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The influence of climatic legacies on the distribution of dryland biocrust communities

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Abstract

Predicting the distribution of biocrust species, mosses, lichens and liverworts associated with surface soils is difficult, but climatic legacies (changes in climate over the last 20 k years) can improve our prediction of the distribution of biocrust species. To provide empirical support for this hypothesis, we used a combination of network analyses and structural equation modelling to identify the role of climatic legacies in predicting the distribution of ecological clusters formed by species of mosses, lichens and liverworts using data from 282 large sites distributed across 0.6 million km^2 of eastern Australia. Two ecological clusters contained 87% of the 120 moss, lichen and liverwort species. Both clusters contained lichen, moss and liverwort species, but were dominated by different families. Sites where the air temperature increased the most over 20k years (positive temperature legacies) were associated with reductions in the relative abundance of species from the lichen (Peltulaceae and Teloschistaceae) and moss (Bryaceae) families (Cluster A species), greater groundstorey plant cover and lower soil pH. Sites where precipitation has increased over the past 20k years (positive precipitation legacy) were associated with increases in the relative abundance of lichen (Cladoniaceae, Lecideaceae and Thelotremataceae) and moss (Pottiaceae) families (Cluster B species) and lower levels of soil pH. Sites where temperatures have increased the most in the past 20k years suppressed the negative effects of plant cover on Cluster B by reducing plant cover. Increased intensity of grazing suppressed the negative effect of soil pH and the positive effect of soil carbon, on the relative abundance of Cluster B taxa. Finally, increasing temperature and precipitation legacies reduced the negative effect of soil pH on Cluster B. Understanding of the importance of climatic legacies improves our ability to predict how biocrust assemblies might respond to ongoing global environmental change associated with increasing land use intensification, increasing temperature and reduced rainfall.

KEYWORDS
bryophyte, drylands, ecological clusters, lichen, liverwort, soil crust

1 | INTRODUCTION

Biocrusts are complex assemblages of lichens, bryophytes (mosses and liverworts), cyanobacteria, fungi and microscopic organisms such as archae and bacteria that occupy the top few centimetres of soil across a myriad of arctic, arid and temperate ecosystems (Weber, Büdel, & Belnap, 2016). Because of their intimate connection with

surface soils, biocrusts play critical roles in soil nutrient cycling and sequestration, soil hydrology, seedling establishment, surface temperature regulation and provide habitat for soil micro-organisms (Delgado-Baquerizo et al., 2016; Weber et al., 2016). Globally, biocrusts play substantial roles in the carbon and nitrogen cycles (Weber et al., 2015). However, despite their huge importance in drylands, where they are often the dominant form of land cover, there have been few fruitful attempts to predict their distribution across large spatial scales (but see a recent global modelling study by Rodriguez-Caballero et al., 2018). Rather, most studies have tended to focus on specific study areas at the local scale (e.g., Eldridge, 1996, Weber et al., 2008; Rodriguez-Caballero, Escribano, & Canton, 2014; Chamizo et al., 2012; Garcia-Pichel, Loza, Marusenko, Mateo, & Potrafka, 2013).

Predicting the distribution of biocrusts is not an easy task. Although the current distribution of these organisms is thought to be related to climatic, edaphic, topographic and biotic factors (Bowker et al., 2016), many areas that would be expected to support particular crust species are often devoid of crusts and vice versa. Overall, therefore, we know relatively little about what determines the distribution of soil crusts at broad regional scales (Steven, Gallegos-Graves, Belnap, & Kuske, 2013). Part of the reason could be that large areas of biocrust worldwide have been heavily modified by land use practices such as overgrazing (Chiquoine, Abella, & Bowker, 2016), and these effects may persist for many years. Surfaces disturbed during nuclear testing in arid Australia in the late 1950 s had still not recovered their full complement of species, particularly foliose lichens, after more than 40 years (Eldridge & Ferris, 1999). Similar scenarios exist for other areas where biocrusts have been disturbed (Kuske, Yeager, Johnson, Ticknor, & Belnap, 2012), reinforcing the notion that it is extremely difficult to accurately predict the current distribution of biocrusts. Given that biocrust community composition is strongly driven by climate (e.g., Rogers, 1971; Reed et al., 2012; Kuske et al., 2012; Lafuente, Berdugo, Ladrón de Guevara, Gozalo, & Maestre, 2017) and that biocrusts are often considered slow-growing communities (decades to centuries), climatic legacies (changes in precipitation and temperature over the last 20k years) might have also played a key role in shaping their current distribution. Recent studies across a range of environments have shown that paleo-legacies are important for predicting the effects of climate on microbial and plant communities (Delgado-Baquerizo et al., 2017; Pärtel, Chiarucci, Chytrý, & Pillar, 2017). Similarly, Lopez-Merino et al. (2017) showed that paleoclimatic erosion events caused by flooding have had substantial effects on the current growth of aquatic communities of *Posodonia*. However, an integrated approach considering past climatic legacies for predicting the contemporary distribution of biocrust communities is lacking and requires knowledge of both current and past climatic condition as well as multiple environmental attributes. An understanding of how biocrusts and their associated taxa are distributed in drylands is a critically important research question that can help us to manage potential change resulting from human-induced land use and climate-related changes. Particularly lacking is an understanding of what historical conditions drive the distribution of biocrust communities; specifically those from previous climates. Information on climatic legacies could therefore provide a useful way to improve our capacity to predict the distribution of ecological assemblies of biocrusts across southern Australia, but potentially other areas.

The contemporary distribution of bryophytes and lichens in soil crusts indicates that they are closely tied to climate, particularly rainfall and temperature. For example, in eastern Australia, the distribution of lichens is strongly driven by temperature and summer rainfall, with biocrust lichens and bryophytes largely restricted to areas of winter rainfall (Eldridge, 1996; Eldridge & Tozer, 1996). Therefore, changes in precipitation and temperature over the last 20k years might help explain the current distribution of mosses and lichen species today. While we have a relatively good knowledge of the current status of biocrusts over many areas (Weber et al., 2016), we still lack a clear understanding of how they might have changed in response to altered climatic conditions over the past 20k years and whether these changes have imposed a legacy effect on the distribution of crusts that we see today. A knowledge of how climatic legacies might have affected, and continue to affect, biocrust distribution is critical if we are to be able to separate changes resulting from human-induced impacts from those that represent a legacy effect of former climates. By climate legacy, we mean the difference between climatic conditions 20k years ago and current conditions. For example, a location would have a "positive temperature legacy" if the temperature at that site is currently greater than it was 20k years ago. A knowledge of climate legacies could help to explain why two locations with a similar current climate do not always support the same community assembly. Predicting how the distribution of biocrusts might have changed and the likelihood of recovery under current climates is critically important to allow us to allocate scarce financial and intellectual resources to those areas most at risk of degradation and to prioritize restoration efforts with limited finances. This could include activities such as inoculation, which is designed to promote biocrust establishment and associated ecosystem services.

Here, we used network analyses and a regional survey including data on the distribution of biocrust lichen and bryophyte species across 0.6 million km^2 of eastern Australia to test the hypothesis that climatic legacies (changes in temperature and rainfall conditions experienced about 20k years ago) can help explain the current distribution ecological clusters formed by biocrust species strongly co-occurring and which might share environmental preferences. For instance, certain species of mosses (e.g., *Fissidens* spp.) and lichens (e.g., *Xanthoparmelia* spp.) are known to prefer more mesic conditions. Our focus here was on biocrust taxa, though vascular plant clusters are also likely to respond to climatic legacies.

2 | MATERIALS AND METHODS

2.1 | The study area

The survey was conducted over an area of about 0.6 million km^2 in New South Wales, Australia and bounded by the Queensland Border

in the north (−29.00°), the South Australian border in the west (141.00°), in the south by the Murray River, and in the east by longitude 147.50°. Annual rainfall across the survey area ranged from ~400 mm in the north-east to ~150 mm in the north-west (Figure 1) and is spatially and temporally variable. Seasonal distribution of rainfall was mainly summer dominant in the north-east to predominantly winter dominant (~30% more rainfall during the winter months) in the south-west. Diurnal temperatures are typically hot in summer (>40°C) and mild in winter (>10°C), and evaporation increases from south to north and from east to west (Bureau of Meteorology, 2015).

Most of the survey area lies within the Murray-Darling Basin, a depositional landscape overlain by a mosaic of Quaternary aeolian sediments, most of which is characterized by high pH soils. These depositional landscapes ranged from level to slightly undulating plains of Quaternary aeolian sediments and colluvial materials (Pickard & Norris, 1994) to footslopes and ranges. Linear and sub-parabolic dunes are superimposed upon broad sand sheets across the plains. Plains of Quaternary alluvium are found on the Riverine Plain in the south-east and along the floodplains of the major rivers, particularly the Darling, Murrumbidgee and Murray Rivers which drain extensive areas of the survey area. Soils across the survey area range from calcareous to neutral earths on the plains to shallow siliceous sands on the ranges to deep sands on the dunes. A more detailed description of the soils and landscapes is given in Keith (2017).

Vegetation across the survey area was highly variable but could broadly be described as semi-arid woodlands dominated by eucalypts (e.g., *Eucalyptus populnea and Eucalyptus intertexta*), white cypress pine (*Callitris glaucophylla*) or mulga (*Acacia aneura*), with a grassy (*Austrostipa* spp. and *Austrodanthonia* spp.) or shrubby (*Dodonaea*, *Eremophila* and *Senna* spp.) understorey. Plains of quaternary alluvium are dominated by shrubs of the family Chenopodiaceae (*Atriplex*, *Maireana*, Eldridge, Travers, Facelli, Facelli, & Keith, 2017), and sandplains and dunefields by assorted eucalypts (Keith, 2017). The predominant land use over much of the area is livestock grazing on native pastures, with smaller areas used for conservation (national parks) and forestry. Small areas of opportunistic cropping occur along the eastern margins and in the south-west.

2.2 | Field methods

We traversed the survey area using roads and major tracks to form a regular grid of sites, at distances of 10–30 km, in order to provide a comprehensive survey of the area. We sampled a total of 282 sites, chosen randomly based on maps of the study area (Figure 1). Areas of particular interest (e.g., long-term grazing exclosures, railway corridors, regeneration sites and national parks) were also included. At each site we used a random process to select an area of 100 m by 30 m along which we centrally located a 100 m transect. The transect was placed at least 100 m from any tracks in order to avoid possible disturbances. If a randomly chosen site was too disturbed (e.g., a dump site), we selected the next site along the road at a predetermined distance from the original site. Along each transect, we placed ten, evenly spaced 0.5 m^2 quadrats, which were used to collect data on biocrust composition, groundstorey plant cover and soils.

Within each quadrat, we assessed the total cover (%) of biocrusts and the relative contribution of three main types lichens, bryophytes and cyanobacteria (Figure 1). Only cyanobacteria that were visible on the surface were assessed. We then collected samples of all different visible types of soil crusts from each quadrat to obtain

FIGURE 1 Distribution of the 282 sampling sites in eastern Australia (inset Australia) and some typical soil crust taxa. (a) *Xanthoparmelia semiviridis* (foliose lichen, Cluster A), (b) scanning electron microscopy image of cyanobacterial filaments (cyanobacterium, Cluster E), (c) *Didymodon torquatus* (moss, Cluster B), (d) *Asterella drummondii* (thallose liverwort, Cluster B). Photographs: D. J. Eldridge

10 bags of composite crust samples. Sufficient samples were collected to provide voucher specimens for lodgement in herbaria. The community composition of biocrust species was identified using keys in Filson (1988, 1992), Filson and Rogers (1979), McCarthy (1991), Scott (1985) and Scott and Stone (1976), as well as more recent generic revisions. Nomenclature followed Buck and Vitt (2006) for mosses, McCarthy (2006) for liverworts, McCarthy (2015) for lichens, and where appropriate, more recent taxonomic revisions, as well as more recent generic revisions. Some taxa, particularly crustose lichens, were infertile and therefore could not be identified (e.g., sterile *Lecidea* spp., *Cladonia* spp.). Two morphological type of *Collema coccophorum* were identified, based on thallus shape, habit and morphology or lobes and isidia (Eldridge, 1996). Lichen nomenclature conforms with McCarthy (1991) or more recent monographs. Voucher specimens were lodged with the National Herbarium of New South Wales (NSW). Within the same 10 quadrats, we estimated the total above-ground vegetation cover and took a sample of the top 2 cm of the surface from every second quadrat. These soils were bulked, air-dried and sieved to >0.2 mm for an assessment of soil organic C using the Walkely-Black oxidation method and soil pH on a 1:5 soil water extract.

2.3 | Statistical analyses

We used correlation network ("co-occurrence networks") analysis to identify ecological clusters ("modules") of strongly associated biocrust taxa according to Delgado-Baquerizo et al. (2018). In brief, we calculated all pairwise Spearman's (ρ) rank correlations between all taxa (% of cover), focussing exclusively on positive correlations because they provide information on species that may respond similarly to different soil, plant, climatic and grazing conditions (Barberán et al., 2012). We considered a co-occurrence to be robust if the Spearman's correlation coefficient was > 0.25 and $p < 0.01$ (see Barberán et al., 2012 for a similar approach). This cut-off has a biological meaning, because we only focus on taxa that are significantly strongly co-occurring, which are therefore more likely to interact with each other within a given plant community. The network was visualized with the interactive platform Gephi (Bastian, Heymann, & Jacomy, 2009). We then used default parameters (network resolution = 2.0 in all cases) from the interactive platform Gephi to identify ecological clusters of the most strongly interacting biocrust taxa. We then computed the relative abundance of each ecological cluster by averaging the standardized relative abundances (*z*-scores) of the taxa from each ecological cluster. Standardizing the data allowed us to exclude any effect of merging data from different biocrust groups, for example, lichen versus moss.

We then used Structural Equation Modelling (*SEM*) to build a system-level understanding of the effects of paleoclimatic legacies on the composition of the two species-rich ecological clusters. We developed an a priori model of how we expected our biocrust system to behave with changes in paleoclimatic legacies over the past 20k years (Supporting Information Appendix S1). In this a priori model, we predicted that paleoclimatic legacies (changes in temperature and rainfall over the past 20k years), grazing (by cattle), differences in soils (pH and total carbon), groundstorey plant cover and location (latitude, longitude) would have direct effects on both biocrust ecological clusters, separately, and that there would be a number of indirect effects, mediated by soils, plants and grazing (Supporting Information Appendix S1). Grazing has been shown to have indirect effects on soil crust composition by altering plant cover (Eldridge & Koen, 1998) but affecting soil surface stability and therefore soil carbon levels (Eldridge et al., 2017). We also included current climate in our models to account for variation in any response due to current climatic conditions. Current and paleoclimatic data were obtained from the WorldClim database. Paleoclimatic data from the Last Glacial Maximum (about 20k years ago) were downscaled from simulations using Global Climate Models (CCSM4) and calibrated (bias corrected) using WorldClim 1.4 as the baseline "current climate." WorldClim provides information on 19 climatic variables, but we only used a subset of three of these (a) for simplicity (we kept the most comprehensive climatic variables, which are largely used in the literature) and more importantly, (b) to avoid strong multicollinearity issues in our models as most of the 19 variables are highly correlated.

Hypothesized pathways in our a priori model were compared with the variance–covariance matrix of our data in order to calculate an overall goodness of fit using the χ^2 statistic. The goodness of fit test estimates the likelihood of the observed data given the a priori model structure. Thus, high probability values indicate that models are highly plausible causal structures underlying the observed correlations. Before fitting empirical data to our a priori models, we examined the univariate correlations among all variables and standardized (z-transformed) the data. The stability of the resultant models was evaluated as described in Reisner, Grace, Pyke, and Doescher (2013). Analyses were performed using the AMOS 22 (IBM, Chicago, IL, USA) software. After fitting our empirical data to the a priori model (Supporting Information Figure S1), we interpreted a good model fit as one with a low χ^2, high Goodness of Fit Index [GFI] and high Normal Fit Index [NFI]).

For our dataset, we found some gaps (~2%) in our soil pH and C data due to loss of laboratory samples. To overcome this, we obtained soil pH data from Hengl et al. (2017), who present global maps of multiple soil properties at a resolution of 250 m. Missing soil C data were obtained similarly. We found a strong positive and significant correlation between the observed and predicted pH (ρ = 0.46; $p < 0.0001$) and soil C (ρ = 0.55; $p < 0.0001$). For each of our sites, we estimated the density of cattle using data from Robinson et al. (2014) that are based on 1 km resolution global maps. A demonstration of the validity of predicted cattle density, soil C and pH for the NSW region and Australia is presented in Delgado-Baquerizo et al. (2018).

3 | RESULTS

We recorded 120 lichen, moss and liverwort taxa across the study area. Mosses accounted for 46% of all taxa, and crustose (18%) and squamulose (15%) forms were the most common lichens. Our

network analysis discriminated six ecological clusters, two of which had 87% of all taxa. These two main ecological clusters included 41 (Cluster A) and 52 (Cluster B) taxa. The additional four small clusters comprising between 2 and 13 taxa (Figure 2a). Clusters A and B had a similar richness of mosses, lichens and liverworts (Supporting Information Appendix S2). Some biocrust taxa were strongly indicative of the two major clusters. For example, taxa from the lichen families Peltulaceae and Teloschistaceae were restricted to Cluster A, while Cladoniaceae, Lecideaceae and Thelotremataceae were restricted to Cluster B. For the mosses, Bryaceae were dominant in Cluster A and there was slightly greater abundance of Pottiaceae in Cluster B (Figure 2b).

Our *SEM* provided a system-level understanding on the role of multiple ecological attributes in predicting the distribution of biocrust communities. Interestingly, we found that climatic legacies have an important influence on the relative abundance of the two major ecological clusters but had no significant effects on the remaining clusters. Specifically, sites with the greatest increases in temperature over the last 20k years (positive temperature legacies) were associated with reductions in the relative abundance of Cluster A taxa (Figure 3), while sites where precipitation has increased over the past 20k years (positive precipitation legacy) were associated with increases in the relative abundance of Cluster B (Figure 4). Climatic legacies also influenced other ecological attributes. For example,

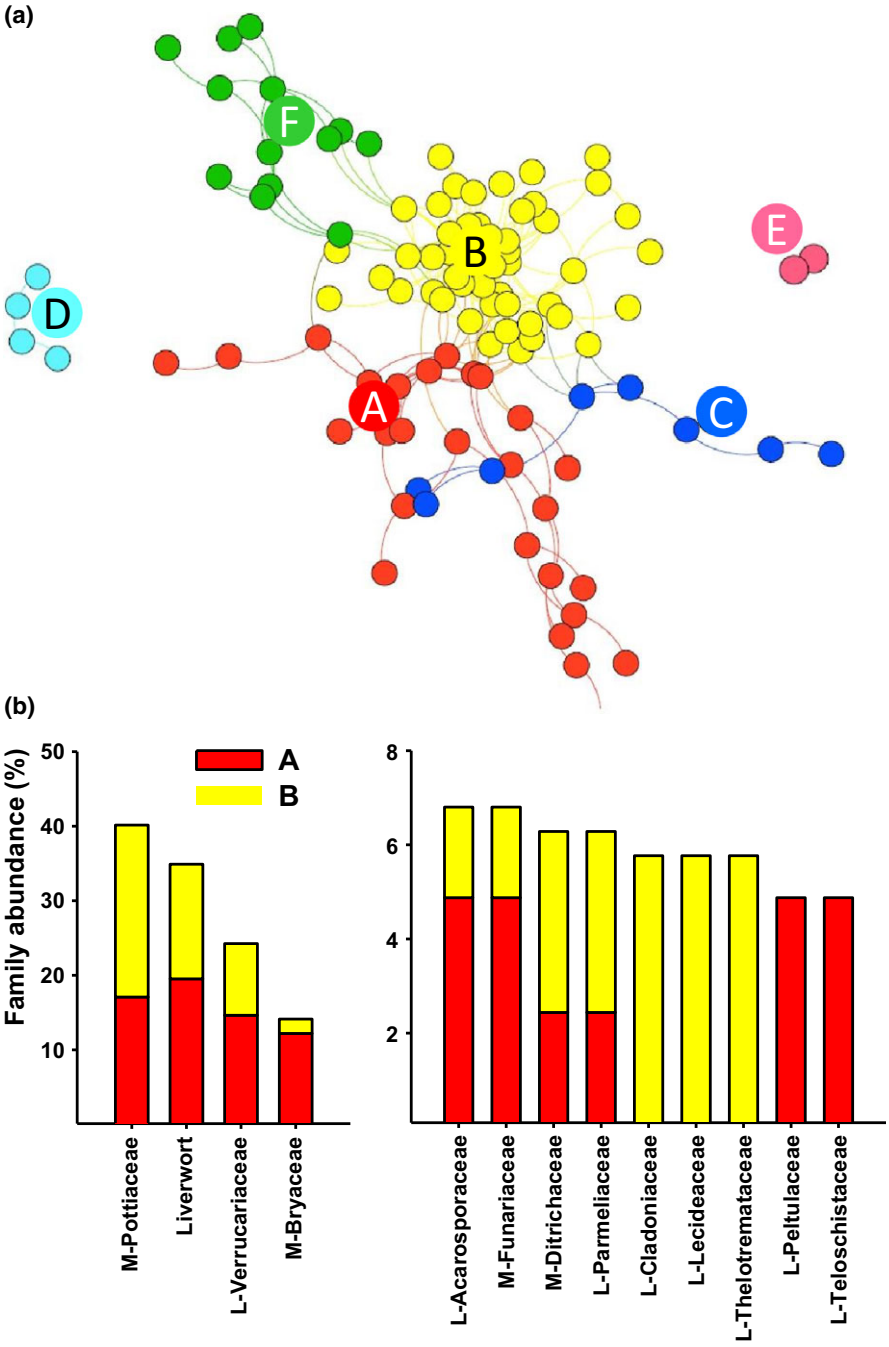

FIGURE 2 Network diagram showing the location of the six clusters (A-F) and histograms showing the abundance of different moss and lichen families in Clusters A (red) and B (yellow). Histograms on the left-hand side show that there is a greater abundance of mosses from the family Pottiacea in Cluster B, and liverworts, lichens (Family Verrucariaceae) and mosses (Bryaceae) in Cluster A

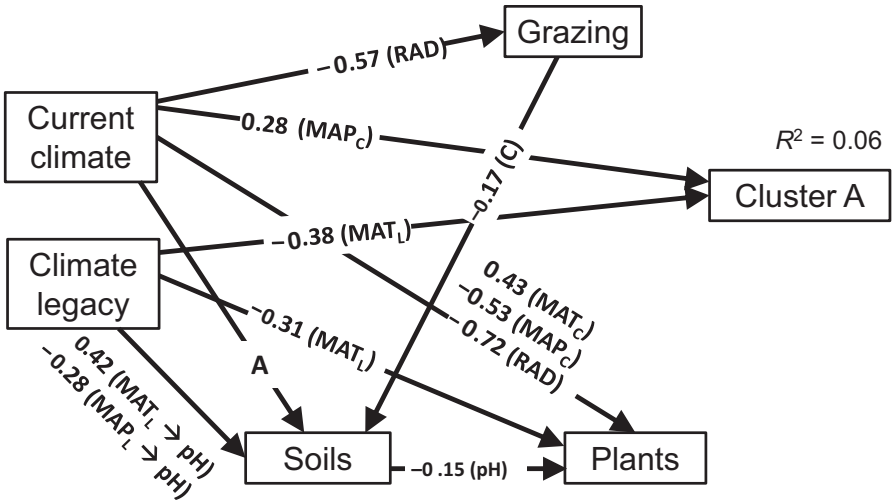

FIGURE 3 Structural equation modelling of the direct and indirect effects of current and paleoclimatic legacies (both including mean annual temperature [MAT_C & MAT_L], mean annual precipitation [MAP_C & MAP_L], and radiation RAD), grazing (cattle grazing), soils (organic carbon [C] and pH) and groundstorey plants (cover) on Cluster A. All variables were included as independent observable variables. Multiple path coefficients are presented on the same arrow in order to reduce the number of boxes and the number of arrows, resulting in considerable simplification of the model structure. Correlations among different groups of variables, for example, pH and C, or legacy MAT and legacy MAP, were allowed to covary. Standardized path coefficients, superimposed on the arrows, are analogous to partial correlation coefficients and indicative of the effect size of the relationship. χ^2 = 5.57, *df* = 3, *p* = 0.134, GFI = 0.996, RMSEA = 0.056, Bollen-Stine = 0.90. Only significant path coefficients are shown. The proportion of variance explained (R^2) appears below the three soil health response variables in the models. For pathway A in both models: MAT_C→pH (−0.68), MAP_C→pH (−0.81), RAD→C (−0.60)

sites where the temperature has declined over the past 20k years (negative temperature legacy) had less groundstorey plant cover, but higher levels of soil pH and sites where precipitation has increased (positive precipitation legacy) compared with current levels also had lower levels of soil pH. We also found some indirect effects of climatic legacies on the relative abundance of Cluster B. Sites exhibiting the greatest increases in temperatures in the past 20k years suppressed the negative effects of plant cover on the relative abundance of Cluster B by reducing plant cover. Similarly, increased intensity of grazing suppressed the negative effect of pH and the positive effect of soil carbon on the relative abundance of Cluster B. Finally, increasing temperature and precipitation legacies reduced the negative effect of soil pH on Cluster B (Figure 4).

Of course, other environmental variables were also important predictors of the relative abundance of ecological clusters of biocrusts (Figure 4). For example, sites with greater current precipitation had a greater relative abundance of both Clusters A and B, and sites with greater radiation were associated with increases in Cluster B. Conversely, locations of greater contemporary temperature were associated with declines in Cluster B (Figure 4). Increases in the relative abundance of ecological Cluster B were associated with lower levels of soil carbon, but less plant cover and lower soil pH. Unlike Cluster B, however, we found no direct effects of soils or plants on the relative abundance of Cluster A.

4 | DISCUSSION

Our study provides empirical evidence that climatic legacies can influence the current distribution of major ecological clusters of biocrust species. Climatic legacies had different effects on the relative abundance of different ecological assemblies of biocrust organisms, with significant effects on two of the six ecological clusters that together comprised 78% of all lichen and bryophyte taxa found across ~0.6 million km^2 of eastern Australia. Thus, precipitation and temperature legacies were associated with the relative abundance of ecological clusters A and B, respectively. Our results could help to explain why biocrusts are absent from particular locations where they would be expected to thrive. Alternatively, our results could also shed light on why some species occur in areas where they are not predicted to occur under current climates, such as the case for foliose lichens in areas of summer rainfall in central Australia (Eldridge, 1996). Our work is important for two reasons. First, it provides insights into why species are absent from the areas that have not been impacted by human-induced disturbance or vice versa. Second, an understanding that climate legacies can explain part of the current distribution of biocrusts safeguards us against unreasonable expectations that species can be predicted from distribution models based on the current known distributions. Third, our research improves our understanding of the effects of long-term changes in climate on organisms that have been little studied but are believed to be relatively resilient to changes in climate. Overall, a knowledge of the importance of climate legacies helps us to moderate our decisions about investing in landscape restoration based on a lack of knowledge of the true drivers.

Our structural equation models provide evidence of the negative correlation between increasing temperature legacies and the relative abundance of taxa in Cluster A. In other words, taxa in ecological Cluster A were associated with the smallest increase in temperature

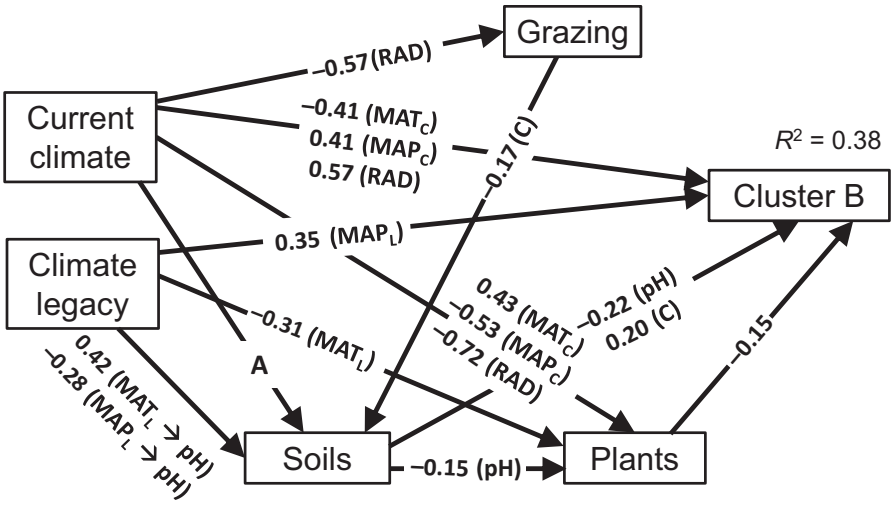

FIGURE 4 Structural equation modelling of the direct and indirect effects of current and paleoclimatic legacies (both including mean annual temperature [MAT_C & MAT_L], mean annual precipitation [MAP_C & MAP_L] and radiation RAD), grazing (cattle grazing), soils (organic carbon [C] and pH) and groundstorey plants (cover) on Cluster B. Multiple path coefficients are presented on the same arrow in order to reduce the number of boxes and the number of arrows, resulting in considerable simplification of the model structure. Correlations among different groups of variables, for example, pH and C, or legacy MAT and legacy MAP, were allowed to covary. Standardized path coefficients, superimposed on the arrows, are analogous to partial correlation coefficients and indicative of the effect size of the relationship. χ^2 = 5.57, *df* = 3, *p* = 0.134, GFI = 0.996, RMSEA = 0.056, Bollen-Stine = 0.90. Only significant path coefficients are shown. The proportion of variance explained (R^2) appears below the three soil health response variables in the models. For pathway A in both models: MAT_C→pH (−0.68), MAP_C→pH (−0.81), RAD→C (−0.60)

over the past 20k years. This cluster was dominated largely by mosses from the family Bryaceae (e.g., *Rosulabryum* spp.; Figure 2B). Dominant biocrust traits for the species within this cluster could help explain this result. For example, ecological cluster A moss species such as *Goniomitrium acuminatum* and *Acaulon integrifolium* have "annual shuttle" strategies, maintaining a high reproductive effort by maintaining a short lifespan and producing a few relatively large spores (Kürschner & Frey, 2012). Although they can withstand high temperatures, their photosynthetic optimum is between 10 and 28°C (Lange, Green, & Reichenberger, 1999), and higher temperatures for prolonged periods may compromise their ability to regenerate (Stark & McLetchie, 2006). This could account for the fact that sites with the lowest increase in temperature over the past 20k years are closer to the photosynthetic optima for Cluster A mosses. Lichen taxa in Ecological Cluster A included *Xanthoparmelia semiviridis* (syn. *Chondropsis semiviridis*), which is known to be strongly influenced by changes in diurnal summer temperatures (Rogers, 1972). Photosynthesis of some lichens can be suppressed when high summer temperatures, particularly when the thallus is hydration (Lange, Green, & Heber, 2001). *Xanthoparmelia semiviridis* is a sessile lichen that cannot maintain gas exchange after exposure to temperatures of only 55°C for 30 min (Rogers, 1972). Thus, locations with the largest increases in temperature over the last 20k years would likely have resulted in a lower relative abundance of this species.

Increasing precipitation legacy was positively related to the relative abundance of Ecological Cluster B taxa. Again, functional traits associated to the species within this cluster might help explain this result. For example, cluster B contained the thallose liverworts *Asterella drumondii*, *Riccia lamellosa*, *R. limbata* and *R. nigrella*, all of which require free water to reproduce and maintain their osmotic balance (Sperry, 2003). Studies in arid northern Australia have shown that *Riccia* spp. tend to occur in areas where water accumulates after rainfall (Rogers, 1994). Highly variable or erratic rainfall will limit the distribution of liverworts (Scott, 1985), and in water-limited environments such as hot deserts, or cold deserts such as Antarctica, their distribution is likely to be restricted to areas receiving supplementary water in the form of snow melt (Kennedy, 1995) or runoff water (Eldridge, 1998; Eldridge & Tozer, 1996). Ecological Cluster B also contained the foliose and fruticose lichens (*Xanthoparmelia* spp., *Cladia* spp., *Cladonia* spp. and *Heterodea* spp.) consistent with our models that indicate a significant positive relationship between this cluster and the contemporary distribution of rainfall (Figure 4). Our previous research has shown that *Heterodea* spp. are more common in zones that intercept runoff (Eldridge, 1998). This extra water may be necessary to support the larger thallus structure of these taxa. Therefore, locations with the largest increases in precipitation over the last 20k years might have resulted in a larger relative abundance for this cluster.

We also found evidence for multiple indirect effects of climatic legacies on ecological cluster B *via* changes in plant cover and soil pH (Figure 4). For example, sites where temperature has increased the most over the past 20k years will likely be associated with a lower plant cover, which was associated with an increase in the relative abundance of ecological cluster B (Figure 4) but no significant effect on ecological cluster A (Figure 3). Increasing plant cover is known to suppress the cover of certain mosses and lichens species

such as Cladonia spp. in cluster B (Pharo & Beattie, 1997) by occupying suitable bare soil niches (Pharo & Beattie, 1997; Vanderpoorten & Engels 2003; Vanderpoorten, Sotiaux, & Engels, 2005; Martínez et al., 2006). Grazing had an overall suppressive effect on Cluster B taxa (standardized total effects [STE] = −0.17), and one potential mechanism was *via* the suppression of the positive effect of carbon on Ecological Cluster B taxa. Carbon is a proxy for organic matter (Schmidt et al., 2011), so taxa from Ecological Cluster A would be expected to prefer high fertility conditions or sites of low soil pH. Support for this comes from a study of the micro-scale distribution of biocrust taxa across three microhabitats within a *Callitris* woodland. The interception zone, an area where a change in slope produces a series of alternating depressions, was dominated by taxa from Ecological Cluster B such as *Asterella drummondii*, *Fossombronia* spp. and the thallose liverworts *Riccia* spp.; Eldridge, 1998). The tendency of these species to occur in areas of water and organic matter accumulation may be related to their preference for sites with high levels of organic carbon.

Another interesting outcome from this study is that the dominant ecological clusters in our region included a similar number of moss and lichen species. A priori, we might have expected that one cluster would be dominated by mosses and the other by lichens, based on the notion that mosses (and liverworts) would dominate areas where precipitation has increased over the past 20k years while lichens would show the opposite response. This is based on the perception that mosses prefer more mesic and lichens more arid environments. However, this was not the case. Rather, both mosses and lichens species were well represented in each cluster, indicating that no dichotomy between the two clusters and suggesting that multiple mosses and lichen species can potentially share environmental preferences. Notwithstanding the effects of current climate and climate legacy, soil chemistry, plant cover and grazing, the low explanatory power of our models (0.06–0.38) indicates that other unmeasured factors could influence the different clusters. Nonetheless, the aim of this study was to examine whether we could identify an association between climatic legacies and contemporary distribution of biocrust taxa after accounting for well-known ecological predictors of biocrust. Future modelling could include other potential drivers flooding or fire, which were not modelled, to improve predictability. Biocrusts are known to be killed by frequent fires (Eldridge & Bradstock, 1994), the return interval for fire in western NSW is relatively long (Leigh & Noble, 1981).

Although climatic legacies and climate change are not directly comparable, mainly because of their different temporal scales (centuries vs. thousands of years), we believe that our results can still provide some potential insights to help understanding the future distribution of biocrusts species across large regions. For example, temperatures are predicted to rise by 1–5°C across Australia's drylands over the next 50 years, depending on location and modelling scenario (Stokes, Ash, & Howden, 2008). Climatic projections for much of our study area include an increase of up to 3°C in temperature, with the greatest increases in the north, an increase of 10%–20% in summer rainfall, but substantial reductions (20%–50%) in winter precipitation (Eldridge & Beecham, 2017). This could mean a contraction of taxa in Ecological Cluster A to areas experiencing lower rates of temperature increase, such as areas in the south of the study area, and a potential expansion of Ecological Cluster B species northward into areas of increased rainfall. The management and ecological implications of these changes have not been adequately addressed. However, there are likely to be changes in ecosystem functions associated with these changes. For example, the cyanolichens *Collema coccophorum* and *Peltula* spp. (Ecological Cluster A), which have cyanobacteria as their phytobionts, may retract to the south, altering the inputs of N into the soil (Belnap, 2002). The extent to which these potential changes lead to ecosystem-wide changes in soil N pools is, however, unknown.

Our work indicates that climatic legacies influence the current distribution of biocrusts ecological clusters of species across large spatial scale. Information on climatic legacies could therefore, provide a useful way to improve our capacity to predict the distribution of ecological assemblies of biocrusts across southern Australia, but potentially somewhere else. Given that biocrusts have such as broad global distribution, we encourage others to use regional biocrust species databases to test whether clusters of similar species from other drylands exhibit similar responses to those in our study. This knowledge can help us to improve our predictions of how biocrust assemblies might respond to ongoing global environmental change associated with increasing land use intensification, increasing temperature and reduced rainfall, with important implications for future sustainable management and conservation policies. It might also help us to prioritize activities such as inoculation that is designed to promote the establishment of biocrusts and their associated ecosystem services.

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SUPPORTING INFORMATION

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