from grazing

In a broader context, our analysis provided some support for general models that predict recovery of biodiversity from grazing. In particular, variables reflecting ecosystem productivity and initial vegetation condition (levels of weed invasion) were among the strongest negative correlates of recovery in York gum woodlands, consistent with Cingolani *et al*. (2005) and Lunt *et al*. (2007*a*, 2007*b*). On the other hand, given the short evolutionary exposure to grazing, recovery appeared to be better than suggested by these models, especially at moderate levels of degradation. Additionally, we suggest that the role of propagule availability (as influenced by land-use history and the mobility and longevity of native propagules) is under-developed in existing grazing-recovery frameworks. Perennial forbs that contribute significantly to plant diversity in eucalypt woodlands typically have short-lived propagules and poorly dispersed seeds, which contributes to slow recovery (Lunt 1997; Lunt *et al*. 2007*a*). However, some species and ecosystems are characterised by long-lived or mobile propagule banks that facilitate recovery, as evidenced by the results for jam.

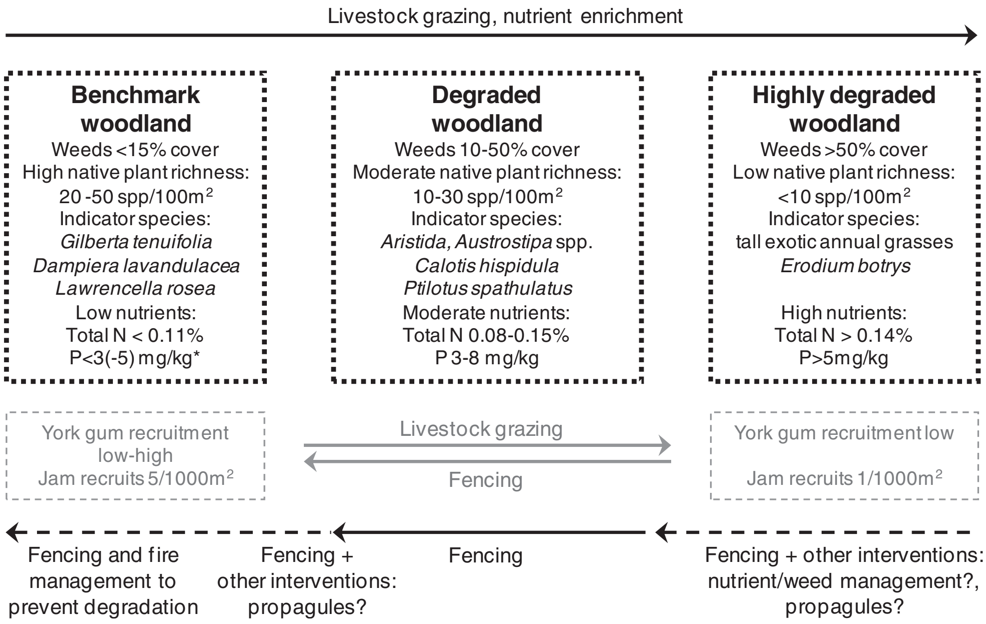

Fig. 7. Framework for guiding restoration decisions in York gum–jam woodlands, based on three generalised woodland states in a degradation sequence from benchmark woodlands, through degraded woodlands with low–moderate exotic invasion and nutrient enrichment, to highly degraded woodlands with high exotic invasion and nutrient enrichment (values provided are indicative only). Each state captures considerable ecological variation, and, as indicated by solid arrows on the restoration (reverse) axis, we suggest that fencing alone is likely to be the most effective for promoting jam recruitment and for enhancing condition of moderately degraded woodlands. Dashed arrows indicate uncertainty regarding the capacity of the ecosystem to recover without additional interventions, such as those indicated. Note that nutrient and water limitation are potential alternative forms of degradation in semiarid woodlands (not detected in the present study) that would require different types of interventions to stimulate soil and vegetation processes (e.g. Ludwig *et al*. 1997; Yates *et al*. 2000*a*, 2000*b*). *Some exceptions noted, e.g. on dolerite dykes.

Management implications

Our data support ongoing investment in fencing to exclude livestock grazing for enhancing biodiversity-conservation values in York gum woodlands and potentially other low-productivity woodlands. We propose an indicative framework to guide setting of conservation targets and clarify where additional interventions may be of highest priority (Fig. 7). Likely benefits of fencing include increased native species richness and cover, reduced exotic species abundance and enhanced tree recruitment, as well as prevention of further degradation from livestock grazing. However, not all benefits will occur in all woodlands within medium (10–20 year) time-frames, and full recovery to benchmark condition will not necessarily occur as a result of fencing alone (Fig. 7; Prober and Wiehl, in press). Rather, depending on initial woodland condition, additional interventions such as nutrient management, weed control, burning or propagule addition, may be needed to achieve conservation goals (Prober and Smith 2009).

Finally, although our proposed framework focused on site-scale factors (Fig. 7), we emphasise that the landscape context of woodlands in agricultural landscapes should also be considered. For example, investment needed to restore highly degraded woodlands is higher than for moderately degraded woodlands; however, if highly degraded woodlands represent the only remaining woodlands in a degraded landscape, they may still be of considerable value to landscape processes and to the local community.

Accessory publication, available on the web

A table on grazing effects on species composition is available as an accessory publication on the Journal's website.

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