Title

“Testing a model of biological soil crust succession”

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Date of manuscript: 27/10/2014

Manuscript word count:

6,445 abstract to end refs; 6,926 including all legends etc.

Number of pages: Article: 18; Supplementary material: 13

Abstract

Question: Biocrust composition is important for the diversity, structure and function of dryland ecosystems globally, but there is no universally applicable model of biocrust succession, and the models that do exist may not apply everywhere. We ask: 1) How do biocrust species vary in their response to time since livestock exclusion (Time) across environmental gradients? 2) Is there evidence for ruderal, mid- and late-successional responses to Time in biocrust species? 3) Can exploration of species attributes within response groups reveal potential mechanisms for biocrust succession? 4) Do our data support an existing standard conceptual model of biocrust succession described in the literature.

Location: Semi-arid woodlands of northwest Victoria, Australia.

Methods: We use data from a space-for-time study of biocrust composition following livestock exclusion and develop a hierarchical regression model of succession amongst a moss-dominated biocrust community.

Results: Time since livestock exclusion (Time) was the most important driver of biocrust community dynamics in our study region; species varied widely in their response to Time; and, succession within this moss-dominated biocrust community did not follow the general sequence predicted by the standard model of biocrust succession presented in the literature. We classified species by their successional response from model coefficients. All late-successional species were short-statured and closely-attached to the soil whereas nearly all tall-statured and loosely-attached species were classified as mid-successional.

Conclusions: This study demonstrates the utility of hierarchical models for investigating successional processes at the species and community level, for testing a standard conceptual model of succession and for suggesting hypotheses about underlying trait-based mechanisms. We propose an alternative model of biocrust succession that distinguishes between succession in favourable and unfavourable environments. We propose species response to Time is mediated by species structural density, which in turn relates to a suite of correlated traits including growth rate and longevity. This alternative conceptual model is useful for its generality.

Key words: Generalised linear mixed effects model; secondary succession; biological soil crust; moss; liverwort; lichen; cyanobacteria; life-form; traits

1 Introduction

2 Biological soil crust (biocrust) organisms are important colonisers of disturbed soils worldwide
3 (Belnap & Lange 2003). While they are subsequently replaced by vascular plants in mesic
4 environments, they remain a dominant component of the ground cover in environments where
5 soil depth or rainfall limits vascular plant growth (Bowker 2007). Succession amongst the
6 cyanobacteria, algae, bryophyte and lichen species of these permanent biocrusts has received
7 limited scientific attention, particularly studies at the species level and across environmental
8 gradients. This limits theoretic and mechanistic understanding of biocrust succession. These
9 scientific gaps are at odds with the recognised importance of biocrust composition for the
10 diversity, function, and conservation status of globally important drylands (Belnap & Lange
11 2003; Bowker et al. 2008). Here, we address knowledge gaps in biocrust ecology with a
12 hierarchical regression model of biocrust succession in a moss-dominated community.

13 Reviews of biocrust ecology present a standard (conceptual) model of primary and secondary
14 succession at the level of broad taxonomic groups (Eldridge & Greene 1994; Belnap & Eldridge
15 2003; summarised in Appendix S1). This is essentially a facilitation model of succession
16 (Connell & Slatyer 1977) in which colonising cyanobacteria and then cyanolichens (lichens with
17 a cyanobacterial symbiont) aggregate soil particles and fix atmospheric nitrogen, making soils
18 suitable for subsequent colonisation by early and late successional mosses and phycolichens
19 (lichens with an algal symbiont). It does not distinguish between primary and secondary
20 succession and assumes the described pattern of community development will overwhelm other
21 environmental effects and will be stable across environmental gradients. While this model has
22 been supported at broad taxonomic levels (e.g. Kidron et al. 2008; Langhans et al. 2009; Dojani
23 et al. 2011), most studies concern coarse-textured, sandy soils, where cyanobacteria naturally
24 dominate the biocrust. To our knowledge, there are no successional studies in relatively mesic
25 conditions and fine-textured soils where moss-dominated biocrusts occur. Whether the sequence
26 in the standard model holds across environmental gradients and regional species pools is largely
27 untested, particularly for moss-dominated biocrusts. Despite this uncertainty, studies of biocrust
28 ecology often classify biocrusts by ‘early-’ and ‘late-’ successional stages, based on dominance
29 by cyanobacteria versus mosses, respectively (e.g. Tighe et al. 2012; Lan et al. 2012). This
30 reliance on the standard model rather than independent observation risks confounding
31 ‘successional stage’ with the effect of environmental gradients. For instance, biocrusts tend to
32 shift from cyanobacteria- to moss-dominated communities along a gradient of increased moisture
33 (Su et al. 2009). No study to date has proposed mechanisms, such as the influence of species
34 attributes on occurrence, which would enable prediction of early- and late-successional moss and
35 lichen species.

36 We present a space-for-time study of biocrust succession following livestock exclusion, for
37 moss-dominated biocrusts in grassy woodlands of northwestern Victoria, Australia. This
38 vegetation occurs on ancestral floodplains with calcareous, clay-loam soils. Biocrusts are an
39 important component of ground cover in these woodlands with a mean 45% cover in minimally
40 disturbed sites, where tree cover is low and soils are relatively stable (Read et al. 2011). Previous
41 work in the region has shown trampling by sheep removes biocrusts from small remnant
42 vegetation patches used for livestock shelter (Read et al. 2008); and biocrusts take approximately
43 20 years following livestock exclusion to recover to cover levels observed in minimally
44 disturbed sites (Read et al. 2011).

Our study uses specialised regression models (hierarchical generalised linear models) to advance understanding of biocrust succession. Prior studies of biocrust succession (and studies of succession generally) have been impeded by available statistical methods. This is largely because it is difficult to generalise patterns of community change over time while accounting for individualistic responses of component species. Probabilistic models of vegetation succession model transitions between community states (e.g. Baasch et al. 2010) and enable prediction of vegetation change at the cost of explaining individualistic species responses. Multivariate methods such as ordination (e.g. Hooper et al. 2004) enable more detailed description of community patterns at the cost of prediction. Neither approach can reveal the role of scarce species in community dynamics – an important issue for biocrusts because data are time consuming to collect hence sample sizes can be low. Recent developments in hierarchical modelling (e.g. Ovaskainen & Soininen 2011; Pollock et al. 2012) present an exciting opportunity to develop predictive models of succession at the species and community level simultaneously, by combining individual species models of occurrence or abundance in a higher-level model of whole community response.

In the current study we identified *a priori* three potential succession response groups: (a) early colonisers and disturbance tolerant species (ruderals) that are replaced by later species and decline in abundance following livestock exclusion; (b) mid-successional species that increase and then decline in abundance, and (c) late-successional species that show a positive response to Time that may increase non-linearly. We used hierarchical models to explore whether examples of each were present in the biocrust community and to classify species accordingly. We compared modeled results with predictions of the standard model. Specifically we asked: 1) How do biocrust species vary in their response to Time, in the context of environmental variation? 2) Is there evidence for ruderal, mid- and late-successional responses to Time in biocrust species? 3) Can exploration of species attributes within response groups reveal potential mechanisms for biocrust succession? 4) Do our data support the standard model of biocrust succession (i.e. sequential colonisation by biocrust species in the following order: cyanobacteria < cyanolichens < early colonising mosses and lichens < late colonising mosses and lichens). 5) In addition, we ask, is this response to Time as important or more important to composition than environmental covariates?

Methods

Study region and site survey

Our study area was within the dryland agricultural region of northwest Victoria, Australia (36°06' – 36°30'S, 142°35'–142°52'E). Study sites were remnant grassy woodlands dominated by *Allocasuarina luehmannii* (Buloke) or eucalyptus species (either *Eucalyptus largiflorens* (Black Box) or multi-stemmed “mallee” *Eucalyptus* spp), distributed across a restricted rainfall gradient (370 to 410 mm mean annual rainfall) on calcareous, clay-loam soils. We surveyed 21 remnant patches (sites; <30 ha in size) where livestock had been excluded by fencing for a known time period (Time, between 1 and ~50 years). Prior to fencing, sheep had typically grazed the remnants for a few months every 1 to 3 years.

Data were originally collected for a space-for-time study of recovery in biocrust cover following livestock exclusion (Read et al. 2011). Three assumptions are important for valid use of this data

in the current study: 1) sites trace the same climatic history; 2) there is no relationship between time since livestock exclusion (Time) and degree of disturbance and; 3) the sampling chronosequence represented a convergent successional pathway rather than multiple successional pathways. Support for the validity of these assumptions is presented in Appendix S2.

Environmental and species survey

Sampling of environmental variables and biocrusts are briefly described here (see Appendix S3 for more detail). At each site we sampled two haphazardly selected locations and recorded dominant canopy trees, collected soil cores for soil analysis and visually estimated cover of vascular plants, bryophyte and lichen species and dark cyanobacterial crust within three 0.5 x 0.5 m (small) quadrats. Quadrat placement was stratified into open and shaded microsites. All bryophyte and lichen taxa were collected and identified to the lowest taxonomic level possible. For simplicity, taxonomic units will be referred to as species from here on. Soil texture data for each site was extracted from remotely sensed radiometric signals for thorium–potassium ratio (Th:K), which is an effective surrogate for soil texture (White et al. 2003) and a strong predictor of biocrust distribution in the study region (Read et al. 2008).

Fifty-five species were recorded. The moss *Triquetrella papillata* was the most frequently recorded species (44 data cases) and had the highest mean abundance across sites (21%). Nine species were recorded in only one site. All but one common species was detected in recently disturbed sites (fenced < 5 years previous to the study).

Statistical analysis

Data preparation

Our data were structured (nested) and we simplified this by averaging (pooling) data from the duplicated small quadrats. This gave a total of 61 pooled quadrats nested in 21 sites with 3 microenvironments in each site. The remaining data structure (quadrats at microenvironments within sites) was addressed in the hierarchical model (see below).

Species abundance data (P_{ij}), where abundance is the proportional cover of species i in quadrat j , was logit transformed to Y_{ij} (with the equation $\text{logit}((P_{ij} * .998) + .001)$) to ensure normality (Warton & Hui 2011). Time and environmental variables were centred and scaled by subtracting their means and dividing by twice the standard deviation to ensure comparability of model coefficients (Gelman & Hill 2007).

Hierarchical linear models of species abundance

We fitted a hierarchical, multi-species model of abundance (Pollock et al. 2012) as a function of time since livestock exclusion (Time) and environmental variables. This was a generalised linear mixed effects model (GLMM) where intercept and slopes were allowed to vary by species and intercept was also allowed to vary by site (Gelman & Hill 2007). We included site as a random effect and microsite as a covariate in the model to reflect data structure (quadrats nested within sites). The model structure is described in detail in Appendix S4.

We selected candidate variables to include in our final model from the complete list of environmental variables in Read et al. (2011). These include relevant measures of vegetation and soil conditions, described in Appendix S3. We only included variables that were not highly

correlated (Pearson's $r < 0.25$). We assumed linear responses for all environmental variables because the environmental gradients were quite short. We included linear and quadratic terms for Time because we expected non-linearity in species response to Time. Previous work with these data showed total biocrust cover plateaued at 20 years, so it is likely the abundance of some species may plateau within the timeframe of this study, resulting in a non-linear response. Also, species interactions such as competition and replacement may result in non-linear responses to Time.

We then compared a suite of candidate models comprising the covariates Time, Time² plus combinations of the eight soil and vegetation variables (Appendix S5), using a step-wise forward selection procedure and identifying the best (final) model with Akaike's information criterion (AIC, Jamil et al. 2012). We allowed a maximum of five covariates because larger models often failed to converge. The size of our dataset precluded us from fitting interactions, so we only included the main effects of environmental variables in our model. All analysis was done using the package lme4 (version 0.999999-2) in R (R Development Core Team 2012). Details of candidate models and model code are provided in Appendices S5 – S6.

Evidence of successional response groups

We described *a priori* three potential species responses to Time that could be identified mathematically and visually from model results. We suggest ruderal species will show a decline in abundance following livestock exclusion and will be evidenced in model coefficients by a negative or weak response to Time that is likely to plateau with time but could be linear:

$$\text{Ruderal abundance: } \beta_1 < 0 \text{ or } \beta_1 \sim 0, \beta_2 \geq 0$$

where β_1 is the coefficient for the linear, and β_2 for the quadratic, term.

Mid-successional species will show an early increase to a maximum abundance that subsequently either plateaus or declines in abundance. This will be evidenced in model coefficients by a unimodal or plateaued response (i.e. a negative non-linearity):

$$\text{Mid-successional species abundance } \beta_1 \geq 0, \beta_2 < 0$$

Late-successional species will have model coefficients with a positive response to Time that is positively non-linear:

$$\text{Late-successional species abundance } \beta_1 > 0, \beta_2 \geq 0$$

Species with at least 3 observations, were classified into one of these three successional response classes following mathematical and visual evaluation of model results, based on these *a priori* predictions and a bivariate plot of species coefficients for Time vs Time². We present three species of each response type for illustration.

Results

Community and species' response to time

Hierarchical modelling showed time since livestock exclusion (Time) was a strong covariate of biocrust species abundance across all species (Fig. 1; species and model coefficients appear in

Appendix S7). Five terms were included in the final model: Time, Time², open microsites (Microsite), Buloke woodlands (Buloke) and soil Thorium:Potassium ratio (Th:K). Coefficients for these fixed effects summarise patterns for the entire community (Ovaskainen & Soininen 2011) by describing response of the average species. Since covariates were centred and scaled, model coefficients are comparable, and correlations between coefficients are meaningful (correlations between coefficients appear in Appendix S8). Coefficients for the random effects (i.e. species) summarise responses of individual species to covariates and how they differ from species mean response.

Time had the largest average effect of all covariates ($\beta_1 = 0.25$, se = 0.12, Appendix S7). On average, species showed a gradual increase in abundance with Time, but their responses varied widely, with a standard deviation of 0.44 across all species responses (Appendix S7). Responses ranged from slightly negative for the tall moss *Pseudocrossidium crinitum* ($\beta_1 = -0.23$) to steeply positive for the mat forming moss *Triquetrella papillata* ($\beta_1 = 2.38$). While the average effect of the quadratic term Time² was small and highly uncertain ($\beta_2 = -0.07$, se = 0.17), species varied widely (Time², sd = 0.60), ranging from a relatively rapid increase followed by a decline in abundance for *T. papillata* ($\beta_2 = -2.99$) to an escalating rate of increase for the short moss *Gemmabryum pachytheca* ($\beta_2 = 0.86$). Variation in species' linear and non-linear responses to Time is illustrated in Fig 2.

Species varied most in their responses to Time and Time² (sd=0.66 and 0.4 respectively) and then less for environmental covariates, the greatest of which was Buloke (sd=0.32, Appendix S8).

Since *Triquetrella papillata* was clearly the dominant species, we re-ran the model without it to test whether it alone was responsible for the patterns detected by our model. Although the strength of mean species responses to Time and environmental covariates was weaker without *T. papillata*, results were consistent (Appendix S9).

Evidence for three successional responses

Most species could be classified into one of three successional response classes (Appendix S7) based on mathematical and visual assessment of model results. Species with low frequency (< 4) could not be classified due to negligible responses detected. Biocrust species showed a continuum of successional responses, from ruderal to mid- and late-successional, as illustrated in the plot of coefficients for Time and Time² (Fig. 2). We present examples of ruderal species (Fig. 3. a-c), mid-successional species with a modal response (Fig. 3 d-f) and late-successional, steady increaser species that show no clear plateau in abundance (Fig. 3 g-i).

Species attributes and successional response

All species classified as late successional were short statured species, closely attached to the soil, including: gel-lichens, crustose lichens, squamulose lichens, short mosses and thallose liverworts (Appendix S7). Dark cyanobacterial and algal crusts embedded in the soil, were also classified as late successional. Nearly all open structured and tall statured species were classified as mid successional (i.e. foliose and fruticose lichens, tall moss, leafy-like liverworts), with the exception of two tall mosses, which were classified as ruderal. Also, all three species with loose

attachment to the soil were classified as mid successional. Only four species were classified as ruderal and these were all mosses, two tall (> 15 mm) and two short (<15 mm) statured species.

Interactions between species successional response and environmental variables were also indicated with all late successional species having a negative association with buloke woodlands and a positive association with open microsites.

Comparison with the standard model of biocrust succession

The standard model predicts a facilitative successional sequence of cyanobacteria and cyanolichens followed by colonisation of later successional bryophytes and lichens. Our results suggest otherwise for those cyanobacterial crusts we measured (dark ones) and cyanolichens. While total abundance of mature cyanobacterial crusts (Black crust) showed a positive response to Time, the response was no faster than a number of moss species (e.g. *Didymodon torquatus* and *Syntrichia antarctica*) and there was no evidence of subsequent decline in abundance due to replacement by other species ($\beta_1 = 0.95$, $\beta_2 = 0.26$, illustrated in Appendix S10a). Similarly, the cyanolichen *Collema coccophorum*, showed no evidence of early development but instead showed a slow, positive response to time ($\beta_1 = 0.27$, $\beta_2 = 0.54$, illustrated in Appendix S10b). Results for the only other recorded cyanolichen *Lemphollemma chalazanum*, showed a similar pattern ($\beta_1 = 0.23$, $\beta_2 = 0.26$).

Testing independence of response to time and environment

Species' responses to Time were correlated with their environmental responses (Table 2). For instance, response to Time was positively correlated with response to open microsites ($R = 0.60$) and with response to Th:K ($R = 0.81$), so species more associated with open microsites and/or coarse textured soils (i.e. soils with a high Th:K) were more likely to increase rapidly after grazing exclusion. Also, response to time was greater for abundant species than species in low abundance, with a high correlation between species intercept and time ($R = 0.82$).

Discussion

Our hierarchical model of biocrust succession provides an efficient summary of the wide variety of species responses to time since livestock exclusion and represents a significant advance in understanding of biocrust community dynamics. This is the first attempt, to our knowledge, to estimate successional trends for a whole biocrust community, from individual species to the community level, including rare species; the first test of the standard model of biocrust succession in a community not dominated by cyanobacteria; the first data-driven exploration of bryophyte and lichen attributes that may explain successional response, and, the inaugural use of hierarchical models to elucidate successional patterns. We relate our findings to current understanding of biocrust succession and general succession theory and propose a modification of the standard model of biocrust succession.

Temporal patterns at the community level

The relative strength of species response to Time (Appendix S7) shows disturbance and recovery are fundamental drivers of biocrust composition in our study region, where soil disturbance by livestock is common (Duncan & Dorrough 2009). Although environmental covariates were

selected from a suite of variables known to be related to total biocrust abundance in the region (Read et al. 2008; 2011), species responses to these covariates were comparatively weak. The strong response of biocrust species to Time is unsurprising, because we sampled within vegetation communities where biocrusts were known to exist and we sampled within a regenerative phase of succession: species must respond to Time as they colonise and grow across previously-disturbed bare ground. While total biocrust cover plateaus in the region within ~20 years (Read et al. 2011), biocrust composition continued to change over the timeframe of this study (~50 years) and did not appear to stabilise. This was evidenced by the continuum of species responses to Time (Fig. 2) and the absence of a plateau in any species response. Unfortunately we could not ascertain whether the successional trajectory of our study sites approached composition of undisturbed biocrusts, because undisturbed remnants were not found in the region, which has a long history of land clearance, agriculture and livestock grazing (Duncan & Dorrough 2009).

Our data suggest all common species (frequency > 5%) were present in recently fenced sites (i.e. livestock excluded for < 5 years), so were likely already present at sites as propagules when livestock were excluded. This result concurs with Walker and Chapin (1987) who proposed buried seed and spores would be more important in secondary succession than colonisation by dispersing seeds and spores.

Mechanisms of biocrust succession

The wide variation in species response to Time likely reflects variation in species relative growth rate, longevity and dispersal mechanism. These are important mechanisms driving secondary succession of vascular plant communities in favourable environments (Noble & Slatyer 1980) and we assume the same is true for biocrust communities.

Here we probe results from our hierarchical model to investigate mechanisms underlying moss and lichen species response to Time, and propose functional traits (*sensu* Violle et al. 2007) to explain the observed alignment of species successional response (classified from model results) with morphological attributes (Appendix S7). Specifically we develop a hypothesis that explains why tall, open structured and loosely attached species (i.e. tall mosses, leafy-like liverworts, foliose and fruticose lichens) were generally classified as mid-successional, whereas short statured, closely attached species (i.e. crustose and squamulose lichens, thallose liverworts and short mosses) were generally classified as late-successional. We note that identification of response groups does not mean species are necessarily early- or late-successional.

Life-form attributes such as height, degree of attachment to soil and structural openness may indicate a functional trait we call species 'structural density' which explains responses of complex, 3-dimensional biocrust species that grow exposed above the soil surface. The concept does not necessarily apply to cyanobacteria and algae, which are simplified, microscopic organisms generally embedded within the soil matrix.

We think moss and lichen species structural density represents a fundamental trade-off between relative growth rate (RGR) and longevity, similar to the leaf economic spectrum widely recognised for vascular plants (Wright et al. 2004). We propose that structural density relates to species 'surface area per unit volume' (SAV) and its analogue 'dry matter content per unit volume' (DMV). Structural density is likely to be particularly important for poikilohydric

organisms such as lichens and bryophytes, which are highly dependent on external, transient water supply and where the clonal or colonial life form rather than the individual forms the ecological unit (Bates 1998). We suggest low density species have an increased surface area per unit volume, and a reduced mass invested in photosynthetic structures per unit volume and this relates to a suite of correlated physiological processes, including: increased light interception (particularly under high solar radiation), increased rates of water absorption per unit mass, increased photosynthetic assimilation rates and a corresponding faster RGR when wet, increased evaporation rate and reduced wetness duration and reduced structural strength and longevity of photosynthetic structures.

These proposed relationships between life form, structural density, growth rate and longevity have not previously been formalised in terms of a measurable, continuous functional trait. While actual measurement of species traits such as SAV and DMV needs to be explored, colony life form has long been recognised as important for cryptogam response to environmental gradients because of its influence on water absorption, delay of desiccation and light interception (Rogers 1992; Glime 2013). Previous studies have observed slower growth rates for cryptogam life forms that are low statured, dense and closely attached to the soil, such as the slower growth of crustose compared to foliose lichens (Hayward, Bruce & Grace 1982; Giordani et al. 2014). Also, trade-offs between light capture and water retention have been identified for dense compared to loose turf mosses (Elumeeva et al. 2011). While life form is a coarse measure of structural density, overall we think it reasonable to conclude that species life form aligns with species successional response in this study because it captures what is likely a fundamental ecological trade-off.

We suggest dispersal strategies and niche preferences are the mechanisms underlying the ruderal response observed in our study. Dispersal by vegetative propagules and buried spores are important mechanisms for early stages of secondary succession for vascular plants (Walker & Chapin 1987) and we assume the same is true for cryptogams. Four species were classified as ruderal with a low abundance at the time of livestock exclusion and a weak, negative response to Time (Appendix S7). Two ruderal species were short, hardy mosses common to disturbed habitats with a capacity to propagate rapidly from vegetative propagules and stems (i.e. *Bryum argenteum* and *Gemmabryum pachytheca*, Spence & Ramsay 2006). The other two ruderal species were tall mosses commonly found under shrubs in arid environments (i.e. *Pseudocrossidium crinitum* and *Rosulabryum campylothecium*, Eldridge & Tozer 1997). Perhaps they survived in unfenced sites because they tolerate shady microsites under trees and shrubs where they avoid livestock trampling

The observed declines in abundance of all ruderal species in early stages of succession are likely due to species competition for space and light (Nobel and Slatyer, 1980) and resources such as soil nutrients (Tilman 1985). The decline in abundance of taller mid-successional species (i.e. unimodal distributions, illustrated in Fig. 3) and their apparent replacement by shorter late-successional species is interesting. We suggest late-successional species have a greater structural density and eventually outcompete low density species, both because of their greater structural strength and survival, and because of shifts in the physical properties of the biocrust over Time. As biocrusts develop, discrete patches of colonising species grow laterally and coalesce to form a continuous homogenous carpet (Cutler et al. 2008). Continuous carpets have greater biomass and enhanced wetness duration compared to scattered patches (Kidron et al. 2010) due to mulching properties of the biocrust, enhanced water conduction from the soil by dense and low growing

1 taxa and reduced evaporation due to boundary layer effects. We think low growing and dense
2 species that form continuous carpets will have extended opportunities for photosynthate
3 assimilation and growth and will eventually outcompete tall and open structured species despite
4 their short stature and slower growth rates. This is because species are more loosely attached to
5 the soil have a reduced capacity to conduct soil water and also dry more quickly.

6 Overall, our hierarchical model combined with species morphological attributes and successional
7 response class provides an exciting opportunity to explore successional patterns and develop
8 testable hypotheses, opening the way to a deeper, mechanistic understanding of biocrust
9 succession, beyond the process of facilitation.

10 ***Towards a generalised model of biocrust succession***

11 Our study suggests biocrusts do not always follow the sequence defined in the standard model of
12 succession, where colonising cyanobacteria (and then cyanolichens) stabilise soils, fix nitrogen
13 and facilitate successive waves of colonisation by bryophyte and lichen species. Instead, mature
14 (black) cyanobacteria crusts and cyanolichens appear to develop slowly in our study region,
15 compared to many moss species (Appendix S10).

16 We hypothesise that while facilitation by cyanobacteria and cyanolichens may indeed be an
17 important mechanism for biocrust succession in severe environments, such as hyper-arid deserts,
18 and mobile, coarse-textured soils (e.g. Zaady et al. 2007), facilitation may not be important in
19 relatively favourable conditions, such as in our study region (with rainfall of ~ 390 mm per
20 annum and fine-textured, moisture-retentive soils). This hypothesis agrees with successional
21 theory developed for vascular plant communities by Walker and Chapin (1987). They argued
22 facilitation is likely to explain succession in severe environments, whereas maximum growth rate
23 and competitive ability would be the important mechanisms of succession in favourable
24 environments. Findings by Lukešová and Komárek (1987) also support our hypothesis, because
25 moss protonema were observed with cyanobacteria in the earliest stage of primary succession in
26 a favourable environment (rainfall 500 - 650 mm and clay rich soils); hence preliminary
27 colonisation and facilitation by cyanobacteria was not essential. Our findings would be
28 strengthened from more rigorous assessment of cyanobacterial abundance during succession,
29 such as with chlorophyll α techniques (Belnap et al. 2008), particularly to determine the extent
30 and potential role of cryptic, light-cyanobacterial species.

31 We suggest the concept of biocrust succession be expanded to consider alternative pathways for
32 primary and secondary succession across environmental gradients, particularly to consider
33 differences in environmental conditions and morphological attributes of species. These different
34 environmental conditions include: unfavourable conditions - xeric with unstable soils;
35 intermediate conditions - either mesic with unstable soils or xeric with stable soils; and,
36 favourable environments - both mesic and stable soils. We suggest the standard model applies to
37 unfavourable or intermediate conditions with unstable soils, where colonisation and stabilisation
38 of soils by cyanobacteria and algae are a pre-requisite to later establishment by mosses and
39 lichens. We propose an alternative model of biocrust succession (Fig. 4) in favourable
40 environments that omits the first stage of soil stabilisation and facilitation by early colonising
41 cyanobacteria and cyanolichens and where SD is important for understanding the range of
42 responses of above-ground biota. Following the reasoning of Walker and Chapin (1987), we
43 suggest competition and relative growth rate will be important in favourable environments,

1 whereas facilitation will be more important in unfavourable environments. We also suggest
2 species successional response may be mediated by species structural density, which may
3 represent a suit of correlated traits.

4 ***Thoughts on the use of hierarchical models for studying vegetation succession***

5 Our hierarchical model of biocrust succession efficiently summarised patterns at the species- and
6 community-level from this sparse dataset. Our study represents the first time to our knowledge
7 that hierarchical models have been used to elucidate successional patterns and demonstrates the
8 value of this method for predicting species- and community-level patterns simultaneously from
9 field data. Classifying species successional responses mathematically and visually from model
10 results and combining this with knowledge of species attributes can help reveal processes
11 underlying patterns in community dynamics and reveal potential functional response traits.

12 Hierarchical models present a powerful tool to explore drivers of community succession with
13 multispecies datasets because they efficiently extract a detailed picture of all species responses to
14 covariates. Hierarchical models of succession are an improvement on alternative statistical
15 techniques such as multivariate ordination because they are model-based, opening the way to
16 prediction (Ovaskainen & Soininen 2011; Jamil et al. 2012). Further, hierarchical models address
17 a major issue for researchers exploring covariates of community structure where data include
18 many species for which there are few records because species with few records can still be
19 modeled by borrowing strength from common species.

20 **Acknowledgements**

21 We thank W. Morris for help developing model code; D. Meagher, A. Downing and J. Elix for
22 help with species identifications; B. Weber and M. Bowker whose comments considerably
23 improved this manuscript; C. Moxham, M. White and personnel from Greening Australia, DPI
24 and the North Central CMA for assistance with site selection; F. Pereoglou for field assistance;
25 landholders and Parks Victoria for access to properties; and, Birchip Cropping Group for
26 assistance with landholder engagement. This project was supported by the Holsworth Wildlife
27 Research Fund, North Central and Mallee CMAs through NHT and the National Action Plan for
28 Salinity and Water Quality, and the Victorian State Government initiative ‘Our Rural
29 Landscapes’. JE was supported by ARC grant FT0991640 and the Centre of Excellence for
30 Biosecurity Risk Analysis, and PV by the ARC Centre of Excellence in Environmental Decisions
31 and National Environmental Research Program-Environmental Decisions.

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23 **Supporting information (online):**

- 24 Appendix S1. Standard (conceptual) model of biocrust succession.
- 25 Appendix S2. Support for valid use of space-for-time data
- 26 Appendix S3. Sampling methods
- 27 Appendix S4. Model description
- 28 Appendix S5. Candidate models and AIC scores
- 29 Appendix S6. Supplementary code
- 30 Appendix S7. Species attributes and parameter estimates for the effect of Time, Time²,
31 open microsite, Buloke woodland and soil Th:K ratio, on the logit of proportion
32 cover of individual and average species.
- 33 Appendix S8. Standard deviations and correlations for hierarchical model coefficients
34 from a generalised linear mixed-model (GLMM)
- 35 Appendix S9. Variation in species successional responses, omitting dominant species *T.*
36 *papillata*.
- 37 Appendix S10. Predicted response of black cyanobacterial crust and the cyanolichen
38 *Collema coccophorum* to time since livestock exclusion

Fig. 1. Mean species response (species coefficients) to Time, Time² and environmental covariates (Microsite open, Buloke and Th:K) from a generalised linear mixed-model (GLMM); where covariates have been centred and scaled. Species are ordered by decreasing frequency across study sites (top to bottom). Error bars are 95% confidence intervals.

1 **Fig. 2** Variation in species successional responses. Covariance plots of species coefficients
2 (centred and scaled) for Time and Time². Species in top-left corner are *ruderals* (R), bottom-right
3 corner are *mid-successional* (M) and top-right corner are *late-successional* (L).

Fig. 3. Partial plots of species response (cover %) to Time (years) plus the quadratic predictor (Time^2), in a generalised linear mixed-model. Environmental predictors are held at their mean. Species plots illustrate three ruderal species (Figs a) *Pseudocrossidium crinitum*, b) *Bryum argenteum*, c) *Rosulabryum campylothecium*), three mid-successional species with unimodal responses (Figs d) *Triquetrella papillata*, e) *Syntrichia antarctica* f) *Xanthomparmelia reptans*) and three late successional species (Figs g) *Didymodon torquatus* h) *Tortula atrovirens* i) *Riccia limbata*). Note the y-axis is scaled to a maximum of one for all species except *Triquetrella papillata* (Fig. 3d) and *Didymodon torquatus* (Fig. 3g), which occur at higher abundance across the region. Dashed lines show 95% confidence intervals.

Fig. 4.

General model of secondary biocrust succession for a) unfavourable and b) favourable environments, where soil stabilisation, growth rate and dispersal are important mechanisms. Three successional response groups for the above-ground component are identified: ruderal species (disturbance avoiders or capable of rapid, vegetative reproduction); mid-successional species with low structural density (SD), fast relative growth rates and short lived photosynthetic structures; and, above-ground late-successional species with a high SD, slow relative growth rates and long-lived photosynthetic structures. Successional stages are early colonisation and regeneration (C), mid-successional (M) and late-successional (L). Arrows indicate physical removal of biocrusts and dashed-lines indicate response range for mid-successional species. The schematic at top illustrates below-ground taxa (i.e. cyanobacteria and algae) establish during the C and M phases in unfavourable environments and facilitate subsequent establishment of above-ground biota. In favourable environments low SD bryophyte and lichen species can establish during the C and M successional phases. This model does not address intermediate environments (see main text for details).