



Surprisingly fast recovery of biological soil crusts following livestock removal in southern Australia

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Keywords

Boosted regression tree model; Grassy woodlands; Lichen; Livestock exclusion; Moss; Restoration.

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Abstract

Question: Biological soil crusts (BSCs) exist in arid and semi-arid ecosystems worldwide, and their recovery following the removal of a disturbance agent is integral to the rehabilitation of degraded landscapes. We asked: what is the likelihood of success and time frame of BSC recovery in vegetation remnants of southeast Australia, following livestock exclusion by fencing.

Location: Dryland agricultural region of northwest Victoria, Australia.

Methods: We conducted a “space for time” study of BSC recovery across 21 sites where livestock have been excluded by fencing between 1 and > 50 years ago, and used boosted regression tree models to explore the response of BSCs to livestock exclusion while controlling for the influence of environmental variables on BSC abundance.

Results: Our results show a relatively rapid, passive recovery of BSCs following livestock exclusion, with cover stabilizing after 20 years. Sites heavily disturbed by livestock grazing at the time of fencing stabilized at a lower cover. In contrast to studies from other countries, our results suggest mosses, not cyanobacteria, are the important colonizers in our study region.

Conclusions: Ecosystem function in degraded remnants of southern Australia can be improved in a relatively short time frame through passive recovery alone. This knowledge will benefit land managers choosing between restoration options in disturbed and fragmented arid-landscapes.

Introduction

Biological soil crusts (BSCs) are a functionally important component of arid and semi-arid ecosystems worldwide, and their removal by livestock trampling accelerates soil degradation (Belnap 1995; Bowker et al. 2008). The soil lichens, bryophytes, cyanobacteria, algae and fungi, which comprise the BSC, stabilize soils against water and wind erosion (Eldridge & Kinnel 1997; Chaudhary et al. 2009), regulate water infiltration and run-off (reviewed in Belnap 2006) and fix atmospheric nitrogen and carbon dioxide (Hawkes 2003; Housman et al. 2006). BSCs also provide habitat for microfauna (Li et al. 2006) and may facilitate recruitment of vascular plants (Prasse & Bornkamm 2000; Langhans et al. 2009; Su et al. 2009).

Although BSC organisms can survive extremes of climate, they are vulnerable to physical disturbance. Many BSC organisms are brittle and weakly attached to

the soil surface, particularly on soils with a higher sand content, and readily disintegrate when trampled by hoofed animals (Anderson et al. 1982; Eldridge 1998b). Because of the numerous ecological functions of BSCs, knowledge of the potential for BSC re-establishment following livestock removal is important for restoration of degraded arid and semi-arid landscapes.

Theories of succession suggest that BSCs are common colonizers of exposed soils and may re-establish as a permanent component of ecosystems with low vascular plant cover, where the ecosystem has not progressed to a degraded steady state (Bowker 2007). BSC cover is important for ecological rehabilitation due to its stabilizing function. It has been shown to re-establish to a state comparable to undisturbed reference conditions following removal of the disturbance agent (Eldridge & Ferris 1999; Kidron et al. 2008); however, rates implied for re-establishment following surface disturbance are generally

slow and highly variable. Estimates range from 5 years for re-establishment of cold desert cyanobacterial cover following human trampling (Cole 1990), to an estimated two millennia for cover of some hot desert lichens recovering from vehicle disturbance (Belnap & Warren 2002).

Whilst total cover of BSC is highly relevant to ecological rehabilitation, aspects of BSC composition, species richness and diversity are important indicators of BSC successional stage and function (Zaady et al. 2000; Zaady & Bouskilaz 2002; Zhao et al. 2010). Observations of BSC succession suggest that cyanobacteria are common colonizers amongst BSCs, stabilizing soils and facilitating establishment of mid- to late-successional mosses and lichens (Anderson et al. 1982; Johansen et al. 1984; Johansen & St Clair 1986; Belnap 1993; Danin et al. 1998; Belnap & Eldridge 2003); however there appear to be no studies of succession pathways for BSCs in which cyanobacteria are not the dominants prior to disturbance. Two recent studies have observed mosses rather than cyanobacteria colonizing bare soils (Li et al. 2002; Langhans et al. 2010), but without explanation of why these differ from the general reported trends, nor about expected succession trajectories for such BSCs. Factors influencing the time frame and trajectory of BSC recovery include annual rainfall, soil texture, land-use history, past climate, vascular plant community structure and availability of inoculation material (reviewed in Belnap & Eldridge 2003).

In the dryland agricultural region of northwest Victoria, Australia, 5% of native vegetation remains, due to extensive clearing for farming since European settlement in the mid-nineteenth century (Duncan et al. 2008; Duncan & Dorrough 2009). In remnant grassy woodlands of the region, BSCs dominated by mosses and some lichens are abundant on fine textured soils with low tree and litter cover in areas where disturbance is minimal (Read et al. 2008). More broadly, BSC cover is reduced or absent in the many remnants used for livestock shelter (primarily sheep; Duncan & Dorrough 2009). There is a strong negative correlation between remnant size and livestock disturbance (Duncan et al. 2008; Duncan & Dorrough 2009), with negligible BSC cover in the highly disturbed small sites (< 5 ha, Read et al. 2008). Restoring BSC cover to disturbed remnants of the region would likely enhance remnant ecological function through the influence of BSCs on processes such as soil stability, soil nutrient cycling and water infiltration (Bowker 2007).

In this paper we present a “space for time” study of BSC recovery in small remnants, those most likely to be degraded by grazing, over the first few decades following removal of livestock grazing pressure. Given the absence of pristine reference sites enabling us to clearly define full recovery, we use a practical approach that focuses on BSC

cover, and define ecological recovery as occurring when total BSC cover asymptotes to a stable level comparable to little disturbed reference sites (*sensu* Bowker 2007). We identified sites spanning the greatest possible range of time since grazing exclusion (from ~1 to ~50 years) and measured total BSC cover and cover of BSC morphotypes (*sensu* Eldridge & Rosentreter 1999), comparing these against each other and against an earlier data set (Read et al. 2008). Specifically, with these data we aimed to: (1) determine whether total cover of BSC could passively re-establish (*i.e.* without assistance) in isolated remnants following livestock exclusion by fencing; (2) estimate the rate of total BSC cover re-establishment over time since livestock exclusion; and, (3) investigate succession of BSC morphotypes as a function of time since livestock exclusion. To do this, we used a modern form of regression model, boosted regression trees, to analyse the important predictors of cover, and to predict time to recovery to former levels of BSC cover, against a null of no relationship between the response and candidate predictors. We did this both for total BSC cover, and for BSC morphotypes with enough data for analysis. From previous work in these grassy woodland ecosystems (Read et al. 2008) and from the sole other study on BSC recovery in Australian semi-arid woodlands (Eldridge 1998a), we expected that mosses might recolonize bare soil areas within a few years, but that morphotypes such as lichens might take at least several decades to re-establish. We were uncertain how long it would take to achieve cover levels comparable to little disturbed sites, and which morphotypes of BSC biota might prove the important colonizers. The literature strongly suggests cyanobacteria, but it was mosses that dominated residual BSCs in disturbed sites in Read et al. (2008). Data from the current study will critically enhance our understanding of the potential for passive BSC recovery in degraded remnants following livestock removal and inform restoration planning decisions in semi-arid environments.

Methods

Study region

This study was conducted in 21 remnant grassy woodlands (sites) in the dryland agricultural zone of northwest Victoria, Australia (36°06'–36°30'S, 142°35'–142°52'E). The study area is low-lying with the highest peak 154 m a.s.l. The area is semi-arid with long-term average monthly temperatures over the year of: minima from 4 to 14 °C and maxima from 13 to 30 °C. Mean annual rainfall ranges across the region from 370 to 410 mm and the wettest months (July, *ca.* 40 mm) have double the rainfall of the driest (January, *ca.* 20 mm).

Remnant grassy woodlands of the region are dominated by trees of *Eucalyptus largiflorens* F. Muell (Black box) or *Allocasuarina luehmanii* (R.T. Baker) L.A.S. Johnson (Buloke), with a sparse shrubby understorey and diverse ground stratum of grasses and other herbs (White et al. 2003). This vegetation occurs on ancestral floodplains with calcareous, clay-loam soils. The species-rich BSCs of this vegetation type are dominated by mosses, including *Didymodon torquatus*, *Tortula atrovirens* and *Bryum* sp., with lichens such as *Xanthoparmelia* sp., *Psora decipiens*, *Diploschistes* sp. and *Endocarpon* sp. also common (C.F. Read, unpubl. data).

Site selection

We adopted a space-for-time substitution and selected 21 isolated vegetation remnants where livestock had been excluded for a known time period (between 1 and ~50 years). We purposefully biased sampling toward remnants where grazing had been excluded relatively recently because we expected that the most rapid change might begin within the first few years of stock exclusion. Also, because BSC disturbance through livestock trampling is known to be negatively correlated with remnant size in this landscape (Read et al. 2008), and because those remnants available for rehabilitation are often small, we sought to limit size variation and to focus on recovery within smaller remnants (< 30 ha). Nineteen of the 21 remnants were located on private land and fenced \leq 31 years ago. The two public land remnants were fenced ~50 years ago. All remnants were isolated within a matrix of cropland where BSC cover was negligible. One study site was assigned within each remnant. The smallest distance between sites was 130 m (mean nearest neighbour distance 3995 m (standard error = 791 m), and the maximum distance between sites was 80.1 km. Ranges of environmental variables across the sites appear in Table 1.

We did not sample currently grazed remnants in this study; however our previous study in the region (Read et al. 2008) showed average total BSC cover as 8.6% (standard error = 1.5%) in currently grazed remnants in the same size range (< 30 ha), with a similar range of soil texture (defined by the thorium to potassium ratio; see below for more information on Th:K).

Site grazing history

The year of livestock exclusion (by fencing) and prior management regime was ascertained through consultation with landholders. Prior to fencing, sheep had typically grazed the remnants for a few months every 1 to 3 years. We used interview data to test for a relationship between time since fencing and historic levels of grazing impact. Fourteen face-to-face interviews were conducted

Table 1. Predictor variables (covariates) available for modelling.

Variable	Range
Time since fencing (years)	1–55
Tree cover (proportion)	0.05–0.65
Native perennial grass and shrub cover (proportion)	0.00–0.65
Bare ground cover (proportion)	0.00–0.95
Exotic plant cover (proportion)	0.00–0.60
Native litter cover (proportion)	0.00–1.00
Community: Black box woodlands or Buloke woodlands	
Available P	108–581
K	205–1395
Total soil N	0.1–0.31
Organic soil C	1.18–3.86
Nitrate	1–178
Thorium to potassium (Th:K) ratio, remotely sensed radiometric signal (minimum values associated with heavy clay soil, maximum values associated with sandy loam)	377–500
Microenvironment	Exposed – centre of canopy interspace (E), Exposed dripline – 1 m north of canopy dripline (ED), Shaded dripline – 1 m south of canopy dripline (SD)
Bareground (start) – cover estimate of bare ground at time of fencing	Low-med-high
Litter and logs (start) – cover estimate of litter and logs at time of fencing	Low-med-high
Native grass (start) – cover estimate of native grasses at time of fencing	Low-med-high

with landholders for 19 private land sites in February and March 2007. We asked landholders to score remnant condition at the time of fencing according to a series of indicative photographs of the vegetation community type in various states of degradation. The photographs were taken from eye height with a hand-held camera using focal lengths in the order of 5 to 50 m. Respondents were asked which image best represented the level of bare ground cover in the remnant at the time stock were excluded (1 = low, 2 = medium, 3 = high). The same question was posed regarding native grass cover and ground cover of litter and logs. The time since fencing and starting condition scores of individual sites were not correlated ($r = 0.15$, $t = 0.64$, $df = 17$, $P = 0.27$ for test of a positive correlation), indicating that there was no systematic bias in relation to time since fencing.

Site sampling

For each site we measured potential environmental predictors of BSC abundance in the field, the lab and from geographic information system (GIS) data to understand variation in BSC recovery. All important predictor

variables for BSC abundance identified from our previous work (Read et al. 2008) and that might influence our models were included in the current survey and appear in Table 1. During October and November 2006, each site was sampled at two haphazardly selected locations > 150 m from an edge. At each location the projected foliage cover of trees was visually estimated within a 20 m × 20 m plot, and BSC cover, projected foliage cover of perennial vegetation (< 1-m tall), exotic annual grasses (both alive and dead), bare ground and native litter were visually estimated within three 0.5 m × 0.5 m quadrats placed along a transect. Each transect extended along a north–south axis from the south side of a randomly selected canopy patch (tree or cluster of trees) to the centre of the interspace (area between canopy patches). Transect length varied with interspace length. Quadrats were stratified into three microenvironments, as follows: (1) *Exposed* – centre of canopy interspace; (2) *Exposed dripline* – 1 m north of canopy dripline; and (3) *Shaded dripline* – 1 m south of canopy dripline. Sun exposure can influence the abundance and composition of BSCs because species differ in tolerance of desiccation and shading (Eldridge 1999; Bowker et al. 2006). BSCs were not sampled under tree canopies where BSC development was inhibited by thick layers of leaf litter (Read et al. 2008).

Total BSC and BSC morphotype cover (Eldridge & Tozer 1997) were visually estimated in each quadrat. Morphotypes included were: cyanobacterial and algal crust (called “black crust”); short and tall moss (< 2-mm and > 2-mm high, respectively); leafy and thallose liverworts; and crustose, squamulose, foliose and fruticose lichens. Cover assessments were made after mist spraying with water to minimize variation in bryophyte cover due to differences in moisture content (Rosentreter et al. 2001). We also recorded cover of four classes of cyanobacterial development based on levels of pigmentation (1 = no pigmentation, 2 = faint pigmentation, 3 = medium/dark pigmentation, 4 = black). Although these classes were not tested against actual measures of cyanobacteria or chlorophyll *a* pigmentation, field assessment of soil pigmentation has been found to have a strong relationship with cyanobacterial development and soil stability (Belnap et al. 2008).

Soils

Five random soil samples were collected (depth 0–10 cm) and bulked within each 20 m × 20 m plot after removal of surface litter. The soil sampling was constrained by design requirements for a parallel study (D.H. Duncan et al., unpubl. data). Consequently, whilst the data indicate the nutrient condition of each BSC sampling site, they do not correspond directly to the sub-sampling locations of BSC

microenvironment. The analyses were performed by CSBP Laboratories, Western Australia. Available P and K were extracted using the Colwell method (1965), and their relative concentrations (mg kg^{-1}) estimated following the method of Rayment & Higginson (1992). Total nitrogen (%) was determined using a LECO combustion analyser. Nitrate (mg kg^{-1}) was determined using a Lachat Flow Injection Analyser. Organic carbon (%) was estimated following Walkley & Black (1934). Soil pH in deionized water was determined following Rayment & Higginson (1992).

We extracted data on remotely sensed radiometric signal for thorium–potassium (Th:K) ratio for each site from a raster data set of 50-m grid cells for Victoria (State of Victoria, unpubl. data), originally collected for the State of Victoria for mineral exploration. At large scales, these data have artefactual banding. To mitigate against this problem in modelling, we used a derived value obtained by first multiplying Th and K data by appropriate constants to provide integer values. Second, the smallest value in the data set was added to each value, to yield non-negative integer values. Then we calculated the ratio of Th to an inverted K scale, as $\text{Th}/((K_{\text{max}} - K) + 1)$. In effect this distributes cells ranging from low Th and high K to high Th and low K. Previous vegetation community mapping from the study region (White et al. 2003) has shown the Th:K ratio is an effective surrogate for soil texture, explaining variation in vegetation composition and structure. The Th:K ratio has also been found to be a strong predictor of BSC distribution in the study region, with highest BSC cover observed on soils with a low Th:K ratio and corresponding high clay content (Read et al. 2008).

Data analysis

We aimed to analyse the multivariate relationship between total BSC cover (the response) and the measured covariates, both to identify important variables and to predict the response for unmeasured conditions (Table 1). This is a typical regression modelling problem, and here we used boosted regression tree (BRT) models for the task. BRTs are a form of regression modelling from the statistical learning disciplines, with demonstrated capability for reliable variable selection, automatic detection of interactions and robust fitting of trends (Hastie et al. 2009). These are important for this problem, because we want to accurately identify the relevant relationships. BRTs are gradually becoming more widely used in ecological studies (Fabricius & De'ath 2008; Leathwick et al. 2008; Vesk et al. 2010; Buston & Elith 2011) and are explained in detail in De'ath (2007) and Elith et al. (2008). In overview, they are so named because they

combine two algorithms: one – regression trees – are a type of decision tree (De'ath 2002) and particularly good at reliably identifying important variables, modelling interactions and dealing with missing data; the other – boosting – is one of several new techniques for combining many simple models in such a way as to improve predictive performance.

Here, we present the main features of our data and their implications for the analysis. Two sampling locations were excluded from our analysis: one location was missing data and the other was identified as a sampling anomaly (from claypans, which represent a distinct BSC habitat). The 120 modelled observations of BSC cover and of morphotype cover were not independent, but hierarchically structured, with quadrat estimates of cover at the three microenvironments, nested within two locations in each of the 21 sites. Microenvironment was included as a categorical predictor in our BRTs. In traditional statistical models, one would treat site as a random effect in a mixed model, because the measurements nested within sites might be more similar than those across sites. In BRTs, cross-validation can be used for model training and testing; this helps to develop a model that fits the main trends in the data but that remains general enough to predict well. Cross-validation can be organized to deal with nested data (e.g. De'ath 2007; Fabricius & De'ath 2008; Buston & Elith 2011). Here, we used ten-fold cross-validation, where the data are split in ten 'folds', and the model built from nine and validated against the tenth. We retained the data hierarchy by keeping all data for any one site in the same fold (i.e. two sites each with their two locations and three quadrats per location in each fold). To test whether this dealt successfully with the data structure, we tested the relationship between site and the residuals of the model using methods detailed in Appendix S1. In all cases there was no detectable pattern, showing that the available predictors and the method of model fitting dealt successfully with the data set-up.

Our boosted regression tree model was fitted in R (v2.10, <http://www.R-project.org>; R Development Core Team 2004) using the "gbm" library (Ridgeway 2004) plus additional code written by Elith et al. (2008). We used a learning rate of 0.005 and a tree with two splits; these allow models of sufficient complexity whilst allowing for the relatively small size of the data set (Elith et al. 2008). The model was run with arc-sine transformed measures of abundance (Sokal & Rohlf 1998), which were then treated as a Gaussian (normal) response. A final set of predictor variables was selected using model simplification code that sequentially dropped the least important predictors, until the model was optimized for minimal prediction error in the held-out data (Elith et al. 2008).

The first important output from the model is a measure of the deviance explained on held-out data (using the cross-validation, and showing whether the model explains important variation at new sites). Second, the relative importance of the different predictors can be assessed through their frequency of selection and their effect on the explained deviance (Elith et al. 2008). Third, the effect of each predictor on the BSC response, holding other covariates at their mean, can be visualized in partial dependence plots. These give information on how BSC cover varies with variation in a predictor, providing important clues about the environmental correlates of BSC cover, and its response to grazing exclusion over time. For these, we also present 95% confidence intervals, estimated over 200 bootstrap samples of the data (Hastie et al. 2009).

We also explored the response of individual morphotypes to livestock exclusion. There were insufficient records for reliable regression modelling of morphotype, other than for short and tall mosses. The moss groups followed the same trends as for total BSC and are therefore not presented.

We finally include a graphical summary of average cover of morphotypes for different age ranges of time since fencing, and include uncertainty estimates.

Estimating potential BSC cover in little-disturbed locations

Our overall aim was to identify at what time since grazing the BSC cover approached an asymptote approximating that of little-disturbed reference sites. In the absence of appropriate reference sites, we used a regression model from a previous study (Read et al. 2008) to predict potential BSC abundance, following Gibbons et al. (2008). This method involves predicting reference conditions by holding significant explanatory variables representing modification since European settlement at values representing the minimum observed level of modification. This regression model (*previous model*) was developed using a larger data set from the region, with data collected from 25 sites over a broader area (the northern bound extended ~100 km further north than the current study) using a different sampling structure (refer to Read et al. 2008 for further details). Potential BSC cover was predicted as a site mean. As a check of model veracity, we visually compared predictions of potential BSC cover in minimally disturbed remnants to observed mean BSC cover at long ungrazed remnants from our current study. For further details on model prediction of potential BSC cover, refer to Appendix S2.

Results

The biological soil crust (BSC) showed signs of recovery from livestock trampling after 20 years. We used two

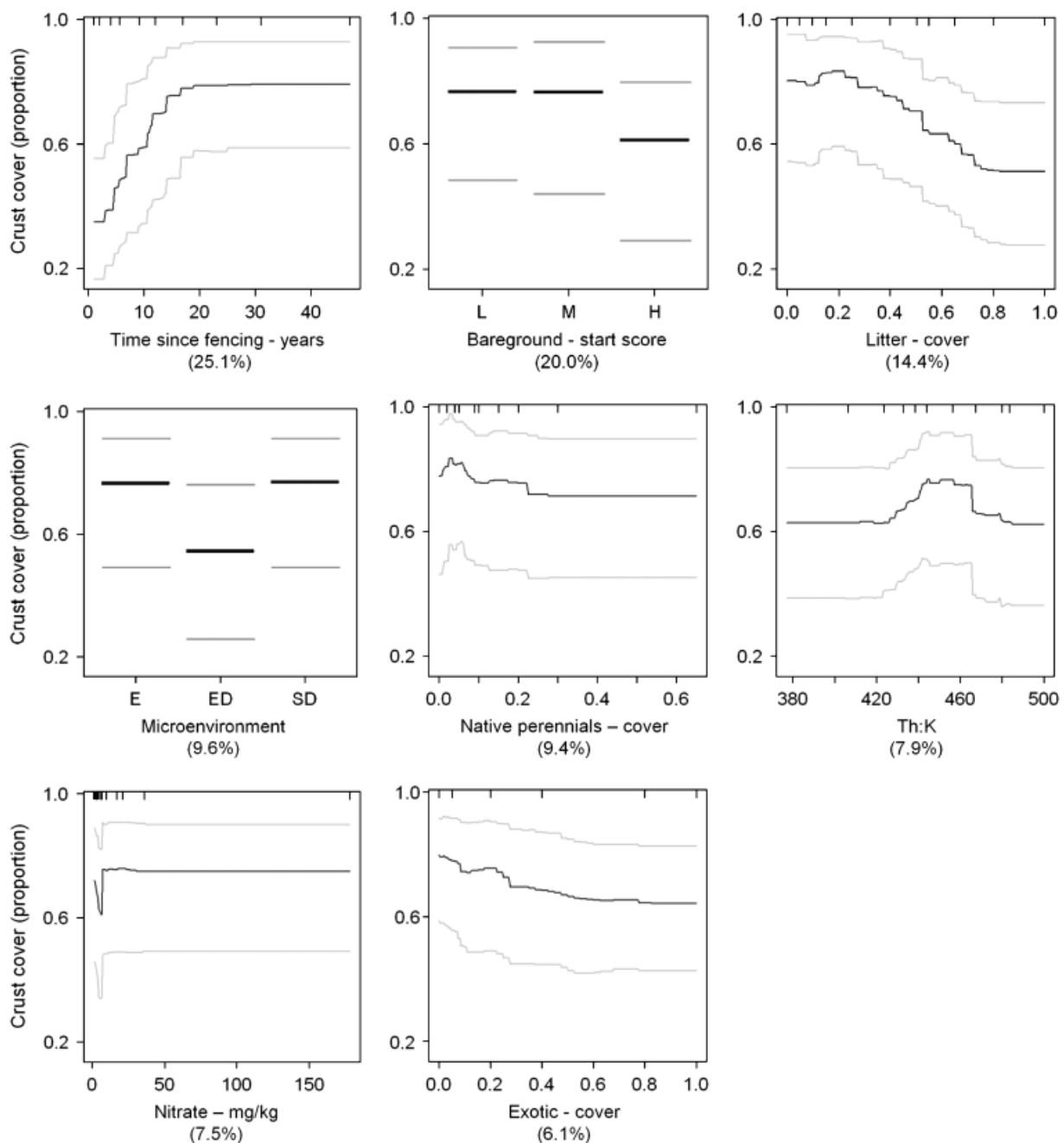


Fig. 1. Partial plots of influential variables in the simplified boosted regression tree model for total biological soil crust (BSC) cover, including Time since fencing; Bareground – start (bareground cover at time of fencing): L = low, M = medium and H = high; Native litter cover (proportion); Microenvironment: E = exposed, ED = exposed dripline – 1 m north of canopy, SD = shaded dripline – 1 m south of canopy; Native perennial cover (proportion); Th:K; Soil nitrate; and Exotic plant cover (proportion). Grey lines represent 95% confidence intervals for the predicted values. Relative contributions of covariates to the boosted tree model of biological soil crust cover are shown in parenthesis.

criteria to assess BSC recovery following livestock exclusion by fencing: (1) stability of BSC cover over time, and (2) comparison of recovered sites with previous model predictions of potential BSC cover. Our data indicated recovery according to both criteria.

First, the modelled BSC response to time since fencing (Fig. 1) shows a stable BSC cover after 20 years, following an initial rapid increase. The final regression model of BSC abundance (Fig. 1) included eight covariates of BSC cover and explained 45.6% of the predictive deviance (i.e.

of the variation in data from sites withheld from model fitting) in BSC response. The model identified time since fencing as the most important covariate of BSC abundance, providing the greatest contribution to model fit. Bare ground cover at the time of fencing was the second most important variable. Environmental covariates of BSC abundance identified in the model were: native litter cover, native perennial cover, Th:K ratio, soil nitrate and exotic plant cover. Sampling microenvironment was influential in the model, with a lower BSC abundance in locations just north of the canopy dripline compared to exposed locations of the interspace and locations just south of the canopy dripline. Our test for residual effects of variation between sites, beyond those explained by the covariates, revealed no identifiable effects. We tested for modelled interactions following the methods of Elith et al. (2008), and found no evidence of interactions between variables influencing the trajectory or time frame of BSC recovery.

Second, a scatterplot of mean site BSC cover against time since fencing shows the mean BSC cover in long ungrazed sites (> 20 years) is consistent with the modelled prediction of potential BSC cover from our previous, larger data set (Fig. 2). Predicted mean site BSC cover was 45% ($\pm 2.75\%$ standard error) for minimally disturbed sites in our study area and this value falls within two standard errors of observed means of long ungrazed sites (> 20 years).

Mosses dominate the BSC community in the study region (Fig. 3) with an average cover of 43% (standard error = 4.1%) in long ungrazed sites (> 20 years), compared to an average lichen cover of 9.3% (standard error = 2.2%). Representation of other morphotypes increased with time since fencing. Short and tall turf mosses represented 97% of biological cover of BSC organisms in recently grazed sites (> 5 years), compared to 78% in long ungrazed sites (> 20 years), which had moderate cover of black-crust (black discoloration of soil from

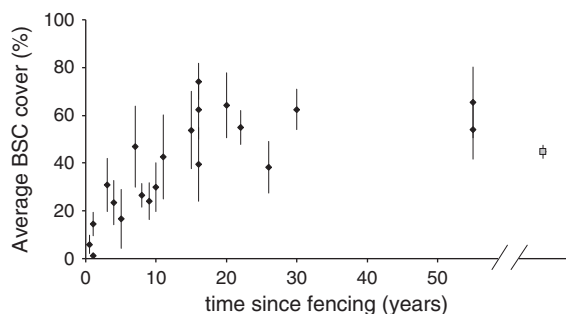


Fig. 2. Scatterplot of mean site BSC cover (%) against time since fencing (black diamonds). The grey square shows potential BSC cover (%; site mean) predicted from a boosted regression tree model developed by Read et al. (2008). Error bars show the standard error of the mean.

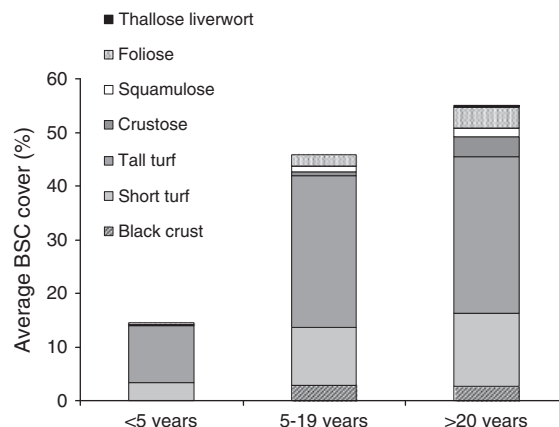


Fig. 3. Mean cover of morphotypes and total biological soil crust in sites grouped according to time since fencing (< 5 years, $n = 35$; 5 to 19 years, $n = 59$; > 20 years, $n = 29$). Morphotypes are: blackcrust (soil discoloration from algae and cyanobacteria), short turf moss, tall turf moss, crustose lichen, squamulose lichen and foliose lichen. Fruticose lichens were observed in intermediate and long ungrazed sites at abundances too low to represent on this figure (cover < 0.01%).

cyanobacteria and algae), and crustose, squamulose and foliose lichens in addition to the moss groups.

Discussion

We found that BSC cover recovered faster than anticipated in the grassy woodlands of northwest Victoria, and that the sequence of recovery of BSC morphotypes is congruent with our previous study, with mosses dominating BSCs in the more recently fenced sites. To our knowledge, this is the first study to draw inference of BSC recovery from regression models based on a one-time sampling of many sites over space, rather than tracking relatively few sites through time. While our estimate is based on past climate, and may not be indicative of recovery under future climatic conditions, the reliability and therefore utility of our estimate is strengthened by inference from existing data.

BSCs can passively recover in grassy woodlands following livestock removal

Biological soil crust (BSC) cover appears to stabilize after 20 years of stock exclusion (Fig. 1). The level at which these sites stabilized is consistent with the predicted cover from our previous data set (Fig. 2), indicating BSCs can re-establish in remnant vegetation without assistance, given sufficient time for recovery; however, repeat measures studies in heavily degraded sites are required to confirm that such sites can recover.

Our boosted regression model of BSC cover (Fig. 1) suggests that site condition at the time of livestock exclusion influences the trajectory of BSC recovery. Although

results based on landholder surveys must be viewed with some caution, due to potential errors in memory and judgement, the performance of starting condition in the model suggests it is important for BSC recovery and worthy of further investigation. BSC cover was lower in sites that had high bare-ground cover at the time of fencing relative to reference conditions (Fig. 1). High bare-ground cover at the time of fencing is assumed to be due to a high level of disturbance from livestock and related to a low BSC cover. No interaction between time since fencing and site condition at the time of fencing was detected. Notwithstanding the subjective and qualitative nature of our data on original site condition, these results suggests that BSC cover stabilizes in poor-condition sites over the same period as good-condition sites, although at a lower cover. Rehabilitation of BSCs in highly degraded sites may face more difficult barriers, such as propagule scarcity, resource limitation and soil erosion (Bowker 2007), whereas BSC rehabilitation in sites of moderate condition may only require sufficient time for passive recovery following livestock exclusion. Climate change may also play some role in the rate of recovery, yet this is difficult to ascertain; high quality, long time series rainfall data in the study region are scarce. However, wider analyses indicate that the autumn rainfall of southeast Australia has been declining since the 1950s (Cai & Cowan 2008) – roughly the period over which the sites here had livestock excluded.

Is fast recovery related to dominance of mosses?

While our estimate of 20 years for BSC recovery in the study region is faster than expected, and faster than many estimates of total BSC recovery rate (Eldridge 1998a; Belnap & Warren 2002; Lalley & Viles 2008), our finding agrees with published estimates of recovery rates for the moss component of BSCs. Moss cover re-establishment was estimated at 17 to 22 years for scalped BSC in the Western Negev Desert (Kidron et al. 2008), 14 to 18 years for livestock-trampled BSCs across deserts of northern Utah, United States (Anderson et al. 1982), and 15 to 20 years for southwestern deserts of the United States (Harper & Marble 1988). The similarity of these recovery rates is surprising as the study regions differ widely from each other in annual rainfall (95 to ~230 mm) and from our study region (390 mm annual rainfall). Moisture is frequently cited as a key factor limiting BSC recovery rates, with faster recovery at higher rainfall (Johansen et al. 1984, 1993; Belnap & Eldridge 2003; Kidron et al. 2008). Reasons for similar recovery rates across the cited studies, despite a large rainfall range, may reflect confounding effects of different disturbance histories, soil texture, temperature extremes or research methodologies. Alter-

natively, perhaps a focus on total BSC recovery rates in the literature has obscured detection of similarities between morphotype recovery rates across environmental and disturbance gradients.

Mosses are key primary colonizers of disturbed soils

A simple summary of mean cover of morphotypes (Fig. 3) gives some insight into succession and differential rates of recovery in our study region. Counter to literature on BSC succession from deserts across the world (Anderson et al. 1982; Johansen et al. 1984; Zaady et al. 2000; Li et al. 2002; Belnap & Eldridge 2003; Housman et al. 2006), mosses, not algae or cyanobacteria, were the dominant colonizers of disturbed soils in our study region. This is consistent with our expectations based on results from our previous study (Read et al. 2008), in which mosses were the only group observed in the most disturbed small remnants. Mosses comprised 97% of BSC cover in recently grazed sites (< 5 years) in the current study. Although dark soil discoloration from cyanobacteria was observed in long ungrazed sites in our study (~3% cover in sites grazed > 20 years ago), discoloration (dark or light) was negligible in recently grazed sites. All lichen groups were slow to recover from disturbance, with the highest cover of each lichen group observed in long ungrazed sites. We hypothesize that the relatively stable, fine textured soils of our study region create favourable conditions for primary colonization by moss. A more detailed study of soil cyanobacterial growth after soil disturbance (through actual measures of cyanobacteria or chlorophyll *a* pigmentation) is required to confirm this finding. Morphotype composition may also differ between seasons (Jimenez Aguilar et al. 2009), and comparison of composition between wet and dry periods is required to confirm overall moss dominance and low cyanobacterial cover. Further, an absence of leafy liverworts in this survey is probably due to lack of rain, as many leafy liverwort species in the region are ephemeral (Milne et al. 2006).

Although we cannot establish whether morphotype composition stabilizes with time in the current study (due to insufficient records for statistical modelling), we observe the composition of BSCs in long ungrazed sites is similar to the composition of minimally disturbed, environmentally equivalent sites from our previous study (Read et al. 2008).

BSCs respond to microenvironment

Our study highlights the need to stratify sampling of BSCs during surveys. The partial plot of BSC cover in different sampling locations showed a reduced cover of BSCs at the exposed canopy dripline compared to the interspace

(Fig. 1). We expect that this is due to higher litter loads near the canopy dripline limiting BSC growth (Read et al. 2008) in the drier, sun exposed microenvironment north of the canopy. The comparatively higher BSC cover to the south of the canopy dripline is likely due to increased moisture from canopy shade, which would be beneficial to the growth of mosses and enable them to survive higher litter loads.

Improved knowledge of BSC recovery will benefit restoration planning

The utility of fencing for conservation is equivocal in some ecosystems where livestock exclusion does not lead to improvements in conservation values such as native plant diversity and composition (e.g. Trémont 1994; Lunt et al. 2007). Our study shows clear benefits from fencing in the study region, with quantitative improvements in BSC cover after destocking degraded sites. BSC re-establishment will enhance the function of degraded remnants as they stabilize soils between plant canopies (Eldridge & Kinnel 1997; Bowker et al. 2008). Whether improvements in native plant species diversity and composition will follow is uncertain; however, some studies from other countries suggest that BSCs may facilitate recovery of native vegetation through increased surface roughness to trap seeds (Boudell et al. 2002) and enhance seed germination (Elmarsdottir et al. 2003; Su et al. 2009).

An estimate of the time frame and likelihood of passive BSC recovery will inform land managers and investors pursuing conservation objectives in their consideration of restoration options for BSCs. We show livestock exclusion through fencing is a successful long-term option for BSC restoration. The likelihood of successfully fast-tracking BSC recovery (reviewed in Bowker 2007) is currently unknown for southern Australia. Our results, if used in conjunction with future information on the likelihood of success for the different active restoration options and their associated economic costs, will enable land managers to make sensible decisions on the allocation of resources, similar to planning restoration options for trees on farms (Dorrough et al. 2008). Results from our study provide crucial information for such decision-making.

Conclusion

The results of our study should provide encouragement for landholders and agencies working to improve ecological function of degraded vegetation across dryland agricultural landscapes. Ecosystem function in degraded remnants can be improved in a relatively short time frame through passive recovery alone. Although recovery of BSC species diversity may take much longer than the return of total ground cover, the rehabilitation of BSC

cover provides benefits to the ecosystem regardless of species composition. Further work is necessary to understand the successional pathways of BSC recovery, particularly to confirm the negligible role of cyanobacteria in colonization (through actual measures of cyanobacteria or chlorophyll *a* pigmentation) and the influence of different disturbance levels on the trajectory of BSC recovery.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. We checked that the structured cross-validation had successfully fitted a model of the response that accounted for the majority of variation between sites by testing the relationship between site and the residuals

of the models using methods suggested by Wood (2006), section 6.5. This involved 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 as (ii) a linear null mixed model with site as a random effect but no fixed effects. An ANOVA comparing the two models showed that there were no site-based patterns in the residuals.

Appendix S2. To estimate potential BSC cover, we used a boosted regression tree model from our previous study (referred to as *previous model*), which identified eight covariates of BSC abundance (Read et al. 2008). We divided these covariates into variables reflecting the intensity of historic disturbance and variables that capture environmental variation between sites. Using our previous model, we held variables reflecting disturbance to values representing minimum impact, after examination

of partial plots from the previous model output. Variables representing minimal disturbance were: large remnant size, sampling location in the remnant centre, high perennial grass cover (%), low available P, high total soil C. Predictors representing environmental variation were held at the mean calculated for the current data set, and included tree cover (%), native litter cover (%) and remotely sensed thorium to potassium ratio (Th:K) as a surrogate of soil texture. Refer to Read et al. (2008) for further details and justification of these specifications.

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