Diversity and abundance of biological soil crust taxa in relation to fine and coarse-scale disturbances in a grassy eucalypt woodland in eastern Australia

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Abstract

Over the last 200 years the box woodlands of eastern Australia have been considerably altered by European farming practices. These changes have been accompanied by a reduction in the size and number of patches of vegetation as well as the quality of the understorey vegetation and underlying soil surface. We measured diversity and abundance of soil crust taxa in relation to habitat complexity, remnant area and width, diversity of vascular plants as well as the number, size and separation of patches of vegetation and grass butts (coarse-scale patchiness), and an index of surface stability derived from measures of seven soil surface features of small microsites (patches of bare/crusted, litter- or grass-covered soil; micro-scale) on both coarse- and fine-textured soils at 35 sites in south-eastern Australia. Fifty taxa were recorded from the 35 sites, and there were more taxa from sites with fine-textured soils (12.7) compared with coarse-textured soils (4.4). The soil crust community was dominated by a few relatively common species, with many species occurring at only a few sites. Half the number of species accounting for < 1% of total abundance. Bare and crusted microsites supported more species and greater cover compared with grassy microsites. Crust diversity declined with increasing coarse-level disturbances (i.e. declines in habitat complexity, remnant area and width, and diversity of vascular plants) but the results were not consistent between soil types. No measures of fine-scale disturbance were related significantly to any of the crust diversity or abundance measures, and there was no evidence of a recent grazing effect on crust composition. The fact that few sites had many species (and visa versa) suggests to us that many sites are probably required to conserve soil crust taxa in these highly fragmented landscapes

Introduction

Box woodlands with a grassy understorey once formed a continuous belt from southern Queensland to western Victoria on the western slopes of the Great Dividing Range in eastern Australia. During the 150 years since European settlement, the box woodlands have undergone dramatic transformation with substantial changes at large (landscape) and finer (patch) scales. Major changes have been associated with widespread vegetation clearance, so much so that isolated clumps and single trees are now a common feature over much of the landscape. Decline in tree cover has been associated with declining soil fertility, increased erosion, greater accession of surface flows to the groundwater, and increasing salinisation resulting from rising ground water tables (Eldridge and Freudenberger, 2005; Robertson, 1996).

At the scale of individual remnants or patches of vegetation, dramatic changes in vegetation

structure have occurred including reductions in plant composition, loss of midstorey and ground-storey flora, declines in many faunal taxa, and invasion by exotic species (Bird et al., 1992; Prober and Thiele, 1995; Yates and Hobbs, 1997; Yates et al., 2000). Livestock grazing and its localised disturbances are associated with reduction in the cover and composition of groundstorey vegetation, reductions in health of individual trees (e.g., dieback and mistletoe infestation), and reductions in the quality of the soil surface and the underlying soil processes (Eldridge and Wong, 2005).

Apart from the vascular plant community, the box woodlands support a rich suite of soil surface organisms which together make up a biological (or cryptogamic) soil crust (Eldridge, 2001a). These crusts are complex associations of mosses, lichens, liverworts, cyanobacteria, fungi and bacteria, and are intimately bound onto surface soils. Crusts, and their constituent non-vascular plant components, are patchily distributed in the landscape, occupying areas of bare ground between individual vascular plants, and in some areas, completely dominating the ground flora (Eldridge and Tozer, 1996). Crusts and their associated taxa play important roles in soil and ecosystem processes. Cyanobacteria in the crusts fix atmospheric nitrogen, and the crusts are sites of enhanced populations of soil meso- and micro-fauna which are important for decomposition and mineralisation processes (Zaady and Shachak, 1994). Crusts influence the germination and survival of vascular plants (Lesica and Shelley, 1992; St Clair et al., 1984), influence water flow and surface stability (West, 1990), and act as sinks for soil carbon (Evans and Johansen, 1999). Because of the large number of processes they moderate, the presence of diverse biological soil crusts is generally regarded as a sign of healthy landscapes (West, 1990).

Biological soil crusts are an important component of spatial patterning in the box woodlands. They have tightly structured surfaces, primarily due to the binding of soil particles by polysaccharides and gels excreted by cyanobacteria (Bertocci et al., 1990). The surfaces are therefore generally hydrophobic, shedding rainfall as runoff to nearby patches of grasses, shrubs and trees where it infiltrates. Thus the crust patches act as resource-shedding zones, redistributing water and nutrients to resource-rich vegetated patches (Eldridge, 2001b). In the undisturbed state, this patterning is strongly controlled and maintained by rainfall, and its redistribution between crust patch and vegetated patch tightly controls how the landscape functions, its level of productivity, and the degree to which it supports a diverse community of plants and animals (Eldridge and Freudenberger, 2005; Tongway and Ludwig, 1994).

Overgrazing and trampling by animals are major degrading processes in the box woodlands. Disturbance reduces the efficiency with which plants trap water and sediment by destroying the natural ability of the cryptogam-covered interspace to shed resources. Disturbances such as fragmentation of vegetation patches leads to changes in the cover and composition of groundstorey vascular plants that are likely to influence both soil crust cover and therefore the extent to which it influences water movement. Any changes in disturbances at the patch scale are therefore likely to influence soil crusts and impact upon ecosystem structure and function. The distribution of both bryophytes and lichens is also strongly influenced by differences in soil factors, particularly clay content and pH. For example, Anderson et al. (1982) found that abundance and species diversity increased with the clay content of the soil, and in a semi-arid landscape in eastern Australia, Downing and Selkirk (1993) found that the sparsest cover of bryophytes occurred on sandy soils which were the least stable.

The objective of our study was to examine three hypotheses about the distribution of the larger, more visible components of the soil crust (i.e. mosses, lichens, liverworts) in relation to disturbance in the box woodlands in southern New South Wales. Firstly, given the strong links between soil texture and landscape stability, we predicted a greater cover and diversity of crusts on fine-textured compared with coarse-textured soils. Secondly, we expected that cover and diversity of non-vascular plants would decline with increasing levels of both fine- and coarse-scale disturbances. Finally, we hypothesised that sites with the greatest level of fine-scale patchiness (e.g., number and size of vegetated patches and basal cover of perennial grasses) would have the greatest cover and diversity of non-vascular plants. These hypotheses were tested by examining the cover and floristics of soil crust communities at fine

(microsite) and coarse (remnant patch and landscape) scales on fine- and coarse-textured surfaces across a gradient in landscape fragmentation and disturbance.

Methodology

The study area

The study was conducted in the Riverina area of south-eastern New South Wales, Australia (35° 50′ S 146°00′ E) near the village of Savernake. The climate is temperate, with a long-term average annual rainfall of 476 mm (Bureau of Meteorology, 1975). Approximately 18% more rain falls in the six winter months (April–September) compared with the six summer months. Summer temperatures average about 30 °C and winter temperatures about 16 °C.

The geology of the general area is Quaternary alluvium, with outcrops of Upper Ordovician material and thinly covered bedrock on the upper slopes and crests of hills and ridges (Beattie, 1972). The Quaternary deposits comprise extensive, level to locally depressed plains of clays and clay loams, traversed by discontinuous low ridges associated with the levees of prior streams. Superimposed on the plains are three smaller units: (i) sand ridges and lunettes to 10 m high dominated by well-sorted loams and sandy loams; (ii) rocky outcrops of shallow, stony loams on exposed granites or meta-sediments to 20 m in relief, and (iii) shallow depressions and lowlands of cracking grey clays (Butler, 1958; Kent et al., 2002).

Thirty-five sites were sampled within the study area, mainly on plains (fine-textured; $n = 24$) and low sandy ridges (coarse-textured, $n = 11$). The dominant soils on the plains are hard, alkaline, red duplex soils referred to as red brown earths (Dr 2.3, Northcote, 1966) or Red Chromosols (Isbell, 1996). These soils have a brownish, loamy A horizon changing abruptly to a reddish-brown blocky clay B horizon at depths of about 30 cm. The surface soils of the sand ridges are generally loose, greyish-brown, neutral red earths (Gn2, Northcote, 1966) or Kandosols (Isbell, 1996), gradually becoming finer (higher clay content) with depth (Northcote, 1966).

The study area occurs within the former distribution of the grassy-box woodlands in the eastern part of the wheat-sheep belt in New South Wales (Moore, 1970). Vegetation on the fine-textured soils was dominated by grey box (*Eucalyptus microcarpa* Maiden), yellow box (*E. melliodora* Schauer.), buloke (*Allocasuarina leumannii* L.A.S. Johnson) and white cypress pine (*Callitris glaucophylla* J. Thomps. & L.A.S. Johnson), and supported a diverse but sparse shrubby understorey of *Acacia*, *Eutaxia*, *Dodonaea* and some *Maireana* species. The groundstorey comprised a moderate cover of native perennial grasses (e.g., *Austrodanthonia* and *Austrostipa* spp.) and introduced annual grasses such as barley grass (*Hordeum leporinum*) and wild oats (*Avena* spp.). The overstorey vegetation at the sites with coarse-textured soils was dominated by grey box, yellow box, white cypress pine and Blakely's red gum (*E. blakelyi* Maiden), and a diverse shrub and groundcover dominated by *Acacia*, *Hibbertia*, *Eragrostis* and *Austrostipa* (Freudenberger and Stol, 2002; Kent et al., 2002).

Site selection

The 35 sites were chosen to encompass, as far as possible, the wide range of remnant types or landuses (e.g., native forests, travelling stock reserves, road reserves, cultivated paddocks), remnant size and shape (large and regular, to small and thin), and condition classes (very poor to very good) found in the area. Consequently, sites ranged from a single tree in a currently cropped paddock to an extensive area of extant native *Callitris* forest with abundant understorey vegetation. All sites were subject to grazing by free ranging kangaroos. Livestock grazing had had been excluded from some sites for 2–3 years prior to our study, while other sites had been excluded from livestock for up to 40 years. Due to the variable nature of grazing history, sites were classified as 'recently grazed' if livestock had been excluded for at least 2 years.

Assessing disturbance at the coarse (individual site or remnant) scale

Indicators of anthropogenic disturbance of individual sites were measured using a variety of methods. The functional integrity of each remnant or site (at the scale of tens to hundreds of

metres) was assessed by measuring the spatial arrangement of stable landscape elements or patches at each remnant (Ecosystem Function Analysis; Ludwig and Tongway, 1995). This analysis provides an indication of the extent to which runoff water, and entrained sediment, seeds and organic matter, is either maintained within, or 'leaks' from patches, and is therefore a useful indicator of landscape function. Along the 25 m transect, the total number, length and width of permanent obstructions such as perennial grasses, shrubs and logs were measured, as well as the length and number of intervening spaces between obstructions (fetches). Three measures were subsequently derived: (1) the number of obstructions per unit length of transect, (2) the total width of obstructions per unit length of transect, and (3) the average distance between obstructions (fetch length; see Ludwig and Tongway, 1995 for a detailed assessment of the technique).

The size (area) and width of sites were measured using GIS software and a SPOT panchromatic satellite image. We also used a habitat complexity scoring system (Catling and Burt, 1995, as modified by Watson et al., 2001), to assess each site in terms of tree cover, shrub cover, groundstorey cover, cover of logs and soil moisture. Values for each of the five attributes were assigned to each site such that a greater number equated with a healthier or more complex site. The maximum possible complexity score is 15, though scores for the Savernake study ranged from 0 to 10 (mean $\pm$ SEM $= 3.6 \pm 0.45$). Complexity has been shown to be highly correlated with bird diversity (Watson et al., 2001). The habitat complexity score was used as a surrogate for site-level condition.

The diversity of vascular plants (Freudenberger and Stol, 2002) was also used as a measure of site health. At each site, tree and shrub species identification and cover was estimated from a 50 m^2 area. Ground species identification and cover was measured in a 20 m^2 area within this 50 m^2 area, and the dominance of forbs and grasses was determined from four 1 m^2 quadrats within the 20 m^2 quadrat. Additional plant species were sought during a timed active search radiating out from the 50 m^2 area. More time was spent searching in large sites and less in small sites in our efforts to find as many different species of plants as possible. We sampled during a wet spring, and most plants flowered profusely making them easier to find and identify.

Assessing disturbance at the fine (microsite) scale

Along the same 25 m transect, detailed measurements were made of soil surface integrity at the microsite level, i.e. at the scale of 0.1 to 10 m. As biological soil crust communities respond to disturbances at small spatial scales (Eldridge, 2001a and b), we stratified the transect according to surface type to the nearest 5 cm, a scale appropriate for cryptogamic crust taxa. Along each transect the soil surface was first divided into a number of readily identifiable microsites which were later amalgamated into three categories: (i) bare or crust, (ii) litter-covered soil and (iii) grassy patches. Bare-crusted microsites were devoid of vascular plants and ranged from a completely bare soil surface to one colonised almost entirely by cryptogamic crusts (lichen, moss or liverworts) or cyanobacteria and algae (indicated by the organic staining). Litter surfaces were defined as those dominated ($> 50\%$ cover) by generally persistent (but sometimes ephemeral) detached plant material. Grass microsites were generally characterised by tussocks of perennial grasses, but also had a variable but generally sparse cover of annual and perennial forbs. The projected foliage cover of grass was often in excess of 70%. Some quadrats may have been dominated by perennial grasses but supported small patches of litter or cryptogams between the grasses. In each case, the dominant microsite was recorded.

Attributes of the soil surface were used to derive an index of stability which relates to the cextent to which the soil resists erosion. At each site we measured seven surface features of bare-crust, litter and grass patches within five 0.5 m^2 quadrats per site: (1) crust coherence (the force required to disrupt the soil surface with the index finger), (2) the degree of surface cracking, (3) stability of the surface soil (determined using the Emerson drop test; Tongway, 1995), (4) degree of erosion, (5) cover of cryptogams, (6) foliage cover, and (7) litter cover (see Tongway, 1995). For a particular quadrat, the value of each attribute was given a score, usually from 1–5, but sometimes from 1–4 such that a larger value equated with a more stable surface. The quadrat's index

of stability is derived as the sum of the scores for the seven attributes expressed as a percentage of 34, the maximum possible score.

Soil crust sampling and identification

At each transect at each site, up to four of the 0.5 m² quadrats used for assessing soil surface morphology were sampled for soil crust organisms. Across all sites a total of 18 bare-crusted, 15 litter and 38 grass-dominant surfaces were sampled, which was sufficient to sample the range of environments found at the sites. At sites which were apparently devoid of surface crusts, only one quadrat sample was taken. Soil covering an area of approximately 25 cm² was taken for assessment of crust species. At all sites additional samples of crust were taken from the immediate area surroundings the transect, and these samples formed the basis for assessing crust diversity at the site level. These additional samples were also used to prepare voucher specimen collections.

Soil crust samples were put through a 2 mm sieve to remove loose soil from the sample, and were then examined under a binocular dissection microscope. All bryophytes and lichens identified, generally to species level, using regional taxonomic keys in Catcheside (1980), Filson and Rogers (1979), McCarthy (1991a) and Scott and Stone (1976), as well as more recent generic revisions. Nomenclature follows Streimann and Curnow (1989) for mosses, Scott (1985) for liverworts, McCarthy (1991b) for lichens, and where appropriate, more recent taxonomic revisions. Across all taxa more contemporary regional keys were used as appropriate.

All species of *Didymodon* were all combined into the one species, *Didymodon torquatus*. Samples of *Desmatodon convolutus* and *Crossidium davidai* were differentiated in this study using laminal morphology characteristics, such that a plant was determined to be *Crossidium davidai* if the lamina maintained a strongly hooded apex after full wetting over a few minutes. If the lamina straightened properly it was deemed to be *Desmatodon convolutus*. In cases of uncertainty a thin section was taken of the leaf to determine species, based upon the knowledge that *Desmatodon convolutus* has single-celled filaments off the costa, and *Crossidium davidai* maintains a multi-cellular filament from the costa of its lamina.

We assessed the abundance of all crust species on all soil fragments collected in the field. All species identified within a sample were recorded and given a weighted abundance score of either < 10, 10–25, 26–100, or 101–1000 individuals or segments (in the case of the foliose and fruticose lichens). The crustose lichens tended to be positively weighted because of their compact character and the high level of segmentation they display on the soil crust. We then calculated a mean abundance for each species over all soil fragments assessed. Abundance rather than cover was used due to the difficulty of assessing cover of individual species in the field. The foliose and fruticose lichens were treated similarly to the thallose liverworts.

Statistical analyses

We used a combination of analysis of variance and multi-variate analyses (Multi-Dimensional Scaling) to test our hypotheses. Relationships between crust cover and diversity, and axis scores from the multi-variate analyses and various environmental disturbance variables were examined using regression analysis and one-way ANOVA after testing for homogeneity of variance (Minitab, 1997) and transforming where necessary.

A matrix comprising the cover of each of 50 species by three microsites (crust, litter, grass) was converted to a similarity matrix using the Bray-Curtis similarity coefficients contained within the PRIMER (Version 4) statistical package (Clarke and Warwick, 1994). This similarity matrix was subjected to non-metric Multi-Dimensional Scaling (MDS) using one of the PRIMER (Version 4) routines in order to determine whether microsites supported a unique assemblage of species. Hypothesis tests of differences between the three types of microsites, defined *a priori*, were performed using ANOSIM, which is comparable to a distribution-free two-way ANOVA (Clarke, 1993). Using a number of random permutations on the similarity matrix, ANOSIM produces a test statistic (Global *R*) with a significance level which we used to determine whether cover of the species varied significantly between crust, litter or grass-covered surfaces.

We fitted power functions of the form $Y = aX^b$ to the data, consistent with island biogeography theory which predicts that diversity increases asymptotically with increasing patch size (Macarthur and Wilson, 1967). Consequently, models for patch area and width pass through the origin. This simple model failed to support the plateau theory for some data sets (the b parameter was > 1), and so other biologically meaningful models were sought. Asymptotic curves of the form $Y = a + b \ (\ln(X))^2$ and $Y = a(1 - \exp(bX))$ were fitted to the non-vascular plant – vascular plant diversity data and patch width for coarse soils, respectively. For number of species and cryptogam abundance versus % of native plants (Figure 5), an exponential growth curve of the form $Y = ae^{bX}$ was used.

Results

Soil crust floristics

In general, the soil crust community was dominated by a few common species, with many species occurring at just a small number of sites. Most species contributed little to mean abundance, with 50% of species accounting for $< 1\%$ of abundance (Figure 1). The moss *Triquetrella papillata* was the most ubiquitous species across the study area, occurring at 23 (66%) of the 35 sites (Tables 1 and 2) and accounting for almost 20% of abundance (Table 1). Only three sites (8.6%) had more than 20 species while 54% of
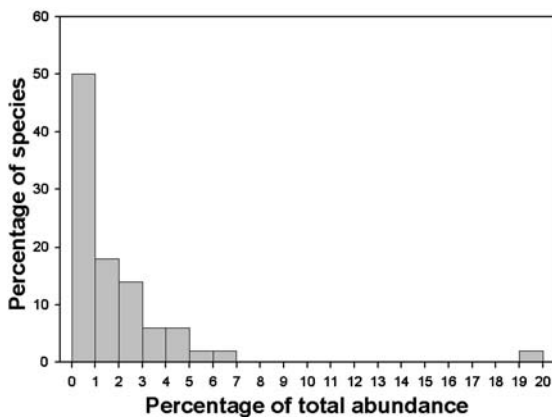

Figure 1. Histogram of the percentage of total abundance contributed by species (e.g., 50% of the species accounted for less than 1% of the abundance).

sites had less than five species. A total of 50 taxa was found across the 35 sites, including 19 lichen species, five liverworts and 26 moss species (Table 1). No species were recorded at eight of the 35 sites. Searches of additional habitat outside the transects at all sites yielded an additional 13 species (8 lichens, 1 liverworts, 4 mosses).

Significantly more taxa were recorded on the fine-textured soils (12.7 ± 1.9 mean $\pm$ SEM) compared with the coarse-textured soils (4.4 ± 1.2; t-test $= -3.73$, $P = 0.001$, df $= 23$; Figure 2). Thirty-four of the 50 species were Only two species, the moss *Campylopus introflexus* and the lichen *Heterodea beaugleholei* were found exclusively on the coarse-textured soils.

Microsite- and site-level relationships

As expected, bare-crust microsites supported significantly more species (approximately 50% more) than grass microsites ($F_{2,68} = 6.62$, $P = 0.002$). Bare-crust microsites also supported a significantly greater crust cover than grass microsites ($F_{2,68} = 3.51$, $P = 0.036$). There were no significant difference however in the abundance of non-vascular species among the three microsites ($F_{2,68} = 0.60$, $P = 0.552$).

When averaged over microsites for each soil type, effectively scaling up the microsite-level data to the site level for all sites containing non-vascular taxa ($n = 27$), significant differences in abundance were apparent between coarse- and fine-textured soils (Global $R = 0.295$, $P = 0.007$; Figure 3). The mosses *Triquetrella papillata* and *Bryum* sp. 1 were more abundant on the coarse-textured soils, while *Barbula calycina, Leptobryum pyriforme, Barbula crinita* and *Eccremidium pulchellum* were more abundant on the fine-textured soils. The SIMPER program identified that these six moss species contributed more than half of the difference in abundance between the coarse- and fine-textured soils (Table 3). For coarse-textured soils, 50% of the total species diversity was captured within only six sites, whereas 13 sites capture total diversity for fine-textured soils (Figure 2).

Soil crust taxa in relation to disturbance

There was some evidence, though by convention only weak, of a livestock grazing effect on the

Table 1. Mean abundance (individuals/25 cm^2; in order of decreasing abundance) of non-vascular plant species found at 35 sites near Savernake, New South Wales

Species	Type	Abundance			Number of sites found at
		By surface texture		Percentage of total	
		Coarse	Fine		
Triquetrella papillata	Moss	123.5	109.9	19.6	23
Barbula calycina	Moss	31.7	72.5	9.9	14
Eccremidium pulchellum	Moss	0.7	58.1	6.5	13
Bryum sp. 1	Moss	39.0	25.1	5.1	13
Barbula hornschuchiana	Moss	8.3	40.0	4.9	8
Fissidens vittatus	Moss	0.0	43.6	4.8	7
Cladonia sp.	Lichen	3.6	34.8	4.1	10
Leptobryum pyriforme	Moss	0.0	31.1	3.4	9
Fissidens pungens	Moss	0.0	28.6	3.2	10
Bryum pachytheca	Moss	0.0	28.2	3.1	6
Cephaloziella sp.	Liverwort	22.0	14.6	2.9	7
Endocarpon simplicatum var. *bisporum*	Lichen	0.0	25.8	2.9	5
Cladia aggregata	Lichen	44.7	1.5	2.9	3
Barbula crinita	Moss	11.5	19.4	2.8	14
Lecidea ochroleuca	Lichen	0.0	23.9	2.6	2
Bryum eremeum	Moss	4.4	21.3	2.6	12
Fossombronia sp.	Liverwort	0.0	18.8	2.1	8
Fissidens taylorii	Moss	0.0	17.5	1.9	4
Bryum billardieri	Moss	3.2	15.0	1.9	7
Bryum argenteum	Moss	1.4	15.2	1.8	5
Collema coccophorum	Lichen	0.0	13.6	1.5	5
Endocarpon rogersii	Lichen	0.0	12.5	1.4	3
Placidium lacinulatum	Lichen	0.0	12.1	1.3	2
Diploschistes thunbergianus	Lichen	0.0	12.0	1.3	1
Trapelia coarctata	Lichen	0.0	12.0	1.3	1
Ceratodon purpureus	Moss	0.0	5.8	0.6	7
Peltula patellata	Lichen	0.0	3.3	0.4	3
Bartramia hampei	Moss	0.0	3.1	0.3	2
Heterodea muelleri	Lichen	0.0	2.7	0.3	4
Xanthoparmelia bellatula	Lichen	0.0	2.7	0.3	3
Endocarpon pusillum	Lichen	0.0	2.3	0.3	3
Bryum sp. 2	Moss	0.0	2.2	0.2	4
Cladia retipora	Lichen	0.0	1.9	0.2	4
Riccia lamellosa	Liverwort	0.0	1.6	0.2	6
Heterodea beaugleholei	Lichen	2.9	0.0	0.2	1
Acaulon introflexus	Moss	0.0	1.4	0.2	1
Lepraria sp.	Lichen	0.0	1.4	0.2	1
Xanthoparmelia amphixantha	Lichen	0.0	1.4	0.2	1
Gigaspermum repens	Moss	0.2	1.1	0.1	5
Desmatodon convolutus	Moss	0.0	0.8	0.1	2
Tortula princeps	Moss	1.1	0.1	0.1	3
Didymodon torquatus	Moss	0.0	0.6	0.1	2
Bryum campylothecium	Moss	0.0	0.5	0.1	1
Riccia limbata	Liverwort	0.0	0.5	0.1	2
Bryum dichotomum	Moss	0.0	0.4	0.0	1

Table 1. Continued

Species	Type	Abundance			Number of sites found at
		By surface texture		Percentage of total	
		Coarse	Fine		
Goniomitrium enerve	Moss	0.0	0.3	0.0	3
Campylopus introflexus	Moss	0.4	0.0	0.0	1
Bryum caespiticium	Moss	0.0	0.1	0.0	2
Cephaloziella arctica subsp. *antarctica*	Liverwort	0.0	0.1	0.0	1
Placidium sp.	Lichen	0.0	0.1	0.0	1

There were no significant differences in abundance of any species between coarse- or fine-textured soils, but note that 34 species were not recorded from the coarse-textured soils. Nomenclature follows Streimann and Curnow (1989), Scott (1985) and McCarthy (1991b).

Table 2. Mean ($\pm$ SEM) diversity and cover of cryptogamic crusts at the three microsites. Different letters within a row indicate a significant difference at $P = 0.05$

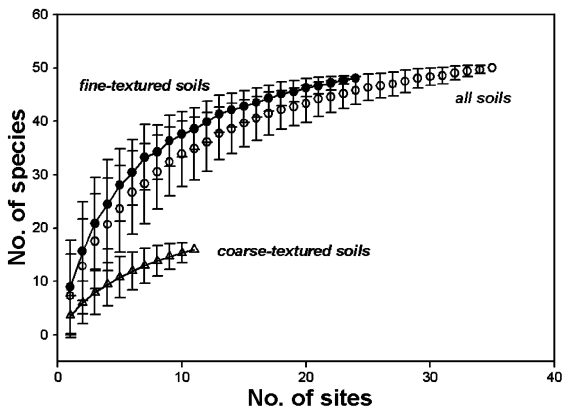|	Bare-crust		Litter		Grass	
	Mean	SEM	Mean	SEM	Mean	SEM
Number of species	15.1[a]	1.8	12.7[ab]	1.5	10.2[b]	1.2
Crust cover (%)	52.2[a]	3.9	43.3[ab]	5.1	35.1[b]	3.9
n	18		15		38	

Figure 2. Cumulative number of species as a function of number of survey sites for all sites (open circles), and sites with coarse-textured (triangle) and fine-textured soils (closed circles) (mean $\pm$ SD).
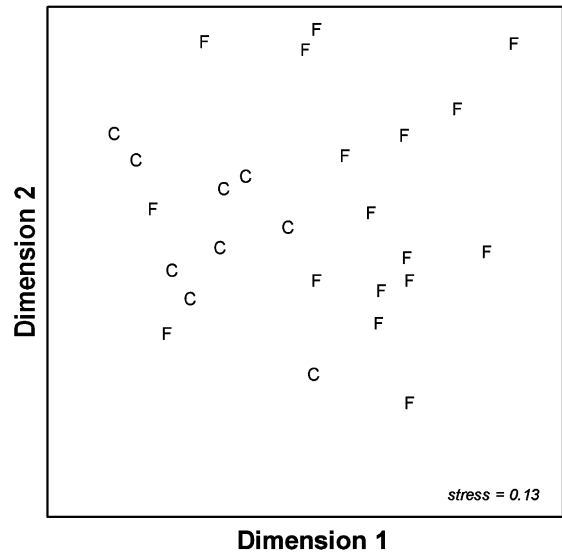

Figure 3. The first two dimensions of the MDS biplot based on 50 species coded for coarse- (C) and fine-textured (F) soils. Note the general separation of fine- and coarse-textured sites along the first dimension.

composition of non-vascular plants in the soil crust when the level of grazing was classified as either currently grazed, recently grazed (stock removed 2–3 years prior to the study) or historically grazed (i.e. ungrazed for > 40 years; Global $R = 0.166$, $P = 0.064$), or simply grazed/recently grazed and historically grazed (Global $R = 0.104$, $P = 0.074$). Further, there was no significant effect of livestock grazing on diversity for either grazed/recently grazed vs. historically grazed

Table 3. Species, mean abundance (individuals/25 cm^2) and percentage dissimilarity contributing to the dissimilarity between coarse- and fine-textured soils in the Savernake District

Species	Mean abundance		Dissimilarity	
	Coarse	Fine	Percent	Cumulative %
Triquetrella papillata	120.0	99.9	21.2	21.2
Barbula calycina	14.7	55.7	7.2	28.4
Leptobryum pyriforme	0.0	53.6	6.8	35.2
Barbula crinita	10.8	25.1	6.2	41.4
Eccremidium pulchellum	0.3	71.4	5.8	47.2
Bryum sp. 1	26.1	19.8	5.1	52.3

($F_{1,33} = 2.0$, $P = 0.167$) or currently, recently or historically grazed ($F_{2,32} = 1.14$, $P = 0.167$). Finally, no livestock grazing effects could be detected when the coarse- and fine-textured soils were analysed separately.

Relationships between diversity of vascular plants and indicators of disturbance were generally stronger on the fine-textured soils (Table 4). The models indicated significant increases in diversity of non-vascular taxa with increases in habitat complexity, patch area, patch width and diversity of vascular plants, when data were analysed separately for different soil textures ($P < 0.05$; Figure 4). However, relationships for both number of vascular plants and site area on coarse-textured soils were not significant ($P = 0.06–0.10$, Table 4).

We detected a relatively strong positive relationship between diversity of soil crust taxa and the proportion of native vascular plants at a site, irrespective of soil texture ($F_{1,33} = 37.1$, $P < 0.001$, $R^2 = 0.50$; Figure 5). Increases in the abundance of crust taxa were also associated with an increasing proportion of native vascular plants at a site, though the relationships were rather weak statistically ($F_{1,33} = 9.9$, $P = 0.01$, $R^2 = 0.18$; Figure 5). Increases in stability were associated with increases in diversity of crust taxa ($F_{1,33} = 9.92$, $R^2 = 0.21$, $P = 0.003$), and larger patches tended to have more stable surfaces ($F_{1,33} = 12.5$, $R^2 = 0.25$, $P = 0.001$). However, again these relationships tended to be rather weak statistically and explain very little of the variance. None of the other measures of site-level disturbance (*sensu* Ludwig and Tongway, 1995) such as the number and size of small-scale patches of grasses or logs on the soil surface, the distance between patches (fetch length), or mean basal cover of perennial grasses, was related significantly to any of the non-vascular plant diversity or abundance measures. Surprisingly, the cover of perennial grasses was not a useful indicator of whether a site was grazed or ungrazed during the past 40 years ($t = 0.84$, df $= 20$, $P = 0.413$).

Discussion

In our study there were important differences in the abundance and diversity of soil crust taxa in relation to soil texture. Abundance was greater on fine-textured soils, and clear differences in floristics could be detected between the two soil types when as few as six sites were sampled (Figure 2). These results are consistent with those from arid and semi-arid areas where soil crust

Table 4. Models parameters relating the number of cryptogamic crust species (Y) to diversity of vascular plants, site complexity, site area and site width for fine- and coarse-textured soils

| Texture	Equation	Adj. R^2	F statistic	P-value
Fine	$Y = 2.52*(\ln(\text{number vascular plants}))^2 - 18.38$	0.54	$F_{1,22} = 30.6$	< 0.001
Coarse	$Y = 1.06*(\ln(\text{number vascular plants}))^2 - 9.66$	0.17	$F_{1,9} = 4.5$	0.06
Fine	$Y = 9.08*\text{complexity}^{0.42}$	0.19	$F_{1,22} = 7.9$	0.01
Coarse	$Y = 2.68*(\ln(\text{number vascular plants}))^2 - 0.33$	0.74	$F_{1,9} = 35.0$	< 0.001
Fine	$Y = 8.14*\text{area}^{0.21}$	0.37	$F_{1,22} = 16.5$	< 0.001
Coarse	$Y = 1.81*\text{area}^{0.28}$	0.08	$F_{1,9} = 3.3$	0.1
Fine	$Y = 21.74*\text{width}^{0.27}$	0.31	$F_{1,22} = 12.8$	0.01
Coarse	$Y = 10.25*(1 - \exp(-1.49*\text{width}))$	0.24	$F_{1,9} = 5.9$	0.04
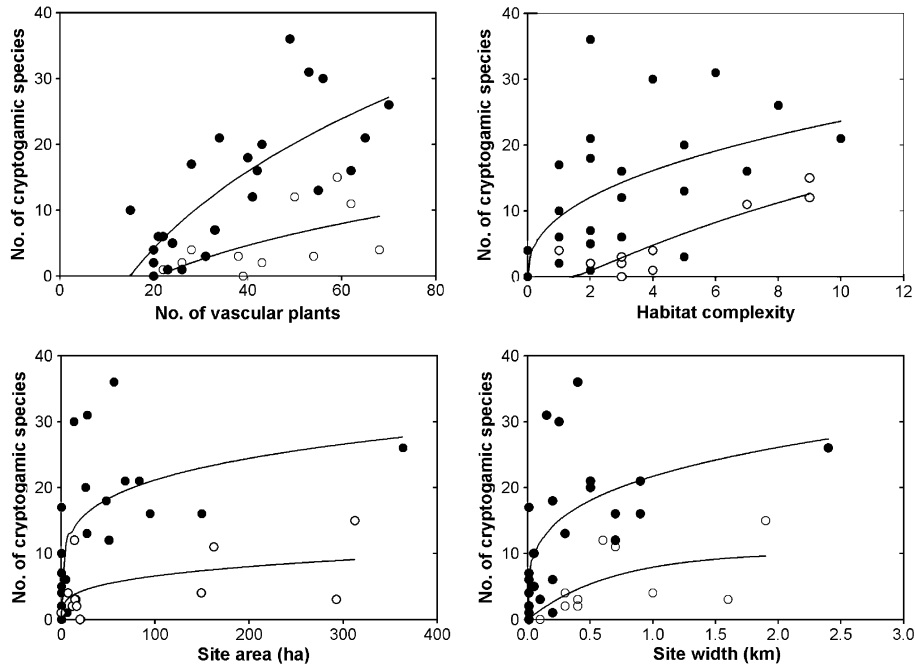
Figure 4. Predicted mean diversity of cryptogamic species in relation to diversity of vascular plants, vegetation complexity, patch area and patch width. Separate models are shown for fine-textured (closed circles) and coarse-textured (open circles) soils. Models are indicated in Table 4.

lichens and bryophytes are more abundant on finer-textured soils (Rogers, 1977; Rogers and Lange, 1972). The mechanisms for this are thought to be related to both the ability of fine-textured soils to hold water and their greater stability to disturbance. The results clearly support our first hypothesis of a soil texture effect.

Our study also confirmed the second hypothesis, that diversity declined with increased coarse-scale (landscape) and fine-scale disturbances. However, it should be remembered that the explanatory value of some of the variables was weak ($<20\%$) and therefore a considerable amount of variance is still largely unaccounted for. Diversity declined with declines in remnant size, habitat complexity, patch width, diversity of vascular plants, and proportion of native plants (Figures 4 and 5), but the results were not always consistent between soil types (Figure 2). We suggest that declining patch size, width, condition, surface stability, vascular plant diversity and weediness are indicators of long-term patch and landscape scale disturbances. However, we were unable to detect an effect of grazing on crust diversity though there were some weak

($P = 0.10$) effects of grazing on crust composition. This lack of a clear trend was probably due to the high temporal and spatial variability in grazing at the Savernake sites. Some of the sites classified as historically grazed had had stock removed only 5–7 years prior to our surveys while other sites had been excluded from livestock grazing for decades. In the absence of livestock, some of the sites were grazed by considerable numbers of free ranging kangaroos. Other sites such as roadside reserves and travelling stock reserves have been grazed only intermittently by travelling livestock for more than a century. We suggest that native plant diversity and habitat complexity are better indicators of long-term disturbances caused by prolonged and intense grazing by livestock and other herbivores than the subjective and variable categories of current, recent or historically grazed.

We were unable to accept our third hypothesis that increased patchiness enhances species diversity, and it is unclear why sites with a high degree of micro-scale patchiness were sometimes floristically rich and sometimes poor. It could have been related to competition for microsites
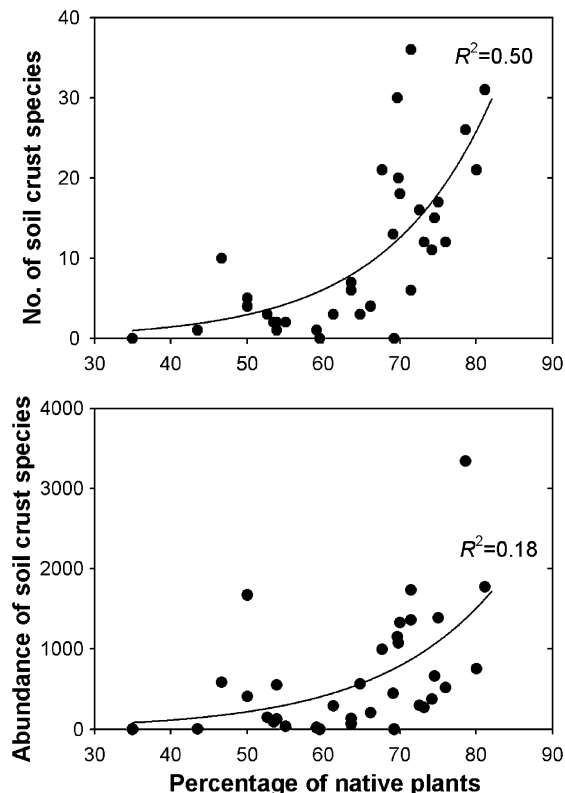
Figure 5. Diversity and abundance of non-vascular plants in relation to the percentage of native plants at a site. Number of soil crust species = 0.0817 exp(0.0719 * % native plants); abundance of soil crust species = 8.7467 exp(0.0644 * % native plants).

between grasses and crust taxa, particularly for light, given that similar levels of patchiness in grasses correspond to different crown characteristics and therefore different levels of light penetration to the soil surface (McIntyre and Tongway, 2005). We found that the bare-crust microsites contained significantly more species and a greater crust cover, which was not surprising, given that these microsites were by definition dominated by crusts. The open sites between individual grass butts were species-rich compared with the sites with continuous grass cover. This is to be expected, as grass-free microsites were unavailable for colonisation by crust taxa which generally cannot compete within a dense grassland sward. Abundance was not related to either surface texture or microsite. This indicates that most of the non-vascular taxa are associated with soil crusts rather than occurring as single elements within a matrix of vascular plants.

Although we were unable to detect an effect of grazing when we characterised sites as currently/ recently grazed or historically grazed, grazing is known to produce dramatic effects at the level of individual crust species (e.g., Cole, 1990; Eldridge, 1998; Rogers and Lange, 1971; Warren and Eldridge, 2001). The mechanisms producing grazing-induced changes are unclear, and could be related to the physical removal of plants and morphological changes to the soil surface brought about by hoof action and trampling (Eldridge, 1998). We suggest that low levels of trampling create intermediate level disturbances which maintain the composition of crust species by helping to maintain open areas amongst dense stands of perennial grasses. In semi-arid landscapes the generation of bare patches by grazing-induced disturbance is well established (Braunack and Walker, 1985; de Soyza et al., 1998; Yates et al., 2000). At low to intermediate levels of disturbance, bare patches provide suitable habitat for non-vascular plants that cannot compete with vascular plants for resources.

The maintenance of biologically crusted surfaces within the grassy matrix is maintained by feedback processes operated by the crusts themselves. Being generally hydrophobic (Eldridge et al., 2002), the crusts shed water, nutrients and organic matter to adjacent grass-dominated microsites, enhancing the capture of water by grasses and shrubs (Dunkerley, 2000) and increasing their cover. Negative feedback processes operate as grasses trap more water and the size of crusted patches decreases (Zaady and Shachak, 1994). Eventually the area of runoff from crust surfaces declines, and grasses begin to retreat as water capture declines, thereby allowing the ingress of biological crusts. For biological soil crust organisms there is a delicate trade-off between water capture and water shedding. Crusts therefore engineer their environment to maximise the amount of moisture they receive whilst minimising water shed to vascular plants which are in direct competition for nutrients and space (Jones et al., 1997).

In the absence of domestic herbivores, the dynamic process of water shedding and water capture at the scale of individual biological soil crust patches would have been maintained by low levels of disturbance by native semi-fossorial animals such as bettongs and bilbies (Garkaklis

et al., 2004). These native animals are highly selective, and their activity results in a patchwork of small diggings rather than the continuous, high intensity, indiscriminate trampling created by domestic herbivores (Fensham et al., 1999). However over large areas of eastern Australia more then two centuries of overgrazing by domestic livestock has lead to substantial reductions in soil health and soil surface condition (Yates et al., 2000). The resulting destruction of surface crusts by high levels of disturbance reduces the efficiency of water shedding by biological soil crust patches, stimulating the growth of annual plants and reducing redistribution of water to the grasses. Persistent trampling and overgrazing then lead to the demise of perennial grasses, replacement with annual plants and ultimately declines in long-term productivity and stability.

Community structure and conservation of soil crust species

An obvious conclusion from our study is that there were few mega-diverse cryptogam sites. Rather, a few species were found at many sites and many species were found at only a few sites (Table 1). The ubiquitous species thus displayed a wide environmental tolerance and therefore no strong preference for sites in a particular condition class nor association with a particular level of vascular plant composition and cover. Conversely, there were a large number of species that were found at only one or two sites (Table 1). In effect, almost three-quarters of the species accounted for less than 2% of total abundance (Figure 1). Those species which were dominant in the poor condition (small patch size, low complexity, low diversity of vascular plants) sites were also dominant in sites with the greatest diversity. About a third of the 36 taxa occurring with abundance <2% are more common in arid soils west of the study area (Eldridge, 2001a) and may be at the eastern edge of their natural distribution. These species are not normally found in extant grassy woodlands, and may have survived by retreating to safe microsites provided by the grassy patches in areas of high quality grassland.

Our results are similar to the results for vascular plants at the study sites where a few sites were extremely diverse while many sites were relatively depauperate (Table 1, Figure 1; Freudenberger and Stol, 2002). Our study indicated that about a third of sites ($n = 16$) were required to capture 75% of non-vascular plants (Figure 2). This supports our view that in these highly fragmented landscapes every remnant of native vegetation has conservation value, particularly those least disturbed. In terms of conserving all of these species, our results clearly suggest that the present system of formal reserves (e.g., Nature Reserves, National Parks, State Forests) is inadequate for conserving and representing the full range of species, many of which may be important for maintaining key ecosystem processes. Rather, conservation of the entire complement of non-vascular taxa is dependent on the maintenance of a network of formalised reserves, *ad-hoc* exclosures, road reserves and the many on-farm remnants of native vegetation that require improved conservation, particularly the management of grazing and reduction in weeds.

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