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

1 Running title: After the fence in WA wheatbelt woodlands

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1

## 2 **Introduction**

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

14 In Australia, the widespread introduction of livestock grazing has resulted in dramatic  
15 impacts on vegetation composition and ecosystem processes (Lunt *et al.* 2007a).  
16 Because these impacts have occurred relatively recently (within 200 years), they have  
17 been well-characterised, perhaps to a greater extent than in any other region with a  
18 short evolutionary history of ungulate grazing (but see Milchunas and Noy Meir 2002).  
19 In eucalypt woodlands of the temperate zone where agriculture is intensive, key  
20 impacts include widespread replacement of dominant native grasses and shrubs by  
21 exotic annuals and secondary native grasses, decline of native forb and shrub species,  
22 and limited tree recruitment (Dorrough and Moxham 2005; Prober and Thiele 2005;  
23 Prober and Smith 2009). These outcomes can result directly from livestock grazing or  
24 indirectly through changes to soil condition, especially enrichment of available nitrogen  
25 or phosphorus in topsoils (Yates *et al.* 2000a; Prober *et al.* 2002; Standish *et al.* 2006;

1 Dorrough and Scroggie 2008; Prober and Wiehl in press). For over 20 years, fencing to  
2 exclude or reduce livestock grazing has been the major tool used in Australian  
3 agricultural landscapes for maintaining and restoring biodiversity in degraded  
4 vegetation, with over 70,000 ha of native vegetation fenced through the Natural  
5 Heritage Trust program in 2005-6 alone (NHT 2007). These programs assume fencing  
6 will result in positive biodiversity outcomes, but this assumption is poorly substantiated  
7 and for restoration goals, is challenged by theoretical predictions of irreversibility  
8 (Cingolani *et al.* 2005). In eucalypt woodlands of agricultural landscapes, several  
9 studies have shown improved tree recruitment, reduced weed abundance or increased  
10 native plant richness or cover in fenced woodlands. However, results have been  
11 variable and all studies have suggested that ecological thresholds limit the recovery of  
12 some or all woodland characteristics (Fox 2001; Petit and Froend 2001; Duncan *et al.*  
13 2007; Lunt *et al.* 2007b; Briggs *et al.* 2008; Spooner and Briggs 2008; Price *et al.*  
14 2010).

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

1 to recovery, and few studies have assessed recovery of topsoil condition (Duncan *et al.*  
2 2007; Price *et al.* 2010).

3 Towards these goals, we evaluated whether fencing for up to 22 years has promoted  
4 recovery of degraded low-productivity forb-rich York gum (*Eucalyptus loxophleba*  
5 subsp. *loxophleba*) – jam (*Acacia acuminata*) woodlands. These were one of the most  
6 common ecological communities of the south-western Australian wheatbelt (Beard  
7 1990), but because they occur on some of the most profitable agricultural land, more  
8 than 90% have been cleared (Hobbs and Saunders, 1993; Shepherd *et al.* 2002). The  
9 remainder is typically heavily impacted by altered fire regimes, livestock grazing, and  
10 nutrient enrichment (Prober and Smith 2009), commonly resulting in reduced tree  
11 recruitment, widespread invasion by exotic annuals, and loss of native plant diversity  
12 (Prober and Smith 2009; Prober and Wiehl in press). We used cross-fenceline  
13 contrasts of grazed and fenced woodlands, and explicit comparisons with near-by  
14 benchmark woodlands to explore two hypotheses regarding recovery of these  
15 attributes: (1) Fencing facilitates recovery of degraded, low-productivity woodlands  
16 towards conditions of benchmark sites, and (2) Without additional interventions after  
17 fencing, complete recovery of degraded woodlands to benchmark condition is  
18 constrained by ecological limits such as propagule availability, nutrient enrichment and  
19 weed invasion.

## 20 **Materials and methods**

### 21 *Survey design*

22

23 We sampled 40 patches of forb-rich York Gum (*Eucalyptus loxophleba* subsp.  
24 *loxophleba*) – jam (*Acacia acuminata*) woodlands (hereafter York gum woodlands)  
25 across the range of this ecological community in the central wheatbelt, Western

1 Australia (Fig. 1). The native understorey of these woodlands comprises a matrix of  
2 sparse to moderately-dense tussock grasses (particularly *Austrostipa* spp.,  
3 *Austrodanthonia* spp. and *Neurachne alopecuroidea*), interspersed with diverse annual  
4 and perennial forbs, patches of bare ground and scattered shrubs (by contrast with  
5 more arid *Eucalyptus loxophleba* woodlands where the understorey can be dominated  
6 by shrubs). Annual net primary productivity of native understorey is typically low (< 200  
7 g/m<sup>2</sup>, S. Prober, unpub. data, Cingolani *et al.* 2005). To infer topsoil and vegetation  
8 changes associated with fencing, we compared plots placed within 29 fenced York  
9 gum woodlands with plots placed in adjacent, grazed woodlands. This sampling  
10 strategy assumed similar starting conditions within each grazed and fenced pair. Our  
11 sample also included 11 little-grazed York gum woodlands across the same range  
12 ('benchmark woodlands, Fig. 1).

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

19 Then, we visited 134 woodlands on 61 farms and selected 29 cross-fenceline pairs that  
20 met the above criteria. They ranged from 1–511 ha (median 20 ha), and had been  
21 fenced for between 2 and 22 years (median 9 years). Sites extended across gradients  
22 in topographic position and vegetation condition and spanned a rainfall gradient of  
23 320–469 mm mean annual rainfall (median 358 mm). Mean annual temperature  
24 ranged from 15.9–17.7°C (median 17.1°C;). Consistent with the distribution of York  
25 gum woodlands, most sites occurred on soils of relatively recent granitic or granitic  
26 gneiss origin, with occasional dolerite or sedimentary influence (consistent across



1 pairs, Department of Industry and Resources 2001). Land managers provided  
2 information on grazing levels before and after fencing (scored on a subjective scale  
3 from 0-5: nil, very low, low, moderate, moderate-heavy, heavy-very heavy).

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

### 9 *Monitoring*

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

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

17 2. Abundance of pre-defined native and exotic plant life-forms was estimated using a  
18 line-intercept technique (see Prober *et al.* 2005). An 8 mm dowel was placed  
19 vertically at each of 50 points spread evenly across each plot; the relative  
20 abundance for any life-form was the percentage of points at which any leaves,  
21 stems or inflorescences of species from that life-form intercepted the dowel. Groups  
22 that were present but did not intercept the dowel at any point were allocated a  
23 nominal abundance of 0.5% points. This technique provided an objective measure

1 of abundance reflecting but not equivalent to projective cover, and is hereafter  
2 referred to as cover.

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

6 4. All plant species occurring within a 10 m x 10 m subplot nested within each 20 m x  
7 50 m plot were recorded, and abundances estimated as above. Subplots were  
8 selected to be representative of the larger plot and comparable to their cross-fence  
9 comparison in canopy cover. Nomenclature follows the Western Australian  
10 Herbarium (2009).

11 5. Topsoil nutrient concentrations were measured by collecting thirty 2 cm diameter, 10  
12 cm deep soil cores spread evenly across the 10 m x 10 m subplots. Samples were  
13 stored at ~4°C and transported within 72 hours to C SBP Futurefarm analytical  
14 laboratories (Bibra Lake, WA). Samples for each plot were mixed, air dried at 40 °C,  
15 and ground to pass through a 2 mm sieve. Analyses were undertaken as follows  
16 (method numbers refer to Rayment and Higginson 1992): available phosphorus  
17 (Colwell method, bicarbonate-extractable phosphorus, 9B1), potassium (Colwell  
18 method, bicarbonate-extractable potassium, 18A1), ammonium and nitrate  
19 (measured simultaneously using Lachat Flow Injection Analyser, soil:solution ratio  
20 1:5, 1M KCl, indophenol blue, Searle 1984, and with copperized-cadmium column  
21 reduction), pH (1:5 soil/0.01M CaCl<sub>2</sub>, 4B2), conductivity (1:5 soil:water extract, 3A1),  
22 organic carbon (Walkley and Black method, 6A1), extractable sulphur (40°C for 3  
23 hours, 0.25M KCl, measured by ICP, Blair *et al.* 1991), and total nitrogen (oxygen  
24 combustion, 950°C with Leco FP-428 analyser).

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

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

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

1 *Data analyses*

2 *Comparisons of fenced, grazed and benchmark plots*

3 Univariate statistical analyses were conducted using Genstat 12.1 (VSN International  
4 Ltd, 2009). Paired t-tests were used to test for differences in average floristic and  
5 topsoil characteristics between fenced plots and grazed plots. Topsoil chemical and  
6 plant cover variables required log transformation ( $\ln(x + 1)$ ) to satisfy the assumptions  
7 of parametric analysis. We also used permutational tests (using 4999 random  
8 permutations) to obtain significance values. These gave similar results to  
9 parametric tests, so are presented only for analyses with more than 20% zeros. Means  
10 and standard errors for benchmark sites were also calculated, and were compared with  
11 fenced plots and grazed plots using independent groups t-tests.

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

17 *Which variables predict benefits of fencing?*

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

1 Preliminary t-tests suggested a small sampling bias, with grazed plots on average 42.6  
2 m from crop edges compared with 48.8 m for fenced plots ( $p=0.045$ ). However, within-  
3 pair differences (fenced – unfenced) in neither distance from crop edges nor landscape  
4 integrity contributed significantly to any models, suggesting the bias did not unduly  
5 influence results.

## 6 *Multivariate analyses*

7 Ordinations were used to explore differences in topsoil and floristic properties of  
8 grazed, fenced and benchmark plots using PC-ORD (McCune and Mefford 1999). For  
9 soil data, we applied Principal Components Analysis (PCA), using the correlation  
10 matrix (data centred and standardised by standard deviation, Greig-Smith 1983) and  
11 Euclidean distance. For floristic data we used non-metric multidimensional scaling  
12 (nMDS). Quantitative floristic data (excluding tree species) were square root  
13 transformed (to reduce the influence of dominant species) and used to produce a  
14 distance matrix using the Bray-Curtis coefficient of dissimilarity (Faith *et al.* 1987).  
15 Preliminary analyses were performed in one to four dimensions using 10 random  
16 starts; these indicated that the three dimensional solution was optimal, and the solution  
17 with lowest stress (0.15) was selected.

18 Direct overlays and biplots were produced to examine relationships between the  
19 ordinations and environmental variables. We used the blocking procedure in PC-ORD  
20 (MRPP), to test the significance of topsoil and floristic differentiation between  
21 benchmark and other plots. To test for apparent recovery of floristic composition  
22 towards benchmark sites due to fencing, we calculated the vector best separating  
23 benchmark sites using the vector-fitting procedure of DECODA (Minchin 1989). Scores  
24 for the position of plots on this vector were extracted and further analysed using paired  
25 t-tests as described above. Scores were also used to order sites and species in two

1 way tables indicating species contributing to the difference between benchmark and  
2 other plots.

### 3 **Results**

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

#### 10 *Topsoil attributes*

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

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

10 Principle coordinates analysis of topsoil properties showed a strong gradient along axis  
11 1, explaining 48% of the variance in the data (Fig. 2a). This was parallel to the  
12 maximum separation between benchmark and other plots (MRPP  $p<0.001$ ), and was  
13 most strongly related to Colwell phosphorus, total nitrogen and organic carbon. Fenced  
14 plots showed no consistent shift from their grazed pair towards benchmark plots along  
15 this axis (Fig. 2b,  $p=0.86$ ), and there was no apparent relationship between position of  
16 fenced plots on this axis and years since fencing. Axis 2 explained only 13% of the  
17 variance in the data and was unrelated to time since fencing.

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

1 *Floristic diversity and composition*

2 There was strong evidence that vegetation condition was better in fenced than grazed  
3 plots (Table 2). In particular, mean native plant richness was on average four species  
4 greater in fenced plots, contributed mostly by annual and perennial forbs. Native shrub  
5 richness was generally very low, but was marginally higher in fenced plots. Despite the  
6 better vegetation condition of fenced plots, native plant richness (especially for forbs)  
7 was still significantly lower than in benchmark plots, by an average of six species. This  
8 difference remained for the subset of 16 sites fenced for nine years or more (Table 2).

9 Cumulative cover of native understorey showed patterns similar to native plant  
10 richness (Table 2).

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

16 The degree of difference in floristic characteristics between fenced plots and grazed  
17 plots in each pair varied significantly in relation to explanatory variables. For difference  
18 in native plant richness, the best-fit model ( $R^2=46\%$ ) had three components. First, a  
19 quadratic relationship with richness of grazed plots suggested high initial richness  
20 limited potential for increase (Fig. 3a), an intuitive result. Second, the model suggested  
21 gains in richness decreased with increasing residual weed cover (Fig. 3b; explaining  
22 low gains at low initial richness). Third, richness decreased with decreasing landscape  
23 integrity (1000 m scale, Fig. 3c, Table 3). If landscape integrity was replaced with prior  
24 grazing levels, only slightly less variation was accounted for, consistent with a



1 significant relationship between these two variables (Table 3). No significant  
2 relationships between native plant richness and years since fencing were detected.

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

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

22 Species contributing to trends along axis 1—reflecting condition in relation to  
23 benchmark sites—included a predominance of exotic annuals (e.g. *Hordeum*  
24 *leporinum*, *Erodium botrys*, *Bromus rubens*, *Avena barbata*) at the greatest distance  
25 from benchmark sites, and at the other extreme, a suite of native species most

1 frequent in benchmark plots (Supplementary Table 1). These included the native  
2 annuals *Gilberta tenuifolia*, *Lawrencella rosea* and *Gnephosis tenuissima*, and the  
3 native perennial forbs *Thysanotus patersonii* and *Dampiera lavandulacea*. Many other  
4 native species were absent from the most species-poor plots, but occurred with  
5 increasing cover along axis 1 (e.g. the native perennial grass *Neurachne*  
6 *alopecuroidea* and the native annuals *Waitzia acuminata* and *Trachymene*  
7 *cyanopetala*).

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

### 13 *Tree and shrub demography*

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

23 Frequency of trees in fenced and unfenced plots was generally not distinguishable  
24 from reference sites. However, jam recruitment was higher in fenced plots compared

1 with benchmark plots, probably owing to past clearing in fenced but not benchmark  
2 plots (Fig. 6b). We did not detect an effect of fencing on mean DBH of any species  
3 except needle tree, which was larger in grazed plots than in benchmark plots (Fig. 6c).  
4 The frequency of standing dead jam, other trees and other tall shrubs was greater in  
5 fenced compared with grazed plots (Fig 6d), but there were more fallen logs in grazed  
6 compared with fenced plots (Table 1).

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

## 14 **Discussion**

### 15 *Benefits of fencing*

16 Our results suggest that if appropriately targeted, fencing can enhance understorey  
17 condition in York gum woodlands degraded by livestock grazing. Our first hypothesis,  
18 that fencing to exclude grazing facilitates recovery towards benchmark conditions, was  
19 supported for native richness of most plant life-forms, native and exotic cover, and  
20 floristic composition. Given theoretical predictions for poor recovery in ecosystems with  
21 a short evolutionary exposure to grazing (Cingolani *et al.* 2005; Lunt *et al.* 2007a,b),  
22 these results are encouraging. Other grazing exclosure studies in temperate eucalypt  
23 woodlands have reported mixed results for these attributes, with declining weed  
24 abundance in three of six studies, enhanced native cover in four of seven studies, and

1 increased native richness in two of three studies (Fox 2001; Pettit and Froend 2001;  
2 Duncan *et al.* 2007; Briggs *et al.* 2008; Spooner and Briggs 2008; Price *et al.* 2010).  
3 However, few showed improvement in as many characteristics as we observed.

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

13 Fenced York gum woodlands also had higher frequency and recruitment of York gum  
14 and jam than grazed woodlands, but this pattern was not observed for needle tree.  
15 Other studies have similarly found benefits of fencing for tree recruitment are species  
16 dependent (Petit and Froend 2001; Duncan *et al.* 2007; Spooner and Briggs 2008;  
17 Briggs *et al.* 2008). As a palatable legume, it is not surprising that jam recruits are  
18 suppressed by livestock grazing, and with a long-lived soil seed store can recover  
19 rapidly after grazing exclusion. Conversely, needle tree has pungent spines that defend  
20 against grazing and so appear unaffected by fencing. For York gum, recruitment was  
21 absent at most sites (81% including benchmark sites), but abundant recruitment in  
22 three fenced plots that were recently-burnt or flooded supports a need for natural  
23 disturbance as well as fencing to promote York gum recruitment (Hobbs and Atkins  
24 1991, Standish *et al.* 2006). Unlike Dorrough and Moxham (2005), we found no  
25 predictors of tree recruitment associated with vegetation condition or ecosystem  
26 productivity (except for a weak, unexplained effect of topsoil potassium on jam

1 recruitment). However, increases in jam recruitment were greater in sites that we  
2 assumed had fewer trees at fencing, an intuitive result but counter to the concept of  
3 better recovery in less degraded sites (noting tree recruitment was not specifically  
4 addressed by Lunt *et al.* 2007a or Cingolani *et al.* 2005).

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

19 Topsoil physical conditions did not follow expected patterns. Other Western Australian  
20 studies have suggested soil bulk density and levels of bare ground increase with  
21 livestock grazing or cultivation (Yates *et al.* 2000b; Standish *et al.* 2006), whereas our  
22 grazed sites were similar to benchmark sites. Lower bulk density and bare ground  
23 associated with fencing might generally be seen as positive outcomes for plant growth  
24 and soil health, but given the deviation from benchmark sites it is difficult to interpret  
25 whether such outcomes are favourable for biodiversity conservation. Exotic annuals  
26 are also associated with lower topsoil bulk density and bare ground (Prober *et al.* 2002;

1 Prober and Wiehl in review), so our results could reflect an interaction between release  
2 from grazing and a greater cover of exotic annuals in fenced compared with  
3 benchmark sites. Soil surface hardness on the other hand, followed more expected  
4 patterns, being lowest on benchmark sites and highest on grazed plots.

5 By measuring vegetation condition, our study indirectly addressed benefits of fencing  
6 for woodland fauna. Differences between fenced plots and grazed plots that suggest  
7 enhanced fauna habitat include higher tree densities, greater structural diversity  
8 associated with higher tree recruitment and shrub frequency, and higher native ground  
9 cover and forb richness (Barrett *et al.* 2008; Montague-Drake *et al.* 2009). Fallen logs  
10 are often cited as an important element of fauna habitat (e.g. Mac Nally 2006), but we  
11 recorded fewer fallen logs in fenced compared with grazed plots. This was  
12 compensated by higher numbers of standing dead trees in fenced plots, suggesting  
13 dead trees were more likely to have fallen over in grazed plots. Few data are available  
14 to evaluate outcomes of fencing for fauna in other eucalypt woodlands, although Briggs  
15 *et al.* (2008) concluded that recovery of fauna habitat is slow.

#### 16 *Limits to recovery*

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

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

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

15 Further, regression analyses pointed to elevated total nitrogen as a limit to recovery  
16 from exotic invasion. Models containing various combinations of the variables organic  
17 carbon, mean annual rainfall, sulphur and Colwell phosphorus explained nearly 70% of  
18 the variation in total N. Hence we interpret these results more broadly as indicating that  
19 exotics are more persistent in high-productivity environments, consistent with Lunt *et*  
20 *al.* (2007a,b), Lenz and Facelli (2006) and related studies that emphasise reduction of  
21 soil nutrient concentrations for restoration of temperate eucalypt woodlands (Prober  
22 and Thiele 2005; Dorrough *et al.* 2006; Standish *et al.* 2009; Prober *et al.* 2009). This  
23 result contrasts with many semi-arid ecosystems, where recovery from overgrazing can  
24 be limited by 'leakage' of nutrients and water due to soil compaction and loss of micro-  
25 catchments on the soil surface (Ludwig *et al.* 1997; Yates *et al.* 2000a).

1

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

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

25 *General models for biodiversity recovery from grazing*



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

### 15 *Management implications*

16 Our data support ongoing investment in fencing to exclude livestock grazing for  
17 enhancing biodiversity conservation values in York gum woodlands and potentially  
18 other low-productivity woodlands. We propose an indicative framework to guide setting  
19 of conservation targets and clarify where additional interventions may be of highest  
20 priority (Fig. 7). Likely benefits of fencing include increased native richness and cover,  
21 reduced exotic abundance and enhanced tree recruitment, as well as preventing  
22 further degradation from livestock grazing. However, not all benefits will occur in all  
23 woodlands within medium (10-20 year) time-frames, and full recovery to benchmark  
24 condition will not necessarily occur due to fencing alone (Fig. 7, Prober and Wiehl in  
25 press). Rather, depending on initial woodland condition, additional interventions such

1 as nutrient management, weed control, burning or propagule addition, may be needed  
2 to achieve conservation goals (Prober and Smith 2009; Standish and Hobbs 2009).

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

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**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. \*\*\*P<0.001, \*\*P<0.01, \*P<0.05, ns=not significant for comparisons as indicated, na=not available, vs=versus. Means are back-transformed for all nutrients, moisture, bare ground, litter, logs and cryptogams.

		bmk		bmk		bmk		fenced	
		vs long-	long-	vs		vs		vs	
		bmk	fenced	fenced	fenced	grazed	grazed	grazed	
		n=22	P	n=16	P	n=29	P	n=29	P
<b>Topsoil chemistry</b>									
Ammonium	mg/kg	2.32	ns	2.61	ns	3.32	**	4.14	ns
Conductivity	dS/m	0.04	*	0.07	***	0.08	***	0.08	ns
Nitrate	mg/kg	3.19	**	6.33	**	5.92	**	5.95	ns
Organic carbon	%	1.13	***	1.61	***	1.83	***	1.76	ns
pH		5.12	ns	5.36	ns	5.22	ns	5.26	ns
Phosphorus	mg/kg	2.43	***	4.38	***	4.66	***	5.04	ns
Potassium	mg/kg	84.1	***	160.7	***	148.6	***	152.2	ns
Sulphur	mg/kg	3.78	ns	4.23	*	5.06	*	5.11	ns
Total nitrogen	%	0.08	***	0.12	***	0.15	***	0.14	ns
<b>Topsoil physical and surface properties</b>									
Bulk density	g/cm <sup>3</sup>	1.32	ns	1.23	***	1.21	ns	1.31	***
Moisture	%vol	na				2.78		2.70	ns
Hardness	MPa	2.80	*	3.33	ns	3.00	*	3.44	0.064
Bare ground	% points	25.8	ns	20.6	**	15.7	ns	26.7	***
Native litter	% points	47.9	***	29.8	**	34.4	***	30.2	ns
Weed litter	% points	0.46	***	4.32	***	4.84	***	7.65	*
Length of logs	m	78.8	ns	75.8	ns	69.0	ns	85.3	*
<b>Cryptogam crust</b>									
All <sup>†</sup>	% points	na		27.40		23.60		19.10	ns
Leafy lichens	% points	na		3.22		3.26		2.31	0.076
Mosses	% points	na		6.70		4.16		2.88	ns
Other	% points	na		17.60		16.20		13.90	ns

<sup>†</sup> Cumulative score derived by summing % points of relevant sub-classes

**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. \*\*\*P<0.001, \*\*P<0.01, \*P<0.05, ns=not significant for paired comparisons as indicated, na=not available, vs=versus. Richness measured in 10 m x 10 m plots; cover (% points) in 50 m x 20 m plots unless 10 m x 10 m indicated. Means for cover are backtransformed.

	bmk		bmk		bmk		fenced	
	vs long-	long-	vs	vs	vs	vs	vs	
	bmk	fenced	fenced	fenced	fenced	grazed	grazed	grazed
	n=22	P	n=16	P	n=29	P	n=29	P
<b>Native cover</b>								
Trees	na		23.39		26.97		23.09	ns
Understorey <sup>+</sup> (50x20)	na		40.72		43.66		34.73	*
Understorey <sup>+</sup> (10x10)	148.75	***	96.91	***	106.45	***	95.25	0.13
Shrubs	na		1.33		1.36		0.95	ns
Ground layer <sup>+</sup>	na		37.21		40.68		31.62	*
Grasses	na		21.53		19.39		16.27	ns
Perennial forbs	na		3.22		3.18		1.61	*
Annual forbs	na		7.07		10.88		9.00	ns
<b>Native richness</b>								
Total	28.23	***	21.81	***	22.41	***	18.28	***
Shrubs	1.50	ns	1.19	ns	1.10	**	0.69	0.077
Ground layer	24.95	***	18.88	***	19.38	***	15.97	***
Grasses	4.82	ns	4.19	ns	4.17	*	3.86	ns
Perennial forbs	7.68	ns	5.81	*	5.86	***	4.24	**
Annual forbs	12.45	***	8.88	***	9.34	***	7.86	**
<b>Exotic cover</b>								
Total <sup>+</sup> (50x20)	na		29.23		34.23		54.37	***
Total <sup>+</sup> (10x10)	12.61	***	38.02	***	41.69	***	53.49	0.078
Annuals <sup>+</sup> (50x20)	na		25.84		31.79		50.52	***
Annuals <sup>+</sup> (10x10)	11.77	***	31.46	***	35.74	***	50.11	*
Annual grasses	na		15.01		19.33		32.45	**
Annual forbs	na		7.93		8.01		12.24	*
Perennial forbs	na		1.75		1.10		1.16	ns
<b>Exotic richness</b>								
Total	1.06	***	8.86	***	9.51	***	9.07	ns

<sup>+</sup> Cumulative score derived by summing % points of relevant sub-classes

**Table 3. Summary of regression models suggesting constraints to woodland recovery.** F=fenced, G=grazed, ln=natural log. Alternative variables and associated  $R^2$  (\*) are provided where relevant. No models were significant for topsoil nutrients (ammonium, organic carbon, phosphorus, potassium, nitrate, sulphur, total nitrogen), length of fallen logs, jam or York gum recruits, or York gum frequency.

Response variable	Form of response variable	n	Best models	Adjusted $R^2$ (%)
Native richness	F-G	29	+(Native richness grazed-Native richness grazed <sup>2</sup> ) - Exotic cover fenced +Landscape integrity 1000m (*or -Prior grazing)	46.0 (*or 45.3)
Exotic annual cover	ln (F+1) – ln (G +1)	29	-Years fenced -ln Total N grazed +Years fenced*ln Total N grazed (interaction)	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
<i>Relationships among predictor variables</i>				
Landscape integrity (1000 m radius)	Untrans- formed	58	-Prior grazing level -ln S (*or -ln P) -Surface compaction	57.5 (*or 53.8)
		58	-Topographic class -ln S -Surface compaction +Rock cover (constrained to exclude prior grazing level)	37.1
Total N	ln (X+1)	58	+ln Organic C +ln Colwell P	69.5
		58	+ln Colwell P +Rainfall +ln S (constrained to exclude organic C)	53.3



## Figure Captions

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

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

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

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

Figure 5. Non-metric multi-dimensional scaling analysis of fenced, grazed and benchmark (bmk) plots based on 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 vs fenced pairs (black lines) and plots beneath trees (bmk tree) vs gaps (bmk gap) for benchmark sites (grey lines).

Figure 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  $\leq 0.5$  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 mean number of individuals per 1000 m<sup>2</sup> predicted by the GLM models of frequency data; different letters indicate significant differences at P=0.05 for each group of comparisons.

Figure 7. Framework for guiding restoration decisions in York gum – jam woodlands, based on three generalized 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 most effective for promoting jam recruitment and for enhancing condition of moderately degraded woodlands. Dashed arrows indicate uncertainty regarding 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 semi-arid woodlands (not detected in this study), that would require different types of interventions to stimulate soil and vegetation processes (e.g. Ludwig et al. 1997, Yates et al. 2000a,b).

\*Some exceptions noted e.g. on dolerite dykes.

Figure 1.

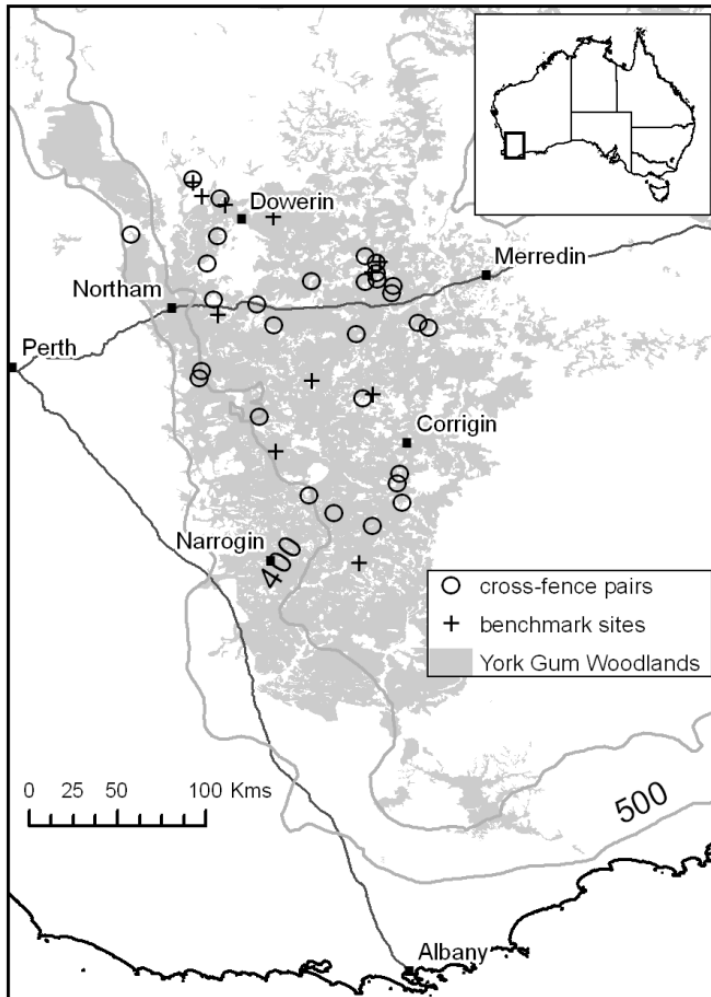




Figure 2.

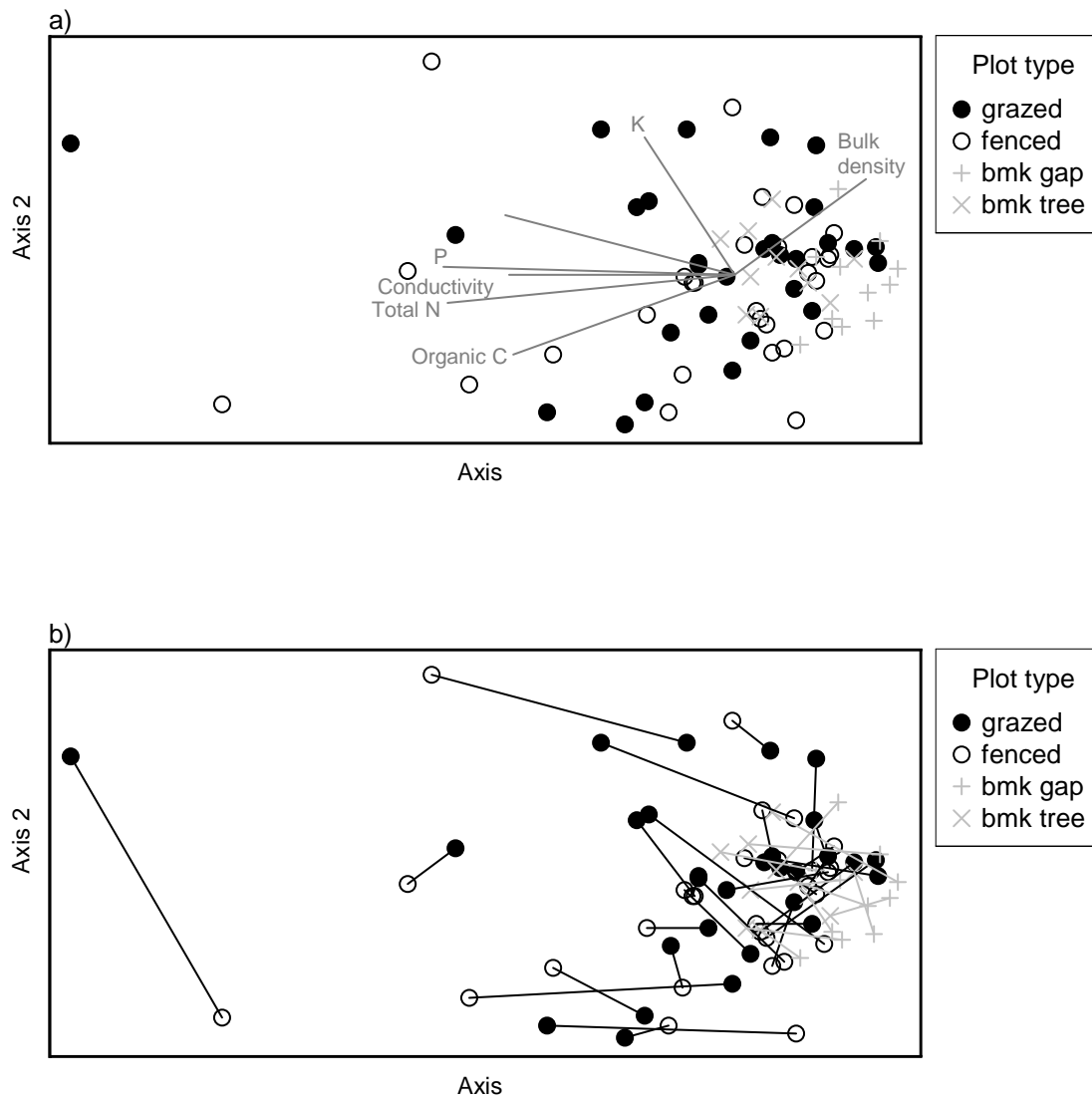
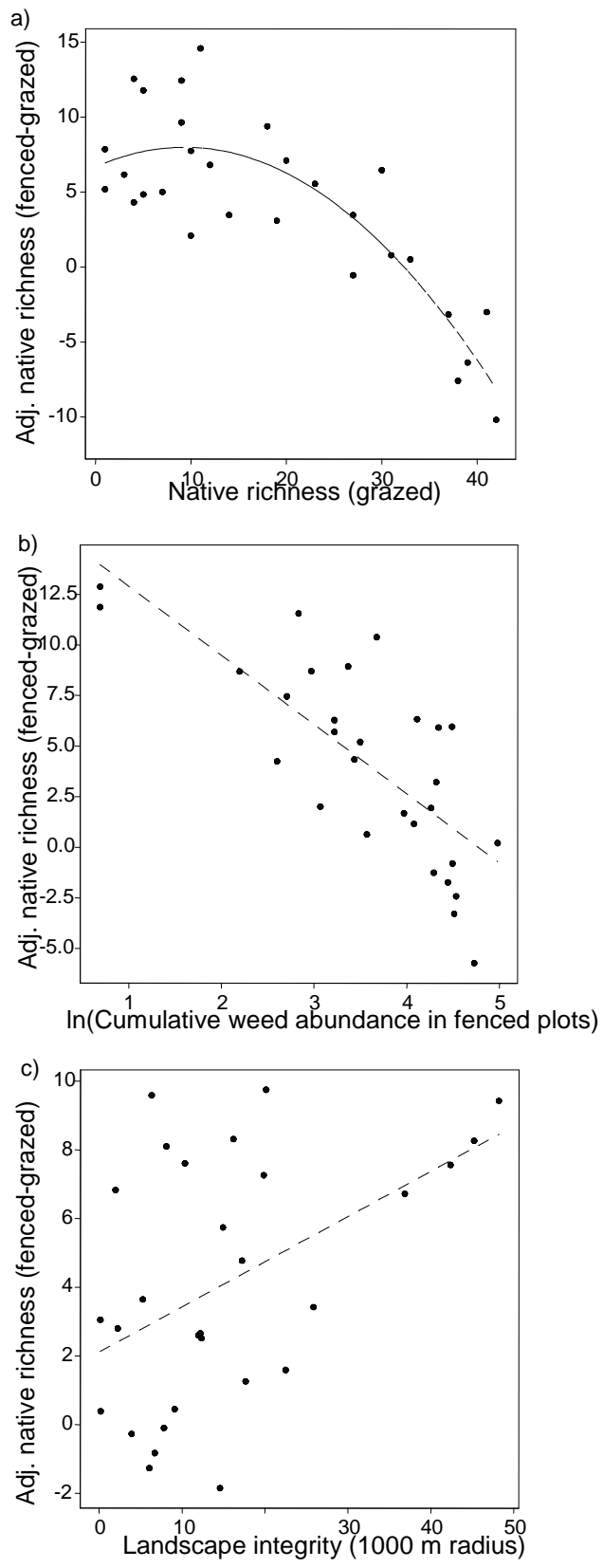


Figure 3.



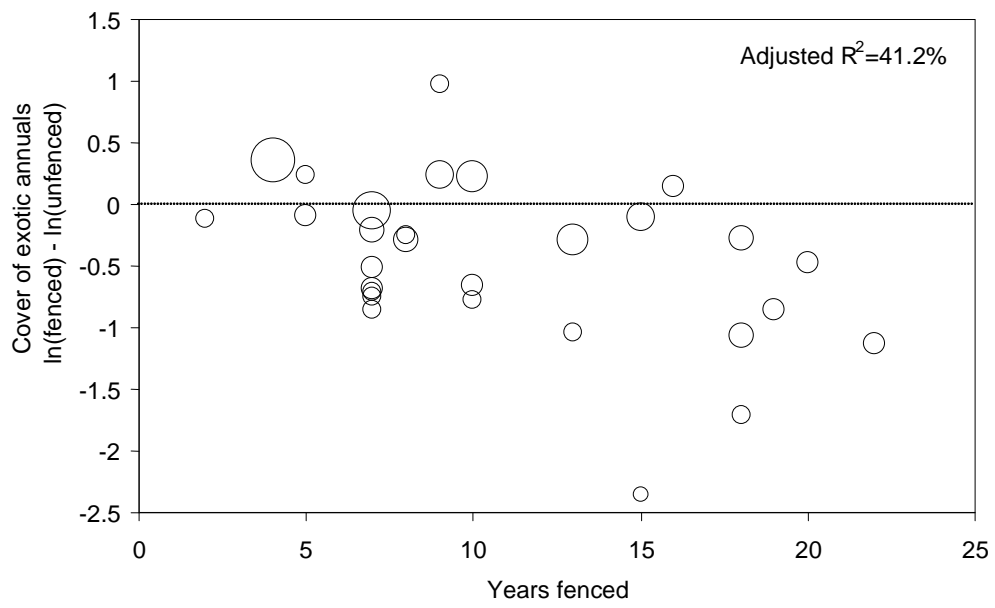


Figure 4.

Figure 5.

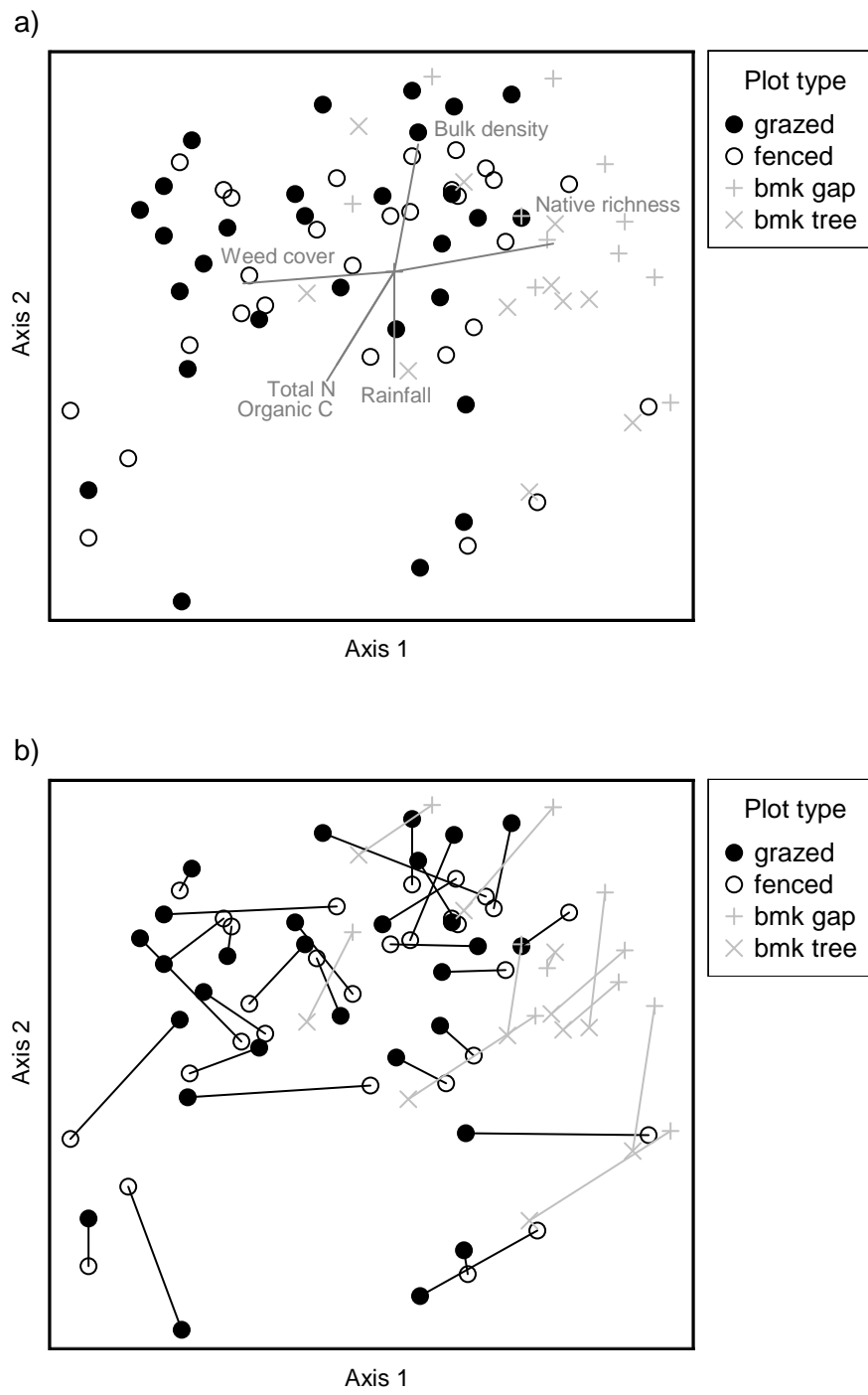


Figure 6.

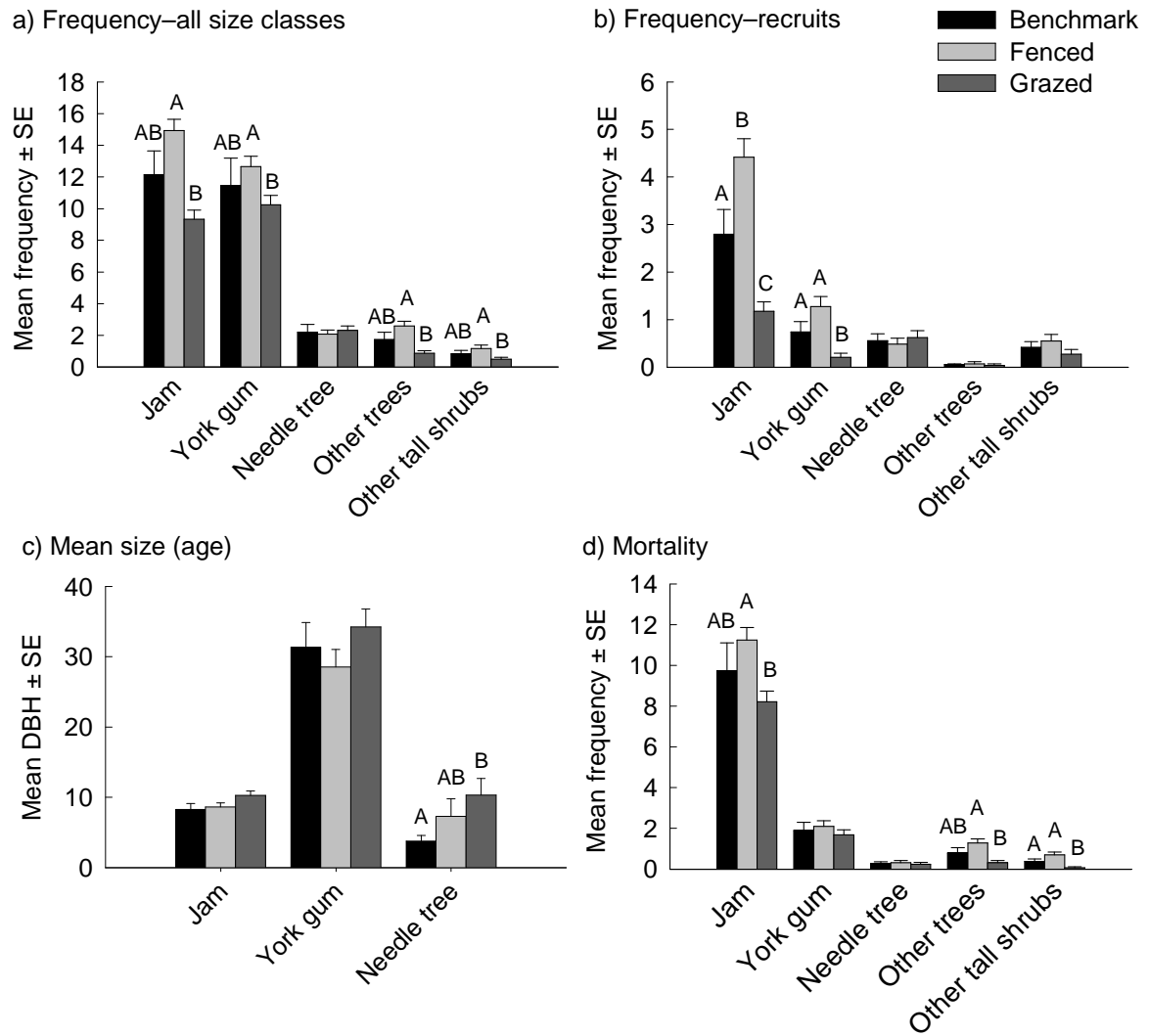


Figure 7.

