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Frequent fire promotes diversity and cover of biological soil crusts in a derived temperate grassland

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Abstract The intermediate disturbance hypothesis (IDH) predicts that species diversity is maximized at moderate disturbance levels. This model is often applied to grassy ecosystems, where disturbance can be important for maintaining vascular plant composition and diversity. However, effects of disturbance type and frequency on cover and diversity of non-vascular plants comprising biological soil crusts are poorly known, despite their potentially important role in ecosystem function. We established replicated disturbance regimes of different type (fire vs. mowing) and frequency (2, 4, 8 yearly and unburnt) in a high-quality, representative *Themeda australis–Poa sieberiana* derived grassland in south-eastern Australia. Effects on soil crust bryophytes and lichens (hereafter cryptogams) were measured after 12 years. Consistent with expectations under IDH, cryptogam richness and abundance declined under no disturbance, likely due to competitive exclusion by vascular plants as well as high soil turnover by soil invertebrates beneath thick grass. Disturbance type was also significant, with burning enhancing richness and abundance more than mowing. Contrary to expectations, however, cryptogam richness increased most dramatically under our most frequent and recent (2 year) burning regime, even when changes in abundance were accounted for by rarefaction analysis. Thus, from the perspective of cryptogams, 2-year burning was not an adequately severe disturbance regime to reduce diversity, highlighting the difficulty associated with expression of disturbance gradients in the application of IDH. Indeed, significant correlations with grassland structure suggest that cryptogam abundance and diversity in this relatively mesic (600 mm annual rainfall) grassland is maximised by frequent fires that reduce vegetation and litter cover, providing light, open areas and stable soil surfaces for colonisation. This contrasts with detrimental effects of 2-year burning on native perennial grasses, indicating that this proliferation of cryptogams has potentially high functional significance for situations where vegetation cover is depleted, particularly for reducing soil erosion.

Keywords Cryptogams · Burning · Fire frequency · Intermediate disturbance hypothesis · Mowing

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Introduction

Disturbances such as grazing, burning and mowing have substantial impacts on the structure, function and composition of grasslands and other ecosystems (Collins et al. 1998; Lunt and Morgan 2002). Ecosystem responses to disturbance are influenced not only by the type of disturbance (e.g. grazing vs. burning), but also by attributes of the disturbance regime such as the intensity, extent, duration and frequency (Collins et al. 1998).

The classic intermediate disturbance hypothesis (IDH) provides a theoretical framework to encompass the effects of a range of disturbance attributes, including scale, intensity

and frequency, on species richness. IDH predicts that richness will display a unimodal (hump-backed) curve in response to variation in a disturbance attribute, with low richness under very low and high disturbance frequencies (or intensities, etc.) and maximum richness under intermediate regimes (Grime 1973; Connell 1978). Mechanistically, IDH assumes that: (1) under infrequent disturbance, competitive species attain dominance and outcompete less competitive species; (2) intermediate disturbance frequencies promote co-existence by constraining potential dominance of competitive species; and (3) frequent (or intense) disturbances reduce diversity either directly, through mortality, or indirectly, by creating abiotic conditions unfavourable to many species (Grime 1973; Connell 1978; Huston 1979).

However, disturbance responses are strongly influenced by site productivity, which controls species colonisation and growth rates (Huston 1979, 2004). Consequently, theory, meta-analyses and modelling studies have highlighted that disturbances are more likely to promote diversity in productive than unproductive ecosystems, where competitive dominance and re-colonisation occur more rapidly (Huston 1979, 2004; Proulx and Mazumder 1998; Kondoh 2001).

Notwithstanding these theoretical expectations, diversity responses to disturbance regimes are highly variable (Mackey and Currie 2001), even in productive grassy ecosystems. Discrepancies can arise when the mechanisms underlying theoretical expectations do not apply. Thus, Collins et al. (1995) found that plant diversity in tallgrass prairie was reduced rather than promoted by increasing fire frequencies, as frequent fires promoted, rather than reduced, competition from the dominant C4 grass. Such examples highlight the need to understand the mechanisms driving species' responses to disturbance regimes (Shea et al. 2004).

In terrestrial vegetation, most studies of the effects of disturbance frequency on vegetation richness and composition have focused on vascular plants. Non-vascular plants, commonly known as cryptogams, are diverse and abundant in many ecosystems, and fulfil many important ecosystem functions including nitrogen fixation, carbon sequestration, enhancing soil surface stability, providing habitat for soil micro-fauna, and influencing germination of vascular plants (Greene and Tongway 1989; Eldridge 2001; Belnap 2003; Morgan 2006). While information is available on successional changes in cryptogam composition following large disturbances such as fire (Timoney et al. 1997; Sim-Sim et al. 2004), few studies address the effects of fire frequency on cryptogam richness and composition (e.g. Mistry 1998).

Fire is commonly recommended for promoting plant establishment, survival and diversity in high-quality remnants of mesic temperate grasslands and grassy woodlands

of south-eastern Australia, consistent with disturbance theory (Tremont and McIntyre 1994; Morgan 1998; Lunt and Morgan 2002). These ecological communities once dominated extensive landscapes of productive agricultural regions, but owing to extensive clearing and livestock grazing, are now highly threatened. Remnants are typically small, degraded and weed invaded (Yates and Hobbs 1997), but relatively intact remnants supporting a range of declining plant species do occur in areas that have escaped significant livestock grazing and nutrient enrichment (Prober and Thiele 1995). These remnants are typically dominated by the large perennial native tussock grasses, *Themeda australis* (R.Br.) Stapf and/or *Poa* species, which dominated these ecosystems before European colonisation (Moore 1973; Prober and Thiele 1995; Lunt 1997), and are believed to have historically been burnt regularly (but at unknown frequencies) through aboriginal and natural fires.

Understanding optimal management needs of rare, high-quality remnants is critically important for conservation of *Themeda*-dominated temperate Australian grasslands and grassy woodlands. However, the effects of fire frequency on plant composition and diversity are poorly understood (Robertson 1985; Prober et al. 2007), and we know of only one observational study that has addressed effects of fire frequency on cryptogam richness in *Themeda* ecosystems: Morgan (2004) documented lower richness of mosses and liverworts under high fire frequencies (1- to 2-year burning) than low frequencies (4– to 20-year burning). Additionally, experimental studies in semi-arid eucalypt woodlands showed that cryptogam crusts took 4 years to recover to pre-burn abundance (Greene et al. 1990), although another study (Morgan 2006) noted rapid recovery. Instead of burning, many remnant grasslands are mown or slashed to limit biomass accumulation; however, no information is available on the effects of mowing on cryptogams in Australian temperate grasslands and grassy woodlands.

In this study, we documented the effects of five replicated burning and mowing regimes on the diversity, abundance and composition of cryptogam crusts (specifically mosses, liverworts and lichens) in a representative, high-quality derived *Themeda australis–Poa sieberiana* grassland in central New South Wales, Australia. Consistent with IDH and the few available studies (Morgan 2004; Greene et al. 1990), we hypothesised that cryptogam richness and abundance would be highest under intermediate fire frequencies (4– to 8-year burning), and would decrease under high (2 year) and low (ca. 15 year) fire frequencies, due to low tolerances to frequent burning, and limited resources beneath thick grass, respectively. Further, we hypothesised that mowing may be less effective than burning for promoting cryptogam crusts due to more limited effects on sward and litter cover (Prober et al. 2007).

Materials and methods

The following site description follows Prober et al. (2008). Experimental plots were established in October 1993 within a high-quality, cleared grassy woodland remnant originally dominated by white box (*Eucalyptus albens* Benth.) and yellow box (*Eucalyptus melliodora* Cunn. ex Schauer), located at Monteagle (34°12′S, 148°21′E, elevation 460 m) on the central western slopes of New South Wales, Australia. Average annual rainfall at the nearest town is approximately 600 mm, with a slight winter maximum. The mean maximum January temperature is 31.3°C and the mean minimum July temperature is 1.4°C. Soils are slightly acidic fine sandy clay loams overlying deep red clays (Red Chromosols, >1 m depth; Isbell 1996), derived from Devonian gran-odiorites.

Based on extensive floristic surveys (Prober and Thiele 1995), the remnant was selected as a representative example of little-grazed, high-quality grassy woodland understorey in the region. It occurs in a rural cemetery with a history of minimal livestock grazing and soil disturbance, although the site was cleared of trees early in the history of settlement (ca. 1900). The ground layer is dominated by *Themeda australis* and *Poa sieberiana*, with a high richness and abundance of native herbaceous plants, few shrubs and relatively low exotic species abundance. The site has a history of frequent burning (ca. 4- to 8-year intervals, last burnt in 1991 prior to experimental burns), so we note that cryptogams not tolerant of this regime are likely to have been absent from the site initially.

Experimental design

Twenty, 5 × 5-m experimental plots separated by 5-m buffers, were established in four blocks arranged along a treeless, gentle slope in October 1993. Three burning frequencies (2-, 4- and 8-year intervals), a biennial mowing treatment and an undisturbed treatment were randomly allocated to plots in each block, creating a five disturbance × four replicate trial arranged in a randomized complete block design.

Treatments began in May 1994 and continued through the experimental period according to the allocated frequency. Burning and mowing were conducted in late autumn to early winter, the typical season for prescribed burning in this region. Mowing height was 10–15 cm, and slash was retained. Grassy swards generally burnt well, leaving blackened tussock bases, minimal live vegetation and sparse litter. Plots were not burnt or mown in 2006 due to extreme drought conditions.

Vegetation and cryptogam measurements

Vascular vegetation and cryptogams were sampled between September 2006 and March 2007, approximately 2.5 years since the most recent 2-year burning and mowing treatment, and 4.5 years after the 4- and 8-year burn treatments. Thus, fire frequency and time since disturbance were confounded in the experimental design. The study area experienced severe drought during the sampling period; the nearby township of Young received 262 mm in 2006, less than half the average annual rainfall.

Grassland structure was measured in spring 2006 using a point-intercept technique following Prober et al. (2007). A tall, 4-mm-diameter rod was placed vertically at 25 points, 200-mm apart, within each plot. The height of the highest vegetation contact with each pin and the total number of vegetation contacts with each pin were recorded at each point. Living and dead material were not separated, and individual species were not distinguished. Percentage vegetation cover was determined from the proportion of the 25 pins per plot that contacted vascular vegetation, and the average number of vegetation contacts per pin (cover repetition) was calculated as a non-destructive estimate of grassland biomass in each plot.

Light infiltration through the grassland vegetation was recorded at each of the 25 pins in each plot, using a Li-Cor light meter (model Li-185) with quantum sensor. Readings were taken above the grass (approximately 600 mm height) and at ground level (<30 mm height) at each point. Light infiltration at each point was estimated from the proportion of incident light (above the canopy) which reached the ground surface. Ideally, light infiltration should be recorded at noon, but because of the large number of readings required, measurements were taken at all times of the day. Resultant shadow effects may have contributed to errors in estimates of light infiltration at each point.

The percentage cover of each of the following attributes was estimated in the field in a 20-mm-diameter circular micro-plot surrounding each of the 25 points: (1) bryophytes (total moss and liverwort cover, as these two groups could not be reliably distinguished in the field), (2) lichens, (3) other vegetation (including other herb species and small annual seedlings), (4) surface litter, (5) grass tussock base, (6) disturbed clear ground (including insect castings and other disturbed soil), and (7) undisturbed clear ground. Note that disturbed and undisturbed 'clear ground' included the ground layer beneath grass tussocks and were not restricted to open canopy gaps.

Twelve of the 25 micro-plots in each plot were removed, and all moss, liverwort and lichen species were identified in the laboratory, following Streimann and Klazenga (2002) for mosses, Scott (1985) for liverworts, McCarthy (1991)

for lichens, and a taxonomic revision of Bryaceae (Spence and Ramsay 2006). The number of individual plants of each bryophyte species and squamules of each lichen species were counted in each sample. From these data we calculated cryptogam species richness at three scales. These included average richness per micro-plot in each plot (species density), richness per 'plot' (i.e. per 12 micro-plots collected from within a plot), and richness per treatment (i.e. per 48 micro-plots per treatment), calculated for total cryptogams as well as mosses, lichens and liverworts. Because abundances varied considerably between treatments (0–600 individuals per plot), we also undertook a rarefaction analysis on plot-scale data to correct for number of individuals encountered (Gotelli and Colwell 2001), using ECOSIM (Gotelli and Entsminger 2006). For further analysis (see below), we selected 'corrected' richness estimates based on predictions for samples of 150 and 25 individuals. The former represented the approximate asymptote of rarefaction curves so in this respect was optimal. However, four plots (two mown and two undisturbed) did not contain this many individuals and were excluded from this analysis. Estimates at 25 individuals were below the asymptote, but included all but one plot that contained no individuals.

We note that no pre-treatment data were available to confirm that experimental plots were initially similar in cryptogam composition and abundance. However, pre-treatment (1993) data from Prober et al. (2007) indicated that there were no initial differences (at $P < 0.1$) among experimental plots in total vegetation cover, bare ground or litter cover. As indicated in the results, these were some of the most important predictors of cryptogam richness and abundance, supporting the assumption that plots were initially similar in this regard.

Data analyses

Treatment effects on vegetation, ground cover and cryptogam attributes were compared at both the micro-plot and the plot scale. Analysis of most univariate variables was undertaken in Genstat 10.1 (Genstat 2007), using ANOVA of the randomized complete block design to test for treatment effects. Where necessary we used natural log and square-root transformations to achieve homogeneity of variance. Fischer's protected least significant differences were used to compare treatment means. In cases where multiple zero values violated ANOVA requirements we used non-parametric Friedman's tests followed by critical difference multiple comparison tests.

We used Spearman's rank correlations and stepwise multiple regression analysis in Genstat 10.1 to explore relationships among structural, treatment and cryptogam variables at the 2-cm micro-plot and 5 × 5-m plot scales (using

pooled data from all micro-plots in each plot). Three stepwise regression analyses were performed for each of total cryptogam numbers and total cryptogam richness (at the plot scale), the first including only structural variables (clear ground, disturbed ground, grass cover, light infiltration, maximum grass height, cover repetition, surface litter cover and % tussock bases), the second including only treatment variables (burning interval, mowing interval, block, years since burnt, number of burns since 1993, number of times mown since 1993), and the third incorporating all variables from these groups. Adjusted R^2-values were used to select optimal models from each of these groups.

Treatment effects on cryptogam composition were assessed using non-metric multi-dimensional scaling (NMDS) ordination and permutational multi-variate ANOVA; the latter provides non-parametric statistical comparisons of floristic composition (Anderson 2005). These were undertaken using PRIMER version 6.1.6 with the PERMANOVA+ module (Primer-E 2007). Data were pooled from the 12 micro-plots in each plot, and analyses were based on a Bray–Curtis dissimilarity matrix calculated from square-root transformed mean abundances (Clarke and Gorley 2006). One 'undisturbed' plot was removed from the dataset as no species were recorded in the sampled micro-plots. Owing to relatively low *df*, we used permutation of residuals under a full model, and Monte Carlo tests (999 permutations) to test significance of comparisons made using PERMANOVA (Anderson 2005). The degree of association of cryptogam taxa with the five treatments was measured using indicator-species analysis (Dufréne and Legendre 1997) in PC-ORD (McCune and Mefford 1999), based on a data matrix consisting of the average abundance of each species in each of the four replicate plots in each treatment. Species data were randomized among the treatments and a Monte Carlo randomization procedure performed with 1,000 iterations in order to determine the statistical significance of the indicator values (McCune and Mefford 1999).

Results

Grassland structure and soil surface characteristics were strongly influenced by fire regime, with increasing grass abundance (height and cover repetition) and surface litter cover with decreasing fire frequency (Table 1). The reverse occurred for light infiltration, dicotyledonous herb cover and undisturbed clear ground, which tended to decrease with decreasing fire. Notably though, there was an increase in disturbed clear ground with decreasing fire, reflecting a high activity of soil organisms such as worms beneath dense grass cover (authors, personal observation), and hence there was no significant difference between

Table 1 Treatment effects on grassland structure and ground cover attributes

Attribute	2-year burn	4-year burn	8-year burn	2-year mow	Undisturbed	P^a
Cover repetition (intercepts/point)	6.4a	11.8b	12.6b	11.6b	21.2c	<0.001
Grass height (mm)	126.7a	205.8b	229.9b	169.5ab	298.5c	<0.001
Light infiltration (%)	49.8a	32.5ab	32.5ab	36.3ab	18.1b	0.037
Vegetation cover (% points)[b]	96	99	100	98	100	NS
Cover (% micro-plot estimates)						
Grass tussock bases	7.4	8.7	8.9	11.4	15.6	NS
Dicotyledonous herbs	5.7a	2.4ab	1.0b	2.6ab	0.6b	0.030
Surface litter	22.0a	27.5a	36.2ab	36.1ab	46.6b	0.040
Undisturbed clear ground	30.5a	18.1ab	15.1bc	16.9bc	4.4c	0.017
Disturbed clear ground	4.6a	18.2b	21.5b	21.7b	23.7b	0.003
Total clear ground	36.2	36.3	37.1	39.8	29.0	NS
Total cryptogams	26.0a	23.5a	16.1a	7.1b	5.6b	0.002
Bryophytes	22.6a	23.2a	16.0a	6.6b	5.0b	<0.001
Lichens[b]	3.7	0.25	0.1	0.8	0.85	NS

Different letters indicate significant differences ($P < 0.05$) between treatments

NS not significant

[a] *P*-values were estimated using ANOVA

[b] For non-parametric data, Friedman's tests were used

treatments in total clear ground. Contrasts were generally greatest between 2-year plots (which were also the most recently burnt) and undisturbed plots, while differences between 4- and 8-year plots were not significant for any structural variables. Effects of mowing were generally intermediate and similar to 4- and 8-year plots (Table 1).

At the micro-plot scale, light infiltration was negatively associated with cover repetition (Rs = −0.603, $P < 0.001$; Fig. 1a) and grass height (Rs = −0.537, $P < 0.001$). Light infiltration was highly variable at low levels of cover repetition, possibly owing to shading effects. However, light levels were typically low when cover repetition exceeded 20–30 leaf contacts per point (Fig. 1a).

Cryptogam cover and diversity

Thirty-four species of cryptogams were recorded from the two hundred and forty, 20-mm-diameter micro-plots, including 22 species of moss, eight liverworts and four lichens (Tables 2, 3). Most species were found infrequently; 22 species (65%) were recorded in less than 5% of micro-plots, whereas only five species were found in more than 10% of micro-plots.

Burning led to an increase in total cryptogam cover and abundance compared with mown and undisturbed plots at both micro-plot (Table 1) and plot (Fig. 2a) scales, driven mostly by mosses, but also reflected in lichen and liverwort abundance. Post hoc comparisons indicated that differences between 2-, 4- and 8-year fire frequencies were not significant.

These results reflected effects of disturbance treatments on grassland structure, with cryptogam cover and abundance at both the plot and micro-plot scales correlating negatively with cover repetition and surface litter cover (Fig. 1b, c), and positively with percent light infiltration (Table 4). However, at the micro-plot scale these relationships were not linear. Rather, cryptogam cover varied widely at low cover repetition (<25 contacts), but was typically low when cover repetition exceeded ca. 20 leaf contacts per point (Fig. 1b). Similarly, surface litter cover appeared to influence the maximum potential cryptogam cover, but cryptogam cover often fell below this maximum (Fig. 1c).

Treatment effects on cryptogam richness were similar to effects on abundance, and were apparent at the treatment scale (Table 2), plot scale (Fig. 2b) and micro-plot scale (Fig. 2c). At the treatment scale, total species richness increased with increasing fire frequency, from just nine species across all undisturbed plots to 27 species across all 2-year burn plots (Table 2). Total species richness across mown plots was relatively low, being intermediate between burnt and undisturbed plots (Table 2). These trends were consistent at the plot scale, where total cryptogam richness was significantly greater in 2-year burn plots than all other treatments, and was significantly lower in undisturbed plots than in all treatments except mown plots. Notably, this trend was also observed for corrected cryptogam richness (after adjustment for number of individual using rarefaction analysis), indicating that increases in cryptogam richness were not solely related to increases in abundance. We note

Fig. 1 Relationships between:
a vegetation cover repetition and
light infiltration (%) beneath the
grass canopy, **b** vegetation cover
repetition and cryptogam cover
(%), **c** surface litter cover (%)
and cryptogam cover (%), and
d vegetation cover repetition
and cryptogam species richness
at the micro-plot scale.
Spearman rank correlation (*Rs*)
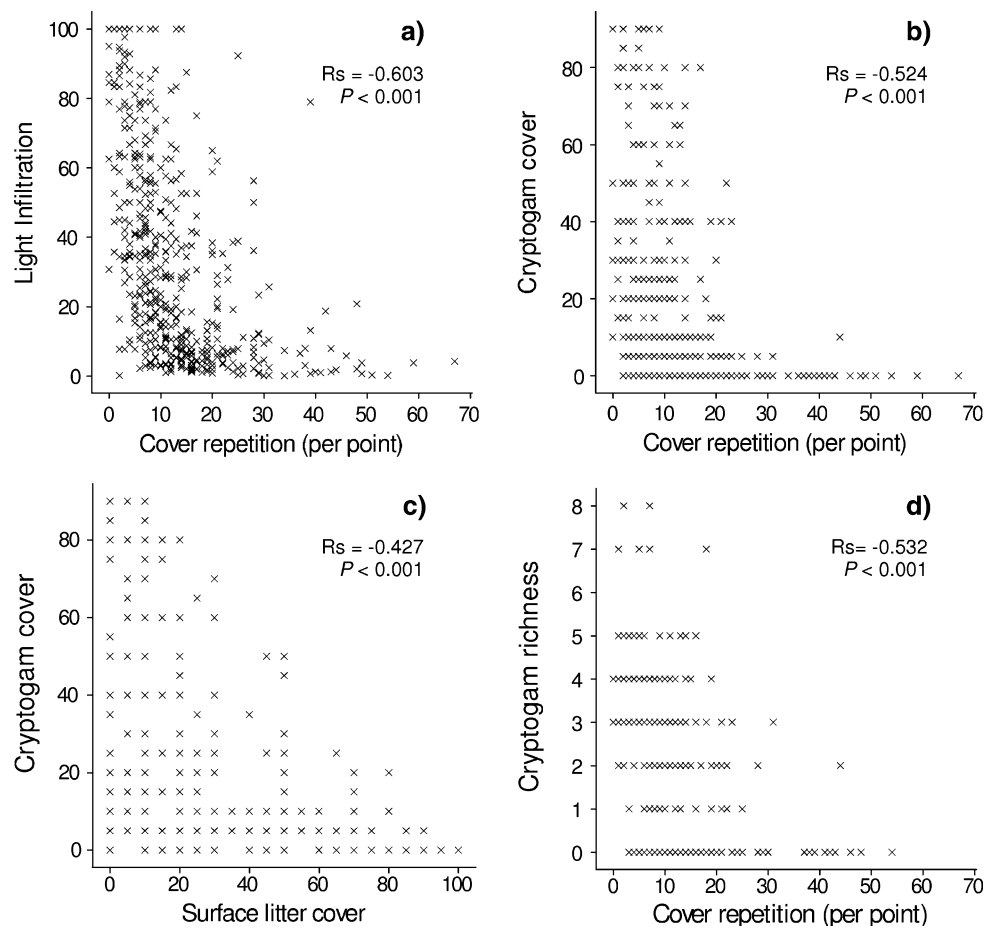and *P* are indicated for each

Table 2 Total number of cryptogam species recorded in each treatment

Treatment	Taxonomic group			
	Total cryptogams	Mosses	Liverworts	Lichens
2-Year	27	17	7	3
4-Year	20	16	3	1
8-Year	20	16	2	2
Mown	17	13	3	1
Undisturbed	9	7	2	0
Total species	34	22	8	4

though that means for mown and control plots at 150 individuals appear somewhat inflated, due to two missing values each (i.e. plots with abundance <150 individuals had low richness but were excluded from analysis due to insufficient individuals sampled; Fig. 2d). Mosses, liverworts and lichens showed similar trends to total cryptogam richness (Fig. 2b), but treatment effects were not always significant. Trends at the micro-plot scale were similar but weaker than trends at the plot scale (Fig. 2c; Table 4).

Cryptogam, moss, liverwort and lichen richness at the plot and micro-plot scales were negatively correlated with

cover repetition, light infiltration and the cover of litter and disturbed clear ground, and were positively correlated with the cover of undisturbed clear ground (Table 4). Similar to cryptogam abundance, cryptogam richness at the micro-plot scale was variable at low cover repetition (<25 grass contacts) but consistently low when cover repetition was high (Fig. 1d).

Stepwise regression analysis indicated that these trends in cryptogam abundance and richness at the plot scale were best summarized by models that incorporated a combination of treatment and structural variables. Using structural variables alone, cover repetition explained 56.3% of the variation in total cryptogam abundance (*P* < 0.001), but no other variables significantly added to this model. Using treatment variables, Number of years since last burn explained 64.1% of the variation in total number of cryptogam individuals per plot (*P* < 0.001). The optimal model incorporating both types of variables included Number of years since last burn (*P* < 0.001) plus light infiltration (*P* = 0.001), explaining 79.6% of variation.

For cryptogam richness, cover repetition alone explained a high proportion of the variation (78.5%, *P* < 0.001), with this increasing to 84.5% with addition of clear ground (*P* = 0.012). Using treatment variables alone, only Number

Table 3 Cryptogam species abundances (mean number of individuals per micro-plot) and frequencies in experimental plots at Monteagle, NSW, Australia

Group	Species	Mean number of individuals/micro-plot					Total no. individuals	Micro-plots (%)
		2-year	4-year	8-year	Mown	Undisturbed		
Moss	*Eccremidium arcuatum*	**10.9**[a]	8.1	8.4	1.3	–	1,377	32.9
Lichen	*Cladonia* spp.	**6.0**	2.1	0.4	1.0	–	454	11.3
Liverwort	*Lophocolea semiteres*	**2.9**	1.4	0.02	–	0.02	212	8.3
Moss	*Barbula calycina*	2.3	2.8	**7.8**	3.4	3.0	928	35.8
Moss	*Breutelia affinis*	1.7	2.0	**2.6**	2.2	0.7	443	19.2
Moss	*Gemmabryum pachythecum*	**1.5**	0.6	0.2	–	–	114	6.7
Moss	*Gemmabryum eremaeum*	**1.4**	–	–	0.2	–	79	4.6
Moss	*Gemmabryum dichotomum*	**1.1**	0.3	0.6	0.1	0.1	109	8.3
Liverwort	*Cephaloziella arctica* ssp. *antarctica*	**1.0**	–	–	–	–	50	0.4
Moss	*Desmatodon convolutus*	**1.0**	0.5	0.2	0.5	0.4	126	6.3
Moss	*Bryum argenteum*	**0.8**	0.04	0.1	0.1	–	50	3.3
Lichen	*Endocarpon simplicatum* var. *bisporum*	**0.6**	–	–	–	–	30	0.4
Moss	*Ceratodon purpureus*	**0.6**	–	0.1	–	–	35	1.7
Liverwort	*Asterella drummondii*	**0.5**	–	–	0.1	–	31	1.7
Moss	*Crossidium davidai*	**0.5**	–	–	–	–	26	1.7
Moss	*Gemmabryum austrosabulosum*	0.5	**0.9**	0.02	0.2	–	76	6.7
Lichen	*Endocarpon pusillum*	**0.4**	–	–	–	–	20	1.3
Moss	*Fissidens taylorii*	0.4	1.0	**3.0**	0.8	1.8	339	19.6
Moss	*Phascum robustum* var. *robustum*	**0.4**	0.2	0.1	–	–	34	2.5
Liverwort	*Riccia crozalsii*	0.3	0.2	–	**0.5**	0.2	57	2.9
Liverwort	*Fossombronia* sp. aff. *pumila*	**0.2**	–	–	–	–	11	2.1
Moss	*Leptobryum pyriforme*	0.2	0.2	**1.1**	0.3	–	90	8.3
Liverwort	*Riccia crinita*	**0.2**	–	–	–	–	10	0.4
Moss	*Pottia brevicaulis*	0.1	**1.7**	0.1	–	–	89	2.5
Moss	*Bryum erythrocarpum* complex	**0.1**	–	–	–	–	5	0.4
Liverwort	*Cephaloziella exiliflora*	**0.1**	–	–	–	–	3	0.4
Moss	*Stonea oleaginosa*	**0.02**	–	–	–	–	1	0.4
Moss	*Bartramia hampei*	–	**3.9**	0.9	0.3	0.4	263	6.3
Moss	*Didymodon torquatus*	–	**1.0**	1.0	0.2	0.8	149	3.8
Liverwort	*Reboulia hemisphaerica*	–	**0.2**	0.02	0.02	–	10	1.7
Moss	*Funaria cuspidata*	–	**0.04**	–	–	–	2	0.4
Moss	*Bryum caespiticium* var. *badium*	–	**0.04**	0.04	–	–	4	0.8
Lichen	*Toninia sedifolia*	–	–	**0.4**	–	–	20	0.4
Moss	*Triquetrella papillata*	–	–	–	**0.02**	–	1	0.4

[a] Maximum treatment abundances are shown in bold

of burns since 1993 was included in the model, explaining 62.8% of variation ($P < 0.001$). The optimal model incorporating both types of variables explained 93% of the variation in cryptogam richness at the plot scale. The model was similar to the structural model (cover repetition and clear ground), with addition of Number of times mown since 1993 ($P < 0.001$).

We note that while some models include Years since burnt and others included Number of burns since 1993, there were only small differences between inclusion of these alternatives, and we do not believe the differences

were adequate to discriminate whether time since fire or fire frequency was most important in determining differences between 2-year burn plots and other burnt plots. Rather, both variables emphasize differences among unburnt plots, 2-year burn plots, and 4- or 8-year burn plots.

Cryptogam species composition

The two-dimensional NMDS ordination showed moderate separation in species composition among treatments (Fig. 3). PERMANOVA indicated that overall treatment
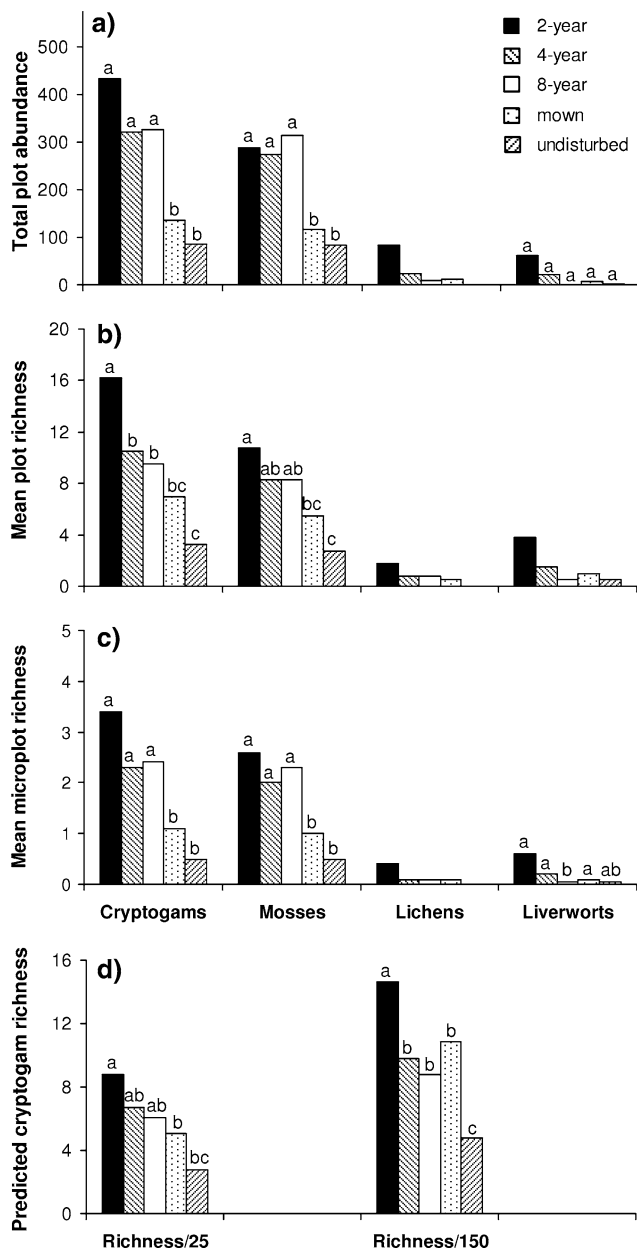
Most species were most abundant in 2-year burn plots (Table 3), and generally declined with decreasing fire frequency, and in mown and undisturbed plots. Indicator-species analysis showed that the bryophytes *Gemmabryum eremaeum* [indicator value (IV) = 89.3, $P = 0.002$], *Fossombronia* sp. aff. *pumila* (IV = 75.0, $P = 0.014$) and *Asterella drummondii* (IV = 62.9, $P = 0.041$), and the lichen *Endocarpon pusillum* (IV = 75.0, $P = 0.023$) were significant and strong indicators of 2-year burn plots. No species were significant indicators of any of the other individual treatments ($P > 0.05$), although the moss *Eccremidium arcuatum* was common only in burnt plots, and several moss species showed a humped relationship with disturbance, with maximum abundance in 8-year plots in most replicates (e.g. *Barbula calycina* and *Leptobryum pyriforme*; Table 3). Thus, undisturbed and mown plots possessed a subset of the species that were more abundant in burnt plots, rather than a distinct cryptogam flora (Table 3).

Discussion

We recorded 34 bryophyte and lichen taxa across the 240 micro-plots (totalling 0.075 m^2), most of which were mosses. This level of richness is comparable with the few other studies of biological soil crusts in box woodlands (e.g. 50 taxa; Eldridge et al. 2006) and *Themeda* grasslands (e.g. 27–32 taxa; Morgan and Rollason 1995; Morgan 2004) in south-eastern Australia, though the latter were sampled across larger areas. Interestingly, while our site contains a high-quality woodland understorey that has rarely been grazed by livestock and includes many regionally declining vascular plant species (Prober and Thiele 1995), the cryptogam flora appears to largely comprise widespread, colonising species (Scott and Stone 1976; Scott 1985; Eldridge and Tozer 1997; Meagher and Fuhrer 2003).

Results demonstrate substantial impacts of different disturbance types (fire and mowing) and regimes (frequency/time since disturbance) on grassland structure and cryptogam composition. As hypothesised, cryptogam richness and abundance were lowest in undisturbed plots. However, contrary to expectations, cryptogams were most diverse in the most frequently and recently burnt sites and biennial mowing led to lower cryptogam abundance and richness compared with biennially burnt plots.

Low disturbance

A high proportion of the variation in cryptogam richness and abundance was explained by grassland cover repetition (79 and 56%, respectively), supporting the IDH prediction that high competitive dominance (albeit by vascular plant

Fig. 2 Treatment effects on **a** cryptogam abundance (total number of squamules or individuals in 12 micro-plots per plot), **b** cryptogam richness at the plot scale, **c** cryptogam richness at the micro-plot scale, and **d** plot-scale cryptogam richness as predicted by rarefaction analysis for samples of 25 and 150 individuals. All main effects were significant ($P < 0.05$), except for lichens (all cases, $P < 0.07$) and liverwort richness at the plot scale ($P = 0.064$). Lichen and liverwort comparisons were made using Friedman's tests as data were non-parametric. Within each taxonomic group, *different letters* indicate significant differences between means

effects were significant ($P = 0.009$), and that the composition of the 2-year burn plots differed significantly from the 8-year ($P = 0.015$), mown ($P = 0.046$) and undisturbed plots ($P = 0.041$). Other pair-wise comparisons were not significant at $P < 0.05$.

Table 4 Spearman rank correlations (*Rs*) and significance (*P*) between grassland structural attributes and cryptogam abundance (number of individuals), cover and richness at micro-plot and plot scales

|	Cover repetition		Light (%)		Litter (%)		Disturbed clear ground (%)		Undisturbed clear ground (%)	
	Rs	*P*	Rs	*P*	Rs	*P*	Rs	*P*	Rs	*P*
Micro-plot scale										
Total abundance	−0.494	<0.001	0.339	<0.001	−0.361	<0.001	−0.221	0.001	0.406	<0.001
Total cover	−0.524	<0.001	0.364	<0.001	−0.423	<0.001	−0.226	<0.001	0.373	<0.001
Total richness	−0.535	<0.001	0.329	<0.001	−0.336	<0.001	−0.226	<0.001	0.474	<0.001
Moss richness	−0.484	<0.001	0.287	<0.001	−0.309	<0.001	−0.188	0.003	0.448	<0.001
Liverwort richness	−0.345	<0.001	0.200	0.002	−0.205	<0.001	−0.118	0.070	0.195	0.002
Lichen richness	−0.271	<0.001	0.246	0.007	−0.158	0.015	−0.260	<0.001	0.310	<0.001
Plot scale										
Total abundance	−0.731	<0.001	0.698	0.001	−0.615	0.004	−0.469	0.037	0.626	0.003
Total cover	−0.665	0.001	0.615	0.004	−0.762	<0.001	−0.537	0.015	0.568	0.009
Total richness	−0.931	<0.001	0.833	<0.001	−0.736	<0.001	−0.662	0.001	0.881	<0.001
Moss richness	−0.875	<0.001	0.774	<0.001	−0.773	<0.001	−0.526	0.017	0.877	<0.001
Liverwort richness	−0.610	0.004	0.566	0.009	−0.506	0.023	−0.634	0.003	0.556	0.011
Lichen richness	−0.765	<0.001	0.684	0.001	−0.588	0.006	−0.640	0.002	0.613	0.004
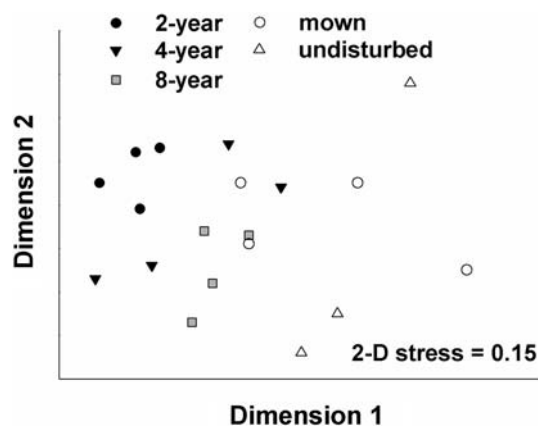
Fig. 3 Non-metric multidimensional scaling ordination showing treatment effects on species composition. Only three replicates of the undisturbed treatment are shown as no species were present in samples from one undisturbed plot

species) leads to lower diversity with infrequent disturbance (Grime 1973; Connell 1978). This is consistent with other studies showing that cryptogam cover in remnant eucalypt woodlands increases with decreasing plant cover (e.g. Eldridge 1998; Cuddy 2000; Eldridge et al. 2000, 2006; Thompson et al. 2006). Cryptogam richness and abundance and grassland cover repetition were in turn significantly associated with incident light and undisturbed clear ground, hence low cryptogam richness and abundance in undisturbed plots is likely to reflect low levels of light (and possibly other resources) beneath the dense grass canopy (Bergamini et al. 2001). Spore germination, in particular, is light dependent (Richardson 1981), and the paucity

of cryptogams in infrequently disturbed plots is not surprising, given the high cover of litter and grass.

Development of a stable cryptogam community in dense swards of 'undisturbed' plots may have been further constrained by high levels of bioturbation (animal-induced soil movement) by earthworms and ants, an interaction not directly predicted by IDH. On average, 24% of the ground surface in undisturbed plots was excavated by soil-active invertebrates, compared with just 5% in the 2-year burn plots. Thus, despite positive associations between cryptogam richness and undisturbed clear ground, there were significant negative associations with disturbed clear ground, consistent with findings that cryptogam crusts commonly require a stable surface on which to establish and grow (Eldridge 2001). Disturbed soil in undisturbed plots was also observed to bury cryptogam mats, although some mosses such as the fast-growing colonists *Gemmabryum* spp. were capable of re-growing through the upturned soil.

An alternative explanation for low cryptogam richness and abundance on undisturbed plots is that the historical regime of 4– to 8-year burning eliminated fire-sensitive taxa from the species pool. After cessation of this regime, recolonisation may have been limited by lack of propagules. In particular, slow-growing foliose and fruticose lichens (e.g. *Xanthoparmelia* spp., *Cladia* spp.; Cuddy 2000), species typical of little-disturbed eucalypt woodlands, were not recorded in our study. However, these species are associated with large patches of exposed soil in little-disturbed sites (Cuddy 2000), and that habitat did not develop in our undisturbed, dense *Themeda* swards. Consequently, we would not expect these species to become

prominent at the scale of our experiment (5 × 5-m plots). Nevertheless, they may be more likely to occur across larger scales that incorporate greater habitat heterogeneity. Similarly, we cannot preclude the possibility that these species may colonize over longer timeframes. For example in more arid regions, lichens have been reported to require more than 30 years to recover in areas where they were removed (Rosentreter and Eldridge 2002).

Mowing versus burning

Biennial mowing had markedly different effects on grassland structure and cryptogams compared with biennial burning. While frequent burning promoted cryptogam richness, cover and abundance, mowing with retained slash led to levels similar to those in less-frequently disturbed plots. By contrast, studies elsewhere have found that mowing promoted bryophyte biomass and cover (Huhta et al. 2001; Peintinger and Bergamini 2006; Billeter et al. 2007). Similarly, a number of grazing-exclusion studies have demonstrated substantial declines in the cover and diversity of soil bryophytes and lichens following increases in vascular plant cover (Brodo 1961; Looman 1964).

Since all cryptogam taxa in our study were considerably shorter than the mowing height (10–15 cm high), mowing was unlikely to have adversely affected cryptogams directly. In part, low cryptogam cover and richness on mown plots compared with 2-year burn plots appears to reflect greater grass and litter cover as we predicted. This is supported by inverse relationships between cryptogam cover and richness versus cover repetition and litter cover, and concomitant reduction in cryptogams on 4- and 8-year burn plots that were structurally similar to mown plots. However, cryptogam abundance, and richness under some measures, was lower on mown plots than 4- and 8-year burn plots, pointing to additional (unmeasured) influences that counteracted positive influences of disturbance on cryptogams. For example, field observations suggest thickness and density of the thatch, rather than litter cover alone, may be important.

Frequent burning

Contrary to expectations based on IDH, cryptogam richness did not decline under our most frequent burning treatment. Instead, cryptogam richness was greatest on plots with the highest fire frequency and the least time since disturbance, even when corrected for differing abundance using rarefaction analysis. This discrepancy suggests that our 2-year burning regime did not meet the assumptions for 'high' disturbance in relation to IDH, in particular that: (1) frequent fire kills or greatly depletes significant numbers of cryptogam species and their recovery rates are slower than the disturbance interval, or (2) conditions created by frequent burning are unsuitable for many cryptogam species.

Regarding the former, surface temperatures in fires in similar *Themeda* grasslands were sufficient to kill surface sown seeds of vascular plants (239–367°C; Morgan 1999), and are likely to have killed cryptogams (e.g. Greene et al. 1990). Nevertheless, cryptogams were clearly able to recover within short timeframes in our study, contrasting with Morgan (2004) and Greene et al. (1990), but consistent with Esposito et al. (1999) and Morgan (2006).

Regarding development of unsuitable abiotic conditions under high disturbance, the opposite may have occurred on 2-year burn plots. Earlier studies at the same experimental site showed that biennial burning reduced grassland productivity (Prober et al. 2007) and increased soil surface compaction compared with other treatments (Prober et al. 2008). Hence, frequent burning may have enhanced habitat suitability for cryptogams both by reducing competing grass cover and creating a stable, bare (albeit compacted) soil surface suitable for cryptogam colonisation (West 1990; Eldridge and Greene 1994; Thompson et al. 2006).

From the perspective of cryptogams then, 2-year burning of *Themeda* grasslands at the study site may not represent 'high disturbance' in the context of IDH. Rather it appears to represent an intermediate disturbance regime whereby competitive dominants (vascular plants) are constrained, but the disturbance regime remains favourable to cryptogam survival, colonisation or vigour. By contrast, more severe disturbances (e.g. fire and grazing combinations) or annual fires might be needed to reduce cryptogam abundance and diversity. This highlights the difficulty associated with expression of disturbance gradients in the application of IDH, and the circularity associated with defining 'intermediate' in terms of conditions under which diversity is maximized (Huston 1994; Li et al. 2004; Shea et al. 2004). Further, application of IDH is dependent on the set of taxa used in diversity analyses. Most IDH studies have focused on primary producers, but few have measured the response of non-vascular plants or biological soil crusts (Shea et al. 2004). Several studies have compared responses among trophic levels, with patterns consistent with IDH in some cases, but more common in basal trophic levels (Shea et al. 2004). In our study, richness of vascular plant species did not significantly increase under 2-year burning compared with other fire frequencies (S. Prober, unpublished data), and perennial grasses suffered high mortality under 2-year burning (Prober et al. 2007), indicating differing disturbance-diversity relationships for different species groups.

By contrast with our results in a mesic Australian grassland, burning destroyed moss- and lichen-dominant cryptogam soil crusts in drier semi-arid woodlands in eastern Australia, and they took 4 years to recover to pre-burn abundance (Greene et al. 1990). These results support

theoretical expectations that disturbances are more likely to have adverse impacts on species diversity in unproductive environments, owing to enhanced stress on limited carbohydrate reserves and slower recolonisation and growth rates (Huston 1979; Proulx and Mazumder 1998; Kondoh 2001). However, Morgan (2004) also found that cryptogam richness was significantly lower in a frequently burnt (1–2 years) *Themeda* grassland compared with grasslands burnt every 4–20 years, in a similar rainfall zone (610–700 mm/year) to our site. Reasons for this contrasting result are unclear, but could reflect annual rather than biennial fires in some cases. Further, Morgan (2004) compared cryptogam composition across six sites with different fire histories, and patterns may have been influenced by other, unknown site features.

Loss of cryptogam cover in semi-arid woodlands leads to reductions in moisture infiltration, structural decline of soil aggregates, increased surface sealing and ultimately increased erosion (Greene et al. 1990; Kinnell et al. 1990). Interestingly, we observed a similar decline in soil surface conditions after 10 years of biennial burning (Prober et al. 2008) even though frequent fires *promoted* rather than eliminated cryptogam crusts. Prober et al. (2008) suggested that soil degradation in frequently burnt plots was due to prolonged exposure to raindrop impact and sunlight rather than a direct result of fire per se. This suggests that cryptogam mats are not functionally equivalent to vascular vegetation cover in terms of maintaining soil surface conditions. Nevertheless, they potentially play a critical role in binding soil and reducing surface erosion when vascular vegetation cover is low (Greene and Tongway 1989; West 1990; Belnap 2003). Prober et al. (2007) noted that 'no other, more fire resilient tussock grasses were readily available to compensate for the decline in *Themeda* on 2-year burn plots'; cryptogams may instead contribute to this important role.

To conclude, we emphasize that previous studies from this experiment found that burning every 2 years, and associated interactions with drought, reduced grassland productivity and resilience (Prober et al. 2007) and had adverse impacts on soils (Prober et al. 2008). Thus, disturbance regimes that maximize small-scale cryptogam richness at the study site differ from those that optimize ecosystem productivity and other elements of ecosystem function.

References

Anderson M (2005) PERMANOVA: a FORTRAN computer program for permutational multivariate analysis of variance. Users guide. Department of Statistics, University of Auckland, New Zealand

Belnap J (2003) The world at your feet: desert biological soil crusts. Front Ecol Environ 1:181–189

Bergamini A, Pauli D, Peintinger M, Schmid B (2001) Relationships between productivity, number of shoots, and number of species in bryophytes and vascular plants. J Ecol 89:920–929

Billeter R, Peintinger M, Diemer M (2007) Restoration of montane fen meadows by mowing remains possible after 4–35 years of abandonment. Bot Helv 117:1–13

Brodo IM (1961) A study of lichen ecology in central Long Island, New York. Am Midl Nat 65:290–310

Clarke KR, Gorley RN (2006) Primer v6: user manual/tutorial. PRIMER-E, Plymouth

Collins SL, Glenn SM, Gibson DJ (1995) Experimental analysis of intermediate disturbance and initial floristic composition: decoupling cause and effect. Ecology 76:486

Collins SL, Knapp AK, Briggs JM, Blair JM, Steinauer EM (1998) Modulation of diversity by grazing and mowing in native tallgrass prairie. Science 280:745–747

Connell JH (1978) Diversity in tropical rainforests and coral reefs. Science 199:1302–1310

Cuddy WS (2000) The distribution and floristics of non-vascular soil crusts in box woodlands on the inland slopes of New South Wales. Honours thesis, School of Geography, University of New South Wales, Sydney

Dufréne M, Legendre P (1997) Species assemblages and indicator species: the need for a flexible asymmetrical approach. Ecol Monogr 67:345–366

Eldridge DJ (1998) Dynamics of moss- and lichen-dominated soil crusts in a patterned *Callitris glaucophylla* woodland in eastern Australia. Acta Oecol 20:159–170

Eldridge DJ (2001) Biological soil crusts of Australia. In: Belnap J, Lange O (eds) Biological soil crusts: structure, management and function. Ecological studies 150. Springer, Berlin, pp 119–132

Eldridge DJ, Greene RSB (1994) Microbiotic soil crusts: a review of their roles in soil and ecological processes in the rangelands of Australia. Aust J Soil Res 32:389–415

Eldridge D, Tozer ME (1997) A practical guide to soil lichens and bryophytes of Australia's dry country. Department of Land and Water Conservation, Sydney

Eldridge DJ, Semple WS, Koen TB (2000) Dynamics of cryptogamic soil crusts in a derived grassland in south-eastern Australia. Aust Ecol 25:232–240

Eldridge DJ, Freudenberger D, Koen TB (2006) Diversity and abundance of biological soil crust taxa in relation to fine and coarse-scale disturbances in a grassy eucalypt woodland in eastern Australia. Plant Soil 281:255–268

Esposito A, Mazzoleni S, Strumia S (1999) Post-fire bryophyte dynamics in Mediterranean vegetation. J Veg Sci 10:261–268

GenStat (2007) GenStat, 10th edn. Lawes Agricultural Trust, VSN International, Oxford

Gotelli NJ, Colwell K (2001) Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. Ecol Lett 4:379–391

Gotelli NJ, Entsminger GL (2006) EcoSim: null models software for ecology. Version 7. Acquired Intelligence, Kesey-Bear, Jericho, VT http://garyentsminger.com/ecosim.htm. Accessed February 2008

Greene RSB, Tongway DJ (1989) The significance of (surface) physical and chemical-properties in determining soil surface condition of red earths in rangelands. Aust J Soil Res 27:213–225

Greene RSB, Chartres CJ, Hodgkinson KC (1990) The effects of fire on the soil in a degraded semi-arid woodland. I. Cryptogam cover and physical and micromorphological properties. Aust J Soil Res 28:755–777

Grime JP (1973) Competitive exclusion in herbaceous vegetation. Nature 242:344–347

Huhta AP, Rautio P, Tuomi J (2001) Restorative mowing on an abandoned semi-natural meadow: short-term and predicted long-term effects. J Veg Sci 12:677–686

Huston M (1979) A general hypothesis of species diversity. Am Nat 113:81–101

Huston M (1994) Biological diversity: the coexistence of species on changing landscapes. Cambridge University Press, New York

Huston MA (2004) Management strategies for plant invasions: manipulating productivity, disturbance, and competition. Div Distr 10:167–178

Isbell RF (1996) The Australian soil classification. CSIRO, Melbourne

Kinnell PIA, Chartres CJ, Watson CL (1990) The effects of fire on the soil in a degraded semiarid woodland. 2. Susceptibility of the soil to erosion by shallow rain-impacted flow. Aust J Soil Res 28:779–794

Kondoh M (2001) Unifying the relationships of species richness to productivity and disturbance. Proc R Soc Lon B Biol Sci 268:269–271

Li J, Loneragan WA, Duggin JA, Grant CD (2004) Issues affecting the measurement of disturbance response patterns in herbaceous vegetation–a test of the intermediate disturbance hypothesis. Plant Ecol 172:11–26

Looman J (1964) Ecology of lichen and bryophyte communities in Saskatchewan. Ecology 45:481–491

Lunt ID (1997) Effects of long-term vegetation management on remnant grassy forests and anthropogenic native grasslands in south-eastern Australia. Biol Conserv 81:287–297

Lunt ID, Morgan JW (2002) The role of fire regimes in temperate lowland grasslands of south-eastern Australia. In: Bradstock R, Williams J, Gill AM (eds) Flammable Australia: the fire regimes and biodiversity of a continent. Cambridge University Press, Cambridge, pp 177–196

Mackey RL, Currie DJ (2001) The diversity-disturbance relationship: is it generally strong and peaked? Ecology 82:3479–3492

McCarthy PM (1991) Checklist of Australian lichens, 4th edn. National Herbarium of Victoria, Melbourne

McCune B, Mefford MJ (1999) PC-ORD. Multivariate analysis of ecological data. Version 4. MjM software design, Gleneden Beach, OR

Meagher D, Fuhrer B (2003) A field guide to the mosses and allied plants of microphytic crust cover: further evidence from a wooded semiarid Australian rangeland. Arid Soil Res Rehab 11:113–126

Mistry J (1998) Corticolous lichens as potential bioindicators of fire history: a study in the cerrado of the distrito federal, central Brazil. J Biogeogr 25:409–441

Moore RM (1973) South-eastern temperate woodlands and grasslands. In: Moore RM (ed) Australian grasslands. Australian National University Press, Canberra, pp 169–190

Morgan JW (1998) Importance of canopy gaps for recruitment of some forbs in Themeda triandra-dominated grasslands in south-eastern Australia. Aust J Bot 46:609–627

Morgan JW (1999) Defining grassland fire events and the response of perennial plants to annual fire in temperate grasslands of south-eastern Australia. Plant Ecol 144:127–144

Morgan JW (2004) Bryophyte composition in a native grassland community subjected to different long-term fire regimes. Cunninghamia 8:485–489

Morgan JW (2006) Bryophyte mats inhibit germination of non-native species in burnt temperate native grassland remnants. Biol Invas 8:159–168

Morgan JW, Rollason TS (1995) Base-line monitoring of a significant grassland remnant at Evans Street, Sunbury, Victoria. Vic Nat 112:148–159

Peintinger M, Bergamini A (2006) Community structure and diversity of bryophytes and vascular plants in abandoned fen meadows. Plant Ecol 185:1–17

Primer-E (2007) Primer 6 and Permanova beta12. Primer-E, Plymouth

Prober SM, Thiele KR (1995) Conservation of the grassy white box woodlands: relative contributions of size and disturbance to floristic composition and diversity of remnants. Aust J Bot 43:349–366

Prober SM, Thiele KR, Lunt ID (2007) Fire frequency regulates tussock grass composition, structure and resilience in endangered temperate woodlands. Austral Ecol 32:808–824

Prober SM, Lunt ID, Thiele KR (2008) Effects of fire frequency and mowing on a temperate derived grassland soil in south-eastern Australia. Int J Wildland Fire 17:586–594

Proulx M, Mazumder A (1998) Reversal of grazing impact on plant species richness in nutrient-poor versus nutrient-rich ecosystems. Ecology 79:2581–2592

Richardson DHS (1981) The biology of mosses. Wiley, New York

Robertson D (1985) Interrelationships between kangaroos, fire and vegetation dynamics at Gellibrand Hill Park, Victoria. PhD thesis, University of Melbourne, Melbourne

Rosentreter R, Eldridge DJ (2002) Monitoring biodiversity and ecosystem function: grasslands, deserts and steppe. In: Nimis PL, Scheidegger C, Wolseley PA (eds) Monitoring with lichens-monitoring lichens. Kluwer, Netherlands, pp 223–237

Scott GAM (1985) Southern Australian liverworts. Australian Government Publishing Service, Canberra

Scott GAM, Stone IG (1976) The mosses of southern Australia. Australian Government Publishing Service, Canberra

Shea K, Roxburgh SH, Rauschert ESJ (2004) Moving from pattern to process: coexistence mechanisms under intermediate disturbance regimes. Ecol Lett 7:491–508

Sim-Sim M, Carvalho P, Sergio C, Garcia C, Rego F (2004) Recolonisation and changes in bryophyte and lichen biodiversity in burned areas from the Serra da Estrela (Portugal). Cryptogam Bryol 25:367–384

Spence JR, Ramsay HP (2006) Bryaceae, Flora of Australia 51, mosses 1. CSIRO, ABRS, Canberra

Streimann H, Klazenga N (2002) Catalogue of Australian mosses, flora of Australia supplementary series. No. 17. Australian Biological Resources Study, Canberra

Thompson WA, Eldridge DJ, Bonser SP (2006) Structure of biological soil crust communities in Callitris glaucophylla woodlands of New South Wales, Australia. J Veg Sci 17:271–280

Timoney KP, Peterson G, Wein R (1997) Vegetation development of boreal riparian plant communities after flooding, fire, and logging, Peace River, Canada. For Ecol Manage 93:101–120

Tremont RM, McIntyre S (1994) Natural grassy vegetation and native forbs in temperate Australia: structure, dynamics and life histories. Aust J Bot 42:641–658

West NE (1990) Structure and function of microphytic soil crusts in wildland ecosystems of arid and semi-arid regions. Adv Ecol Res 20:179–223

Yates CJ, Hobbs RJ (1997) Temperate eucalypt woodlands: a review of their status, processes threatening their persistence and techniques for restoration. Aust J Bot 45:949–973