RESEARCH ARTICLE

Biological soil crust distribution is related to patterns of fragmentation and landuse in a dryland agricultural landscape of southern Australia

Cassia F. Read · David H. Duncan · Peter A. Vesk · Jane Elith

Abstract The dryland agricultural landscape of north-west Victoria, Australia, includes isolated remnants of eucalypt woodland that are exposed to ongoing disturbance from sheep grazing and cropping activity. Biological soil crusts are a functionally important feature of these woodland communities. We used a modern form of regression (boosted regression tree (BRT) models) to investigate relationships between crust abundance and environmental and landscape variables. We also investigated whether the use of broad morphological groups of crust organisms is more informative than simply measuring total crust cover. Remnant size was the single most influential variable for crust abundance, with negligible crust cover in small patches (<5 ha). The BRT model also identified relationships between crust abundance and available P, soil C and perennial grass. We argue that disturbance from stock grazing and camping is the mechanism driving these relationships. Other variables related to crust abundance were proximity to the windward edge, litter cover and tree cover. Morphological groups showed a differential response to some variables, suggesting assessment of total cover may mask important patterns in community structure. Crust disturbance represents a serious issue for maintenance of ecosystem function in the study region, particularly loss of crusts from small remnants because the majority of remnants are small.

Keywords Cryptogamic crusts · Moss · Lichen · Patch size · Grazing · Landscape disturbance · Boosted regression tree models

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Introduction

Biological soil crusts are assemblages of bryophytes, lichens, algae, cyanobacteria and fungi that exist at the soil surface and are a prominent feature of arid and semi-arid ecosystems worldwide. Research has demonstrated that conservation of soil crusts is fundamental to maintaining core ecosystem processes. Soil crusts are known to stabilise soils (Williams et al. 1995; Eldridge and Kinnell 1997; Belnap and Gillette 1998), regulate the balance between water infiltration and run-off (George et al. 2003; Yair 2003), fix nitrogen and carbon (Beymer and Klopatek 1991; Hawkes 2003; Housman et al. 2006) and influence the germination, survival, and nutritional status of vascular plants (Prasse and Bornkamm 2000; Sedia and Ehrenfeld 2003; Su et al. 2007). Mechanical disturbances such as stock trampling and vehicle traffic

cause changes in crust cover and composition, with severe or repeated disturbance resulting in complete crust removal (Andrew and Lange 1986; Beymer and Klopatek 1992; Ponzetti and McCune 2001). Knowledge of where crusts occur in the landscape and where they are most susceptible to disturbance would enhance prioritisation of conservation and restoration activities, particularly in landscapes where degrading processes are unevenly distributed within and among patches of remnant vegetation.

Descriptions of mature, long-undisturbed vegetation in the dryland agricultural zone of Victoria, Australia, identify soil crusts as an important ecosystem component (Department of Sustainability and Environment 2004); however, specific information on crusts is limited. The few published studies of soil crusts have been undertaken in conservation reserves on sandy soils (Eldridge 2001) that are not representative of the more fertile soils preferred for agriculture. To date there have been no studies to determine drivers of crust distribution in this landscape or to assess crust disturbance across patches of remnant vegetation within the agricultural matrix.

Woodlands in this region have been reduced to less than 5% of that present at the time of European settlement (mid nineteenth century in this region). Remnants can be publicly or privately owned, and may be fenced or unfenced, and either protected or subject to grazing. They are part of a broader landscape that is mostly used for broad-scale wheat and sheep farming and are therefore often exposed to disturbances from grazing and camping by domestic stock. High wind speeds are common and remnants may act as sinks within the agricultural matrix, trapping sediments lost from unprotected soils. Land management agencies have recognised that remedial action is required to maintain and restore ecosystem processes across this landscape (Mallee Catchment Management Authority 2003).

We had three broad objectives in this study. Our first objective was to identify environmental covariates of soil crust distribution across the dryland agricultural zone of Victoria to improve our understanding of the potential for crust cover across this landscape. Studies investigating crust distribution worldwide suggest covariates of crust abundance and composition are soil type (Bowker et al. 2005; Eldridge et al. 2006; Thompson et al. 2006), soil pH (Eldridge and Tozer 1997a; Ponzetti and McCune

2001), calcium carbonate content (Rogers 1972; Downing and Selkirk 1993) and precipitation (Rogers 1972; Eldridge and Tozer 1997a; Thompson et al. 2006). Our study region is fairly uniform with very little topographic variation, relatively low rainfall variation (between 330 and 450 mm year^{-1}) and long-term stable landuse. Within this environmental space we investigated whether crust abundance tends to be relatively uniform or whether it varies along gradients of soil chemistry, nutrient content and texture, vascular vegetation cover and litter cover. We excluded siliceous sands that are unstable and unsuitable for crust habitat.

Our second objective was to identify where crusts are most susceptible to disturbance. We examined the influence of landscape variables (remnant size and location within the remnant) and whether there is an interaction between these variables and soil texture. We expected: (1) disturbance is not evenly distributed within and among remnants, because grazing intensity is higher in small remnants relative to large remnants (Duncan et al. 2008) and crusts are removed by trampling from stock; (2) deposition of aeolian particles is greater at the windward edge of remnants, resulting in crust death from burial; and (3) crust disturbance is exacerbated on coarse textured soils. Fine textured soils have a higher aggregate stability, are less susceptible to erosion and mechanical disturbance and have faster rates of crust recovery following disturbance compared to sandy soils (reviewed in Belnap and Eldridge 2003). We expected an interaction between the extent of crust disturbance and soil texture, such that crust disturbance is higher in small remnants on coarse textured soils compared to fine textured soils.

Our third objective was to investigate whether assessment of broad morphological groups is more informative than simply measuring total crust cover. Specifically we investigate whether morphological groups show a differential response to environmental and landscape variables. Eldridge and Rosentreter (1999) argue that the use of morphological groups is an efficient and functionally meaningful approach to monitoring soil crust organisms. Because the function of soil crust species is largely related to their gross morphology, particularly their influence on soils and their response to disturbance, the relationship lends itself to a functional classification useful in rapid assessments (Eldridge and Rosentreter 1999). Since

the inception of the morphological group concept, few studies have tested whether morphological groups show a differential response to landscape and environmental gradients (except see Eldridge and Koen 1998; Martinez et al. 2006).

Methods

Study region

The study was conducted within the dryland agricultural zone, an area 28,777 km^2 in extent, in the northwest of Victoria, Australia (Fig. 1). Of the 5% native vegetation remaining in the region approximately 30% exists in patches <5 ha in size (Duncan and Durrough in review). The entire study area is low lying with a highest peak of 154 m above sea level at Mt Wycheproof. Long-term minimum monthly temperatures range from 4 to 14°C and maxima range from 14 to 30°C, with an upward shift of a few degrees from south to north. Median annual rainfall declines from around 440 mm in the south to 330 mm in the north and the wettest months (July, ca 50 mm) have around double the rainfall of the driest (January, ca 20 mm).

Sampling design

We sampled 25 patches of remnant vegetation selected in a stratified random design across the study region
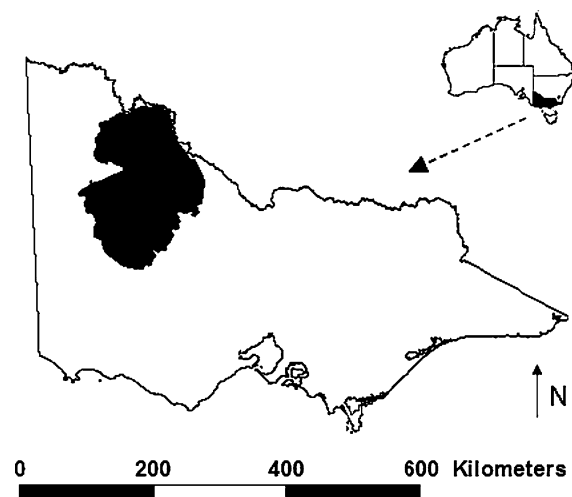

using vegetation maps. Sites were chosen from within the two dominant soil-vegetation associations in the study region. These are: (1) Calcareous Dunes, characterised by multi-stemmed "mallee" *Eucalyptus* spp. woodlands occurring on light sandy soils (White 2006), and (2) Alluvial Plains, characterised by grassy woodlands dominated by *Eucalyptus largiflorens* F. Muell or *Allocasuarina luehmannii* (R. T. Baker) L. A. S. Johnson, occurring on heavier clayish soils. We used these dichotomous soil-vegetation associations in stratification; however, there is a gradient in soil texture and vegetation composition (Duncan et al. 2008).

Remnant patches were allocated to size classes: small (0.5–5 ha), medium (5–10 ha) and large (>20 ha), and we selected 3–5 sites from each size class in each soil-vegetation association. We sampled vegetation and soils at three locations in each site; these were the remnant interior (centre), the windward edge (west edge) and leeward edge (east edge). Edge quadrats were located within 20 m of the remnant edge. At three small sites fewer than three quadrats were sampled as it was not possible to fit three quadrats in very small sites. In all, a total of 71 locations were sampled.

Vegetation sampling

At each sampling location we estimated the projected canopy cover of trees within a 20 m by 20 m quadrat. The 400 m^2 quadrats were then sub-sampled using 10 randomly placed 0.5 m × 0.5 m quadrats to estimate projected cover of bare ground, biological soil crust, leaf litter, perennial native grasses, shrubs, and annual exotic grasses. For the crust measures, we assessed total soil crust cover and morphological group cover in each quadrat. We assigned soil crust organisms to morphological groups based on examination of physical characters in the field. Morphological groups recorded were: moss, leafy and thallose liverworts, and, crustose, squamulose, foliose and fruticose lichens (Eldridge and Tozer 1997b).

Soils

Three soil samples were collected at each sampling location from the top 10 cm of soil and bulked for soil nutrient analysis by CSBP Laboratories (Bibra Lake, Western Australia). Available phosphorus and

Fig. 1 Study area (highlighted) in northwest Victoria, Australia (inset)

potassium were extracted using the Colwell method (Colwell 1965) and their relative concentrations estimated following the method of Rayment and Higginson (1992). Total nitrogen was determined using the LECO combustion method (Sweeney and Rexroad 1987). Organic carbon was estimated following Walkley and Black (1934). Extractable sulphur following Blair et al. (1991). Soil pH and electrical conductivity in deionised water was determined following Rayment and Higginson (1992). Soil texture was determined by kneading a moistened bolus of soil in the hand and assigning the sample to one of five texture classes based on the length of the soil ribbon.

We used continuous, remotely sensed Thorium and Potassium (Th:K) data as surrogate of soil texture in analyses. Th and K are strongly and positively related to soil clay content (Pracilio et al. 2006). Because Th and K are major gamma emitting elements in the soil their concentration in the top 0.3 m of soil can be calculated from measurements by a gamma ray spectrometer (Pracilio et al. 2006). Previous vegetation community mapping from the area (White et al. 2003) suggested that Th and K explained variation in vegetation composition and structure. We calculated a synergistic Th:K ratio as follows:

$$\frac{Th_{max} - Th}{K}$$

where Th_{max} is the highest value of Th in the set. This transformation provides more contrast between soil textures across the study region because it gives the combined response of Th and K to soil texture. These radiometric data were available at a grid resolution of 50 m over the whole area. The Th:K ratio was related to soil texture measured from point samples in the field ($r^2 = 0.40$). Minimum Th:K values of 3.5 were associated with heavy clay soils (clay content >50%) and maximum Th:K values of 5.5 were associated with sandy loam soils (clay content $\sim$5%).

Grazing

Total grazing intensity was assessed within remnants and scored as follows:

(1) Light–No or little evidence of biomass removal, herbivore dung or disturbance by hooves.
(2) Moderate–Localized signs of grazing, tussock structure still evident, some dung and soil

disturbance present, understorey vegetation biomass moderate.
(3) Heavy–No evidence of patchy localized grazing, understorey vegetation biomass low and even, considerable dung and soil disturbance.

Statistical analyses

Our main aim with the modelling was to identify the most influential predictors of crust abundance, and to explore the responses of crust to these predictors. Regression models are useful for such analyses. The response was cover (%), which is best modelled within regression as either a binomial distribution in a quasi-likelihood model (Venables and Dichmont 2004), or arc-sine transformed then treated as a gaussian response (Sokal and Rohlf 1998). The observations were structured, with the 71 windward, centre and leeward sites nested within 25 locations. However, it is possible that the 71 sites act as independent records in the sense that, for example, a windward site is no more similar to a central site at the same location than to any other central site with the same environmental conditions. Hence, we tested the two alternatives of modelling the data as nested or independent. Remnant size (ha) was log transformed to normalise the data, but all other predictors were untransformed. The highest pairwise Pearson correlation coefficient between the final set of predictor variables was 0.85, between some of the soil chemical measures. We included all these in the model, but most variables had much lower pairwise correlations. We did not model the response of Liverwort morphological groups as there were too few occurrences recorded.

Different regression approaches have different strengths and weaknesses for modelling these kinds of data. We explored a range of alternatives— generalized linear models (GLMs) and generalized additive models (GAMs) and their nested counterparts (generalised linear mixed models, GLMMs, and GAMMs), using either a quasi-binomial or gaussian family, and boosted regression trees (BRT) using a gaussian family. Following Wood (2006) we tested the need for including site as a random effect by first running a GLM, GAM or BRT, then modelling the residuals as: (i) a *linear null model,* based on an intercept term and error terms with no predictor factors or covariates, and then running; (ii) a *linear null mixed*

model with site as a random effect but no fixed effects. An ANOVA comparing the two models shows whether modelling the nestedness has an important effect on variance.

Because the main thrust of this paper is exploring the relationships between crust cover and predictor variables, we do not focus on the difference between the methods here. Briefly, our comparison of techniques showed that: (a) if the modelling method could only model simple environmental trends, a site effect appeared important; (b) if the modelling method could define more complex trends, the site effect was no longer significant; (c) BRT models combined reliable variable selection and robust fitting of trends in a more straightforward implementation than any of the alternatives; and (d) while the broad trends were consistent between GAMs, GLMs and BRTs, we were most confident that the BRT models were consistent with our field observations. We therefore decided to use BRT models for analyses.

Boosted regression trees are a form of regression that combines machine learning and statistical techniques. BRT models comprise two algorithms: a regression tree algorithm that predicts a normally distributed response from a measured response and one or more continuous and categorical predictor variables; and a boosting algorithm that, using a forwards stage wise procedure, combines regression trees into a suite or ensemble of trees. This gives a more robust estimate of the response than single tree. As in other generalised regression models, BRT uses a link function that enables prediction of a range of response types including binomial, poisson and gaussian (Hastie et al. 2001). Whilst the use of BRT for ecological applications is in its infancy, there are now several examples that demonstrate its analytical usefulness (De'ath 2007; Leathwick et al. 2008).

BRT models were fitted in R (v2.3.1, www. R-project.org; R Development Core Team 2004) using the 'gbm' library (Ridgeway 2004) plus additional code written by Elith and Leathwick (Elith et al. 2008). BRT models were fitted using a learning rate of 0.001 and a tree size of two nodes, allowing interactions between single predictor variables. A final set of predictor variables was selected for each BRT model using model simplification code that sequentially dropped the least important predictors, until the model was optimised for minimal prediction error in the held-out data (Elith et al. 2008). In summary, the full

set of models for crust distribution were: (i) crust abundance in relation to all predictors; (ii) crust abundance in relation to two specific landscape-scale predictors, log Area and soil texture; and (iii) four models of crust morphological group abundance in relation to all predictors. All BRT abundance models were run with arc-sine transformed measures of abundance.

Results

Biological soil crusts were found to be a common feature of remnant woodlands across the study region, with crusts found in nearly 65% of all sites ($N = 25$) and 100% of large sites. Crusts were more abundant on the Alluvial Plains (mean = 21.1%, standard error of the mean = 3.5) than the Calcareous Dunes (mean = 8.0%, standard error = 3.5) and crust abundance reached over 50% cover in some sites. The final boosted regression tree (BRT) model identified eight covariates of crust cover across the landscape (Fig. 2) and explained nearly 55% of the predictive deviance in soil crust response (Table 1).

Influence of landscape on crusts distribution

Remnant size (log Area, ha) was the single most important predictor of crust abundance across the Calcareous Dunes and Alluvial Plains, providing the greatest contribution to model fit in the regression model (Table 1). Crusts were absent or greatly reduced in small sites (0.5–5 ha), which on average had less than 15% of the cover of large sites (Fig. 2a). Grazing level and remnant size were correlated in this study ($r = 0.60$). Location within a remnant also had a small contribution to model fit in the BRT model of crust abundance. Our results suggest a reduced cover of soil crusts at the remnant edge compared to the remnant interior, with sparsest crust cover found at the windward edge (Fig. 2g).

An explicit test for an interaction between soil texture (Th:K) and log Area did not directly support our hypothesis that crusts are more susceptible to disturbance on coarse textured soils. Although the model of crust response to log Area (ha) and Th:K ratio showed interaction effects between these predictors (Table 2 and Fig. 3), the interaction does not show a greater rate of crust decline on coarse
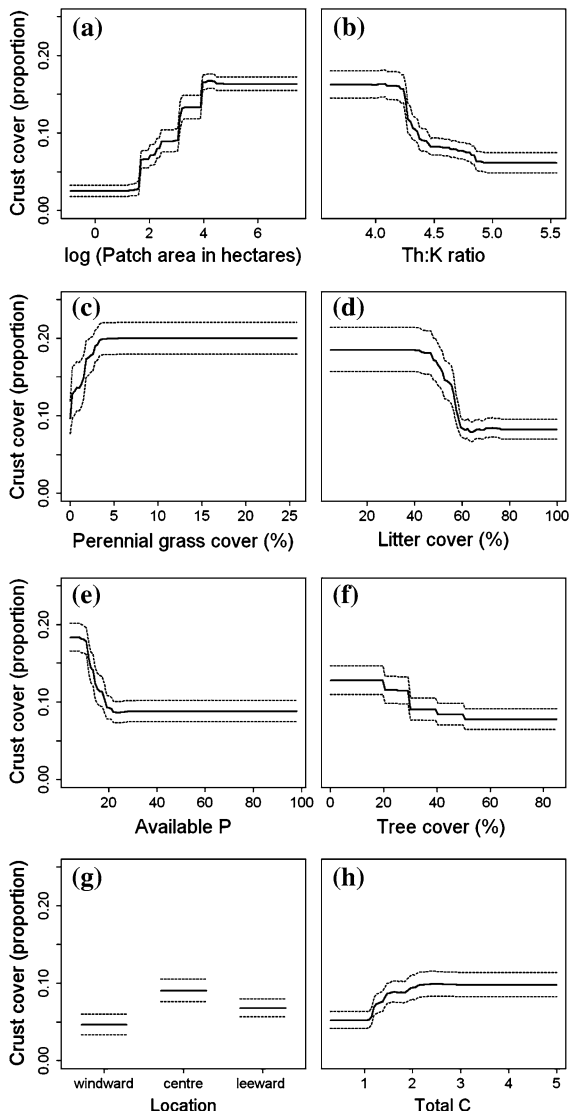
Fig. 2 Partial plots for the eight variables in the simplified BRT model for total biological soil crust cover, ordered by decreasing relative importance in the model (top right to bottom left). Dashed lines represent the standard error of the mean for the predicted values. The y axes for the right column are identical to those in the left

textured soils with remnant size. However, crusts were absent from small sites on coarse textured soils, whereas some crusts remain in small sites on fine textured soils. Peak crust abundance occurred in large sites on fine textured soils. In the final model with all covariates as candidates, a weak interaction was detected between Th:K ratio and location (Table 2).

Environmental covariates of crust abundance

The final BRT model identified six environmental covariates of crust abundance: soil texture (Th:K ratio), perennial grass cover, leaf litter cover, available phosphorus, tree cover and total carbon (Fig. 2, Table 1). Soil texture had the greatest contribution to model fit in the BRT of crust abundance, with peak crust abundance on fine textured soils (low Th:K values). Crusts were more abundant on soils with low P and high total C. Crust cover declined sharply when litter was >40% cover and declined gradually when tree cover was above 20%. Crust cover increased sharply when perennial grasses increased from 0 to 5% cover. The model detected an interaction between log Area and litter cover (Fig. 4, Table 2), such that the positive effect of lower litter cover was increased in large remnants.

Differential response of morphological groups

Models were fitted for the four most abundant groups. Leafy liverworts and thallose liverworts were too rare (Fig. 5) to enable sound model fitting. BRT models for the remaining four morphological groups suggest that groups are differentially affected by their environment and landscape, with often large differences in the importance of measured variables in the fitted models for each morphological group (Table 1). Given that some of these groups are less well explained than others (e.g. the model for crustose lichen explained only 20% of the predictive deviance, compared to 55% for mosses), we discuss broad trends rather than details when comparing the responses of different groups to measured variables.

The Th:K ratio strongly influenced all morphological groups except foliose lichens, with the Th:K ratio ranked the third most influential variable in BRT models for moss, squamulose and crustose lichens. Foliose lichens were positively associated with acidic soils, whereas soil pH had a weak influence on other groups. Another clear difference in morphological group response was the influence of exotic annual weed and native shrub cover, which were only important for crustose and squamulose lichens (a negative and positive relationship,

Table 1 Relative contribution of predictor variables to boosted regression tree (BRT) models of total biological soil crust cover (Total BSC) and morphological group cover (moss, foliose lichen, squamulose lichen and crustose lichen)

	Total crust	Moss	Foliose lichen	Squamulose lichen	Crustose lichen
Predictive deviance (% explained)	54.7	55.0	30.0	33.3	20.0
Log Area (Ha)	24.0	18.9	27.5	25.7	26.1
Location in remnant (windward, centre, leeward)	5.6	4.4	8.8	7.0	–
Th:K ratio (soil texture)	16.1	15.7	–	12.2	24.1
Litter cover (%)	14.6	9.4	16.0	14.5	–
Shrub cover (%)	–	–	–	8.5	21.0
Native perennial grass cover (%)	15.7	16.3	24.2	6.3	–
Tree cover (%)	6.4	6.7	–	–	–
Exotic annual grass cover (%)	–	–	–	7.2	28.7
Grazing factor (high, medium, low)	–	–	–	–	–
Available P (mg/kg)	12.6	11.7	9.0		–
Soil K (mg/kg)	–	–	–		–
Soil S (mg/kg)	–	–	–	3.9	–
Organic C (%)	5.3	2.6	–	5.5	–
Soil pH (H$_2$O)	–	3.3	14.6	4.9	–
Total soil N (%)	–	2.7	–		–
Soil Conductivity (dS/m)	–	2.8	–	4.2	–

Table 2 Summary of pairwise interactions in the simplified boosted regression tree model for total crust cover, and interaction between Th:K ratio and log Area in a reduced model that included only these two predictors

Predictors	Relative strength of interaction
Litter (%), log Area (Ha)	0.37
Total soil N, Th:K ratio	0.05
Th:K ratio, log Area (simplified model)	0.03
Th:K ratio, log Area (reduced model)	0.33

respectively). Tree cover was only included in the model for mosses. Differences between morphological group response to soil S, available C, total soil N and soil conductivity are not discussed, because when these variables were included in the final models their influence relative to other variables was small.

Remnant size (log Area) was consistently identified in the BRT models as an important predictor of abundance across all groups. Closer examination of the data (Fig. 5) shows that mosses are the only group of crust organisms detected in small sites.

Discussion

Crust disturbance across and within vegetation remnants

Our study clearly demonstrates that moss and lichen dominated crusts are an important component of remnant woodlands in the Wimmera Mallee, occupying up to 50% of the ground surface in large remnants with low litter cover. Further, this study shows that crusts are threatened by fragmentation and grazing-induced disturbance in this landscape. Because crust cover is negligible within small remnants <5 ha in size (Fig. 2) and the majority of remnants in the Wimmera Mallee are within this size class (Duncan and Durrough in review) few patches of vegetation in the region retain biological crusts. This loss of crusts is likely to reduce the function of remnants across the landscape, through increased soil erosion (Belnap and Gillette 1998; Eldridge 1998b), decreased soil fertility (Beymer and Klopatek 1991; Hawkes 2003; Housman et al. 2006), and modification of the water run-off infiltration balance (reviewed in Belnap 2006).
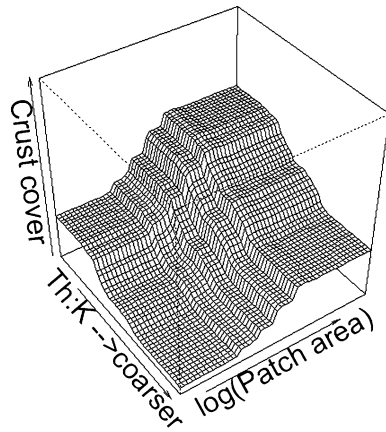
Fig. 3 Proportion cover of soil crust cover in response to interaction between log Area and Th:K ratio, from a boosted regression tree model with only these two predictors. The scale on the vertical axis is zero to one, and arrows show direction of increasing values on all axes
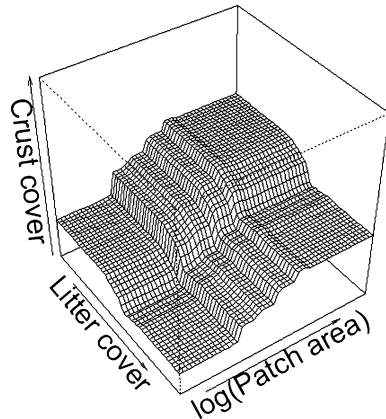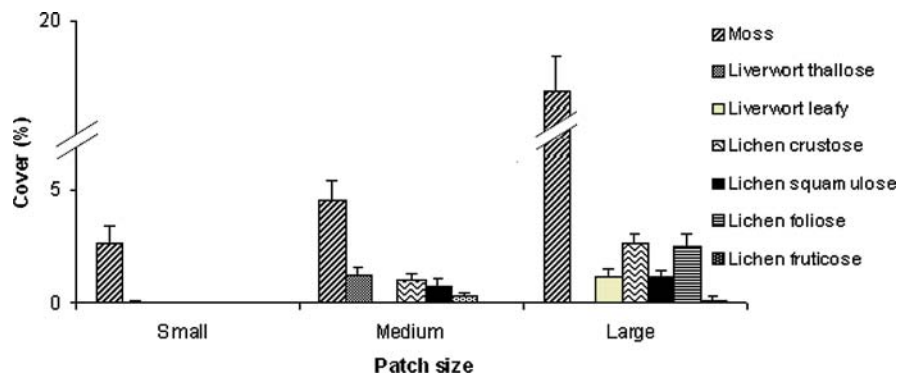

Fig. 4 Variation in total BSC cover in response to interaction between litter cover (%) and log Area, predicted by the boosted regression tree model for crust cover with eight predictor variables. The scale on the vertical axis is zero to one, and arrows show direction of increasing values on all axes

Patterns of fragmentation and landuse are the primary determinants of crust disturbance across remnants. The strong positive relationship between remnant size and crust abundance in the BRT model (Fig. 2) is likely due to an interaction with stock sheltering behaviour. A related study by Duncan et al. (2008) found evidence from patterns in nutrient enrichment in remnants across the study region that stock favour remnants for shelter from prevailing winds and heat. As remnant size increases the frequency and density of stock grazing and camping declines. The destruction of soil crusts by heavy or ongoing stock trampling is well recognised (Anderson et al. 1982; Beymer and Klopatek 1992; Yates et al. 2000). We believe that higher grazing intensity in small remnants has resulted in a decreased cover of crusts relative to large remnants.

There are several plausible explanations as to why we did not detect a correlation between grazing level (high, medium and low) and crust abundance in the BRT model. Firstly, variation in crusts due to grazing may be absorbed by variation in response to other influential variables. Secondly, this coarse measure of grazing is based solely on extant indicators and it is therefore unclear to what extent it reflects levels of historic grazing. Because natural recovery rates of soil crust cover are generally very slow, with estimates as high as 30–40 years for similar lichen and moss crusts in southern Australia (Eldridge 1998a), the legacy effect of grazing within the last ∼30 years is likely to still be evident. Thirdly, our classification of extant grazing pressure may be a poor measure of grazing-induced disturbance. Comparable studies have also failed to detect meaningful relationships between grazing pressure and crust taxa,

Fig. 5 Abundance (cover %) of morphological groups in small (0.5–5 ha), medium (5–10 ha) and large (>20 ha) sites. Error bars show standard errors

when using similarly crude measures (e.g. Eldridge et al. 2006).

Fragmentation and surrounding landuse also influenced crust distribution within remnants. Location within a remnant (windward edge, patch centre and leeward edge) was a covariate of soil crust abundance in the BRT model and exposure to the windward edge impacted negatively on soil crusts (Fig. 2). This impact may be from sediment deposition. Remnants act as sinks in the agricultural matrix with vascular vegetation trapping windblown sediments that can cover the ground (reviewed by Okin et al. 2006). Burial by eroded sediments has been observed to kill photosynthetic crust biota (West 1990). Desiccation of microclimate sensitive groups may also be a cause of decreased abundance at the windward edge, however, to our knowledge such sensitivity has only been observed in closed-canopy forests (e.g. Baldwin and Bradfield 2007) and not in arid, open-woodlands. Further research is needed to establish how far into the remnant the effect of wind extends.

Our data do not support our hypothesis that soil crusts are more susceptible to disturbance on coarse textured soils. Although the regression model detected a weak interaction between remnant size and the Th:K ratio (Fig. 3), this result was primarily due to fine textured soils providing optimal crust habitat relative to coarse textured soils. The rate of decrease in crust abundance with decreased patch size did not differ between coarse and fine textured soils as would be expected if crusts on coarse textured soils were more susceptible to disturbance by stock trampling.

Environmental covariates of soil crust abundance

The radiometric Th:K ratio was the most important environmental covariate of soil crust distribution identified by the BRT model. This result suggests the Th:K ratio has potential to be a useful, remotely sensed variable for explaining crust distribution across the landscape. As a surrogate of soil texture, the influence of the Th:K ratio on crusts is consistent with other studies that have found higher crust abundance and diversity on fine textured soils than on sandier soils (Anderson et al. 1982; Eldridge et al. 2006; Thompson et al. 2006). The mechanisms explaining the influence of soil texture on crust abundance and diversity are poorly understood,

however, they may relate to complex gradients in water and nutrient availability (Bowker et al. 2005). Fine textured soils such as silt and clay hold more water and have a higher nutritional status than coarse, sandy soils (Briggs et al. 1995) and this may promote growth of soil crust biota. Soil texture may also indirectly influence crust abundance through its effect on vascular plant distribution, however, tests for a correlation between the Th:K ratio and various plant life-forms in this study did not show strong relationships.

The influence of tree cover and leaf litter on crust abundance can be explained by a reduction in suitable crust habitat due to increased shading and decreased bare ground (Downing and Selkirk 1993; Eldridge 1999; Dougill and Thomas 2004). Eucalypt species dominant in the study region accumulate thick layers of leaf litter in the absence of fire (Bradstock and Cohn 2002) covering soil that would otherwise be suitable for crust establishment and reducing light reaching the soil surface (Eldridge and Bradstock 1994). It is likely that tree cover inhibits crust cover indirectly through the effect of litter accumulation (litter and tree cover are weakly correlated, $r = 0.45$) as well as directly through shading (Sedia and Ehrenfeld 2003).

Unlike the direct influence of tree and litter cover on crust abundance, we suggest the positive relationship between crust and perennial grass cover (at low levels of cover: 0–5%) is primarily the consequence of a shared response to past grazing rather than a facilitative effect of perennial grasses. Native perennial grass species are known to decline under high grazing pressure from selective browsing and trampling (Vesk et al. 2004). We believe that sites where perennial grasses have declined due to stock grazing are sites where soil crusts have been reduced by stock trampling. This agrees with Beymer and Klopatek (1992) who found both crusts and native C-3 grasses declined with increased grazing intensity in Pinyon-juniper woodlands.

Grazing history may also drive the negative relationship between crusts and available phosphorus. This relationship may be due to a negative impact of nutrient enrichment on soil crust biota or because enrichment of available phosphorus is an indicator of general disturbance at a site. Similar to a study by Bowker et al. (2006) we found a reduced cover of crusts on sites with increased available phosphorus.

Bowker et al. (2006) postulate that this negative relationship is due to uptake of available P by lichens and mosses which convert the P to unavailable organic forms. We suggest for our study region this result is due to a relationship between P enrichment and habitat disturbance, particularly excreta from stock. A related study by Duncan et al. (2008) identified enrichment of available P in small remnants in the study region and argued that the primary cause was from stock camping behaviour, which in small remnants swamped effects from other depositional processes such as dumping of windblown sediments. Similarly, Yates et al. (2000) found elevated levels of available phosphorus in heavily grazed compared to rarely grazed eucalypt woodlands. Australian soils are relative infertile and phosphorus is a key limiting nutrient in many areas (Beadle 1966, Standish et al. 2006).

Disturbance from stock trampling may also explain the weak positive relationship between soil crusts and soil carbon in the study region rather than a causal effect of soil carbon on crust abundance. A decline in nutrient cycling and a break-down in the capacity of arid landscapes to retain litter and soil surface resources are consequences of land disturbance. (Belnap 1995; Yates et al. 2000). In particular, overgrazing and trampling results in decreased soil carbon because of decreased soil organic matter from plants (Renzhong and Ripley 1997; Lechmere-Oertel et al. 2005), destruction of carbon fixing organisms that make up the soil crust (Beymer and Klopatek 1991) and a loss of carbon-rich surface horizons. Sites with reduced soil carbon due to disturbance are also likely to have a reduced cover of soil crusts.

Because the environmental space sampled in this study was defined by Mallee and woodland communities we did not capture the limits of crust distribution in terms of soil stability and vegetation structure. These soil-vegetation associations consistently have suitable crust habitat when undisturbed, with stable soils that are stone and litter-free between the vascular plant canopies. We did not extend our sampling into dense vegetation communities with thick and evenly distributed leaf litter or into landscapes with shifting sands. It would be interesting to determine the limits of crust distribution with respect to soil texture and vegetation structure and the extent of crust abundance across broader gradients for the environmental variables identified in this study.

Differential responses of morphological groups

The results of our study suggest that morphological groups do show a differential response to measured variables. Most striking are the strong responses of foliose lichens to soil pH but not to soil texture and the negative responses of crustose lichens to shrub and annual exotic grass cover (Table 1). Foliose lichens may not be influenced by soil texture as they are loosely attached to the soil surface compared to other morphological groups, and may be less disturbed by movement of unstable, coarse textured soils. Groups also differ in their resilience to disturbance, with mosses the only group with moderate cover in small sites (Fig. 5). Our results suggest that assessment of morphological groups provides information on environmental conditions and disturbance history that would be hidden with data on total crust cover only. However, there is a need for explicit studies to investigate top–down and bottom–up classification of crust biota in relation to environmental variables and disturbance, to determine the optimal level of classification, and whether lumping species and genera into morphological groups masks important responses of crust biota. We expect the appropriate level of classification used in an assessment will depend on the question being investigated.

Conclusion

Our study demonstrates that biological soil crusts are sensitive to environmental conditions indicative of disturbance and therefore threatened in the Mallee and Wimmera bioregions. We believe that grazing history is the mechanism driving many of the relationship identified in this study. The loss of soil crusts from small remnants in this fragmented, agricultural landscape is likely to exacerbate declines in ecosystem function through increased soil erosion, changed patterns in water infiltration and run-off, reduced nitrogen and carbon fixation, and a change in opportunities for seed entrapment and seedling germination. Small remnants should be considered for restoration projects such as fencing from stock if we are to maintain and restore ecosystem function across the Mallee and Wimmera.

References

Anderson DC, Harper KT, Rushforth SR (1982) Recovery of cryptogamic crusts from grazing on Utah winter ranges. J Range Manage 35:355–359. doi:10.2307/3898317

Andrew MH, Lange RT (1986) Development of a new piosphere in arid chenopod shrubland grazed by sheep 1. Changes to the soil surface. Aust J Ecol 11:395–409. doi:10.1111/j.1442-9993.1986.tb01409.x

Baldwin LK, Bradfield GE (2007) Bryophyte responses to fragmentation in temperate coastal rainforests: a functional approach. Biol Conserv 136:408–422. doi:10.1016/j.biocon.2006.12.006

Belnap J (1995) Surface disturbances: their role in accelerating desertification. Environ Monit Assess 37:39–57. doi:10.1007/BF00546879

Belnap J (2006) The potential roles of biological soil crusts in dryland hydrologic cycles. Hydrol Process 20:3159–3178. doi:10.1002/hyp.6325

Belnap J, Eldridge DJ (2003) Disturbance and recovery of biological soil crusts. In: Belnap J, Lange OL (eds) Biological soil crusts: structure, function and management. Springer-Verlag, Berlin, pp 363–383

Belnap J, Gillette DA (1998) Vulnerability of desert biological crusts to wind erosion: the influences of crust development, soil texture, and disturbance. J Arid Environ 39:133–142. doi:10.1006/jare.1998.0388

Beymer RJ, Klopatek JM (1991) Potential contribution of carbon by microphytic crusts in pinyon-juniper woodlands. Arid Soil Res Rehabil 5:187–198

Beymer RJ, Klopatek JM (1992) Effects of grazing on cryptogamic crusts in Pinyon-juniper woodlands in Grand Canyon National Park. Am Midl Nat 127:139–148. doi:10.2307/2426329

Blair GJ, Chinoim N, Lefroy RDB, Anderson GC, Crocker GJ (1991) A sulphur soil test for pastures and crops. Aust J Soil Res 29:619–626. doi:10.1071/SR9910619

Bowker MA, Belnap J, Davidson DW, Goldstein H (2006) Correlates of biological soil crust abundance across a continuum of spatial scales: support for a hierarchical conceptual model. J Appl Ecol 43:152–163. doi:10.1111/j.1365-2664.2006.01122.x

Bowker MA, Belnap J, Davidson DW, Phillips SL (2005) Evidence for micronutrient limitation of biological soil crusts: importance to arid-lands restoration. Ecol Appl 15:1941–1951. doi:10.1890/04-1959

Bradstock RA, Cohn JS (2002) Fire regimes and biodiversity in semi-arid Mallee ecosystems. In: Bradstock RA, Williams JE, Gill AM (eds) Flammable Australia: the fire regimes and biodiversity of a continent. Cambridge University Press, Cambridge

Briggs D, Smithson P, Addison K, Atkinson K (1995) Fundamentals of the physical environment. Routledge, London

Colwell JD (1965) An automated procedure for the determination of phosphorus in sodium hydrogen carbonate extracts of soils. Chem Ind 22(May):893–895

De'ath G (2007) Boosted trees for ecological modelling and prediction. Ecology 88:243–251. doi:10.1890/0012-9658(2007)88[243:BTFEMA]2.0.CO;2

Department of Sustainability and Environment (2004) Ecological vegetation class bioregion benchmark for vegetation quality assessment. Victorian government department of sustainability and environment

Dougill AJ, Thomas AD (2004) Kalahari sand soils: spatial heterogeneity, biological soil crusts and land degradation. Land Degrad Dev 15:233–242. doi:10.1002/ldr.611

Downing AJ, Selkirk PM (1993) Bryophytes on the calcareous soils of Mungo National Park, an arid area of southern central Australia. Great Basin Nat 53:13–23

Duncan DH, Dorrough J, White M, Moxham C (2008) Blowing in the wind? Nutrient enrichment of remnant woodlands in an agricultural landscape. Landscape Ecol 23(1):107–119. doi:10.1007/s10980-007-9160-0

Duncan DH, Durrough JW (In review) Historical and current land use shape landscape restoration options in the Australian wheat and sheep farming zone. Landscape and Urban Planning

Eldridge DJ (1998a) Soil crust lichens and mosses on calcrete-dominant soils at Maralinga in arid South Australia. J Adel Botanic Gardens 18:9–24

Eldridge DJ (1998b) Trampling of microphytic crusts on calcareous soils and its impact on erosion under rain-impacted flow. Catena 33:221–239. doi:10.1016/S0341-8162(98)00075-7

Eldridge DJ (1999) Distribution and floristics of moss- and lichen-dominated soil crusts in a patterned *Callitris glaucophylla* woodland in eastern Australia. Acta Oecol 20:159–170. doi:10.1016/S1146-609X(99)80029-0

Eldridge DJ (2001) Biological soil crusts of Australia. In: Belnap J, Lange OL (eds) Biological soil crusts: structure, function, and management. Springer-Verlag, Berlin, pp 119–131

Eldridge DJ, Bradstock RA (1994) The effect of time since fire on the cover and composition of cryptogamic soil crusts on Eucalyptus shrubland soil. Cunninghamia 3:521–527

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. doi:10.1007/s11104-005-4436-0

Eldridge DJ, Kinnell PIA (1997) Assessment of erosion rates from microphyte-dominated calcareous soils under

rain-impacted flow. Aust J Soil Res 35:475–489. doi: 10.1071/S96072

Eldridge DJ, Koen TB (1998) Cover and floristics of micro-phytic soil crusts in relation to indices of landscape health. Plant Ecol 137:101–114. doi:10.1023/A:1008036214140

Eldridge DJ, Rosentreter R (1999) Morphological groups: a framework for monitoring microphytic crusts in arid landscapes. J Arid Environ 41:11–25. doi:10.1006/jare.1998.0468

Eldridge DJ, Tozer ME (1997a) Environmental factors relating to the distribution of terricolous bryophytes and lichens in semi-arid eastern Australia. Bryologist 100:28–39

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

Elith JE, Leathwick JR, Hastie T (2008) Boosted regression trees—a new technique for modelling ecological data. J Anim Ecol 77:802–813. doi:10.1111/j.1365-2656.2008.01390.x

George DB, Roundy BA, St Clair LL (2003) The effects of microbiotic soil crusts on soil water loss. Arid Land Res Manage 17:113–125. doi:10.1080/15324980301588

Hastie T, Tibshirani R, Friedman JH (2001) The elements of statistical learning: data mining, inference and prediction. Springer-Verlag, New York

Hawkes CV (2003) Nitrogen cycling mediated by biological soil crusts and arbuscular mycorrhizal fungi. Ecology 84:1553–1562. doi:10.1890/0012-9658(2003)084[1553:NCMBBS]2.0.CO;2

Housman DC, Powers HH, Collins AD, Belnap J (2006) Carbon and nitrogen fixation differ between successional stages of biological soil crusts in Colorado Plateau and Chihuahuan Desert. J Arid Environ 66:620–634. doi:10.1016/j.jaridenv.2005.11.014

Leathwick JR, Elith J, Chadderton L, Rowe D, Hastie T (2008) Dispersal, disturbance, and the contrasting biogeographies of New Zealand's diadromous and non-diadromous fish species. J Biogeogr 35:1481–1497. doi:10.1111/j.1365-2699.2008.01887.x

Lechmere-Oertel RG, Colwing RM, Kerley GIH (2005) Landscape dysfunction and reduced spatial heterogeneity in soil resources and fertility in semi-arid succulent thicket, South Africa. Austral Ecol 30:615–624. doi:10.1111/j.1442-9993.2005.01495.x

Mallee Catchment Management Authority (2003) Mallee regional catchment strategy 2003–2008. Mallee CMA, Mildura

Martinez I, Escudero A, Maestre FT, de la Cruz A, Guerrero C, Rubio A (2006) Small-scale patterns of abundance of mosses and lichens forming biological soil crusts in two semi-arid gypsum environments. Aust J Bot 54:339–348. doi:10.1071/BT05078

Okin GS, Gillete DA, Herrick JE (2006) Multi-scale controls on and consequences of aeolian processes in landscape change in arid and semi-arid environments. J Arid Environ 65:253–275. doi:10.1016/j.jaridenv.2005.06.029

Ponzetti JM, McCune BP (2001) Biotic soil crusts of Oregon's shrub steppe: community composition in relation to soil chemistry, climate and livestock activity. Bryologist 104:212–225. doi:10.1639/0007-2745(2001)104[0212:BSCOOS]2.0.CO;2

Pracilio G, Adams ML, Smettem KRJ, Harper RJ (2006) Determination of spatial distribution patterns of clay and plant available potassium contents in surface soils at the farm scale using high resolution gamma ray spectrometry. Plant Soil 282:67–82. doi:10.1007/s11104-005-5229-1

Prasse R, Bornkamm R (2000) Effect of microbiotic soil surface crusts on emergence of vascular plants. Plant Ecol 150:65–75. doi:10.1023/A:1026593429455

Rayment GE, Higginson FR (1992) Australian laboratory handbook of soil and chemical methods. Inkata Press, Melbourne

Renzhong W, Ripley EA (1997) Effects of grazing on a Leymus chinensis grassland on the Songnen plain of north-eastern China. J Arid Environ 36:307–318. doi:10.1006/jare.1996.0214

Ridgeway G (2004) gbm: generalized boosted regression models. R. package, version 1.3–5. Available at: http://www.i-pensieri.com/gregr/gbm.shtml

Rogers RW (1972) Soil surface lichens in arid and subarid South-eastern Australia. III. The relationship between distribution and environment. Aust J Bot 20:301–316. doi:10.1071/BT9720301

Sedia EG, Ehrenfeld JG (2003) Lichens and mosses promote alternate stable plant communities in the New Jersey Pinelands. Oikos 100:447–458. doi:10.1034/j.1600-0706.2003.12058.x

Sokal RR, Rohlf FJ (1998) Biometry. W. H. Freeman and Company, New York

Su Y-G, Li X-R, Cheng Y-W, Tan H-J, Jia R-L (2007) Effects of biological soil crusts on emergence of desert vascular plants in North China'. Plant Ecol 191:11–19. doi:10.1007/s11258-006-9210-8

Sweeney RA, Rexroad PR (1987) Comparison of LECO FP-228 "nitrogen determinator" with AOAC copper catalyst Kjeldahl method for crude protein. J Assoc Off Anal Chem 70:1028–1030

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. doi:10.1658/1100-9233(2006)017[0271:SOBSCC]2.0.CO;2

Venables WN, Dichmont CM (2004) GLMs, GAMs and GLMMs: an overview of theory for applications in fisheries research. Fish Res 70:319–337. doi:10.1016/j.fishres.2004.08.011

Vesk PA, Leishman MR, Westoby M (2004) Simple traits do not predict grazing response in Australian dry shrublands and woodlands. J Appl Ecol 41:22–31. doi:10.1111/j.1365-2664.2004.00857.x

Walkley A, Black IA (1934) An examination of the Degtjareff method for determining soil organic matter, and a proposed modification of the chromic acid titration method. Soil Sci 37:29–38. doi:10.1097/00010694-193401000-00003

West NE (1990) Structure and function of microphytic soil crusts in wildland ecosystems of arid to semi-arid regions. Adv Ecol Res 20:180–209

White M, Oates A, Barlow T, Pelikan M, Brown J, Rosengren N et al (2003) The vegetation of north-west Victoria: a report to the Wimmera. North Central and Mallee Catchment Management Authorities, Arthur Rylah Institute for Environmental Research, Melbourne

White MD (2006) The Mallee vegetation of north western Victoria. Proc R Soc Vic 118:229–243

Williams JD, Dobrowolski JP, West NE, Gillette DA (1995) Micrphytic crust influence on wind erosion. Trans ASAE 38:131–137

Wood S (2006) Generalized additive models: an introduction with R. Chapman and Hall/CRC Press, Boca Raton, Florida

Yair A (2003) Effects of biological soil crusts on water redistribution in the Negev Desert, Israel: a case study in longitudinal dunes. In: Belnap J, Lange OL (eds) Biological soil crusts: structure, function, and management. Springer-Verlag, Berlin, pp 303–314

Yates CJ, Norton DA, Hobbs RJ (2000) Grazing effects on plant cover, soil and microclimate in fragmented woodlands in south-western Australia: implications for restoration. Austral Ecol 25:36–47. doi:10.1046/j.1442-9993.2000.01030.x