







## RESEARCH ARTICLE

# Limited range shifting in biocrusts despite climate warming: A 25-year resurvey

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## Abstract

1. The ranges of many species globally have already shifted to maintain climatic equilibrium in the face of climate change.
2. Biocrusts—soil surface dwelling communities of lichens, bryophytes and microbes—play important functional roles in many ecosystems, particularly in drylands. Compared to better studied animal and plant taxa, dryland biocrusts have different establishment requirements and have never been assessed for historical range shifts.
3. Here, we revisited the sites ( $N=204$ ) of a 25-year-old biocrust survey across a large area ( $400,000\text{ km}^2$ ) of drylands in south-eastern Australia. We used quadratic models to quantify changes in the climate niches of 15 lichen, eight moss and five liverwort taxa, as well as biocrust cover and richness.
4. Our models showed that the observed climatic niches of most taxa have become hotter and drier in the past quarter century, yet the responses of the vast majority of taxa are consistent with remaining in the same geographic space. A similar pattern was observed at the community level, where the peak of biocrust cover and richness now occurs in a hotter, drier environment. Notable exceptions were the liverwort *Riccia lamellosa* and lichens in the genera *Cladonia* and *Xanthoparmelia*, which showed signs of contraction at their arid range edges.
5. Unlike more mobile taxa, most biocrust species have yet to shift geographically and may already be lagging behind the pace of climate change. One explanation for the mortality lag is that long-term climate variability in the system is extensive, which may have selected for the ability to withstand multi-year warm periods as long as there is an eventual return to milder conditions. However, no forecasts of future climate include a return to milder conditions, suggesting there will be an eventual loss of ecosystem multifunctionality at the contracting front. Expansion lags are most likely due to delays in the mortality of competing vascular plants.
6. *Synthesis:* Our study provides a valuable contribution to the knowledge of range shifts in understudied taxa and highlights a future need to promote the expansion

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of biocrusts to maintain the provision of ecosystem functions and services across their range.

#### KEYWORDS

biocrust, biogeography, climate change, cryptogam, historical, mortality lag, niche, range shift, resurvey

## 1 | INTRODUCTION

As Earth's climate becomes hotter and drier in many places, parts of the geographic ranges of species are being pushed beyond niche limits (Sexton et al., 2009). One response of species is to shift their geographic range to maintain a climatic niche that enables populations to be self-sustaining (Gaston, 2009; Lenoir & Svenning, 2015). Long-term surveys have revealed that the ranges of many species have already shifted (Morueta-Holme et al., 2015; Tingley et al., 2009) yet not always in the direction predicted by average temperature change (e.g. Auld et al., 2022; Crimmins et al., 2011). Aside from average temperature, range shifts can be driven by changes in water availability, climate extremes, microclimate, biotic interactions and disturbance regimes (Germain & Lutz, 2020; Lenoir et al., 2010; Rapacciuolo et al., 2014). Unsurprisingly given their lack of mobility, many plant taxa are shifting slowly or not at all (Lenoir et al., 2020; Zhu et al., 2012), posing an alarming extinction risk if the climate within their geographic range exceeds their niche limits and adaptive capacity (Catullo et al., 2015; Sax et al., 2013).

Biocrusts—soil surface dwelling communities of lichens, non-vascular plants and microbes—occur in nearly all terrestrial biomes and occupy an important functional position in these ecosystems (Mallen-Cooper et al., 2020; Weber et al., 2022). In their role as nutrient cyclers, biocrusts are functionally analogous to an additional layer of leaf area (Mallen-Cooper & Cornwell, 2021), fixing about 5% of carbon and 36% of nitrogen in terrestrial systems globally (Elbert et al., 2012). Biocrusts also play critical roles in soil hydrology, stability and microclimate (Chamizo et al., 2016; Eldridge et al., 2021; Mallen-Cooper et al., 2021), and they provide habitat for a variety of microfauna (Darby & Neher, 2016). Little is known about the dispersal capacities of biocrust organisms, and thus the ability of species to shift their ranges. Yet, dryland biocrust taxa rarely produce spores (Warren et al., 2019), which is typically the only mode of dispersal on the scale of several kilometres (Bailey, 1966; Damialis et al., 2017), apart from rare animal dispersal events (Lewis et al., 2014). An additional difficulty is establishment after dispersal, which, for biocrust species, is virtually only known from studies of restoration and inoculation (e.g. Faist et al., 2020). These studies indicate that biocrusts usually fail to colonise soils that have become compacted or unstable, because they cannot anchor to the surface and are easily buried by sediment (Weber et al., 2016). If dispersal and establishment limitations can be overcome, many generalist biocrust species have the potential to expand in total area at the global scale (Mallen-Cooper et al., 2023).

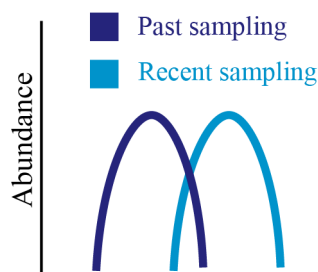
Despite the functional importance of biocrusts, particularly in drylands, only three studies to our knowledge have quantified historical shifts in species ranges over time (Bergamini et al., 2009; Lenoir et al., 2008; Virtanen et al., 2010). One example is a study by Bergamini et al. (2009), who used herbarium records to reconstruct the elevational ranges of cryophilous bryophyte species over time across Switzerland, reporting a mean upslope shift of  $0.9 \text{ m year}^{-1}$ . Critically, no studies have assessed historical biocrust range shifts in drylands, where biocrusts are most dominant (Rodríguez-Caballero et al., 2018) or along non-elevational gradients. A handful of studies have been conducted at small spatial scales, and these provide a 'spatial snapshot' of changes in biocrust composition (Ferrenberg et al., 2015; Finger-Higgins et al., 2022). For example, one recent study examined shifts in biocrust community structure at a semi-arid grassland site over 53 years, finding a long-term multi-year trend that lichens and mosses were particularly sensitive to summer maximum temperatures (Finger-Higgins et al., 2022). While these spatial snapshot studies are critical for assessing correlations over time, they lack the spatial extent to distinguish broad climate-driven shifts from local land use effects (e.g. pollution, fire regime).

Our current understanding suggests that the arid range edges of biocrust species are ultimately controlled by the amount of time in which the organisms are hydrated because it is only in this state that they can fix carbon (poikilohydry; Raggio et al., 2021). There are many climatic factors that can influence hydration time. For example, temperature has a large influence on evaporative demand, which affects how long water resides on the soil surface. Another major control on hydration time is the total input of precipitation, through rainfall or other sources (Chamizo et al., 2021). Here, it is important to consider variables such as total annual rainfall, total number of rain days, and rain falling in the non-summer months when water is slower to evaporate (Darrouzet-Nardi et al., 2015; Sancho et al., 2016; Stark, 2005).

Research in the last decade has identified a third important factor: the frequency and timing of hydration events. For example, increasing summer rainfall and short rainfall events have been implicated in the widespread mortality of the moss *Syntrichia* in the arid drylands of North America (Coe et al., 2012; Reed et al., 2012). The mechanism is related to increased rehydration costs and cellular damage under high temperatures when the organisms are hydrated (Nörr, 1974; Oukarroum et al., 2012). If this mechanism applies broadly across biocrust species, other climate variables relating to hydration cycles could be important, such as the average number of days between rainfall events or the frequency of very hot days

with rainfall. However, there is currently little evidence of the effects of rehydration costs in biocrust genera other than *Syntrichia*, or in milder dryland regions where vascular plants often buffer microclimate conditions (Bowker et al., 2016; Breshears et al., 1998; Li et al., 2010). On the cool leading edge of the range, biocrusts are likely to be limited by vascular plant competition, via shading and

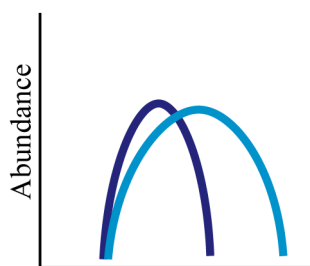
### i) Geographic stasis



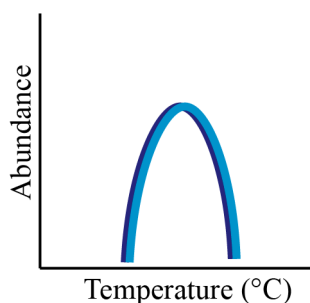
### ii) Range contraction



### iii) Range expansion



### iv) Climate tracking



**FIGURE 1** Four responses of species ranges to climate change, shown along a gradient of increasing temperature: (i) geographic stasis, where a species occupies the same spatial position, and the observed temperature niche has become hotter over time; (ii) range contraction, where a species retains the same leading range edge, which has become hotter, but experiences mortality at the trailing range edge; (iii) range expansion, where a species retains the same trailing range edge, which has become hotter, and geographically expands at the leading range edge; and (iv) climate tracking, where a species maintains its temperature niche via expansion at the leading range edge and mortality at the trailing range edge.

litter burial, rather than the direct effects of water availability (Corbin & Thiet, 2020; Mallen-Cooper et al., 2022; Zhang et al., 2016). In this case, variables relating to the total amount of rainfall may be a good proxy for the abundance of vascular plants and, in turn, the strength of competition (Wang et al., 2010).

Range shifts are typically quantified as changes in the range mean, limit, area and/or shape (Yalcin & Leroux, 2017). Area and shape are usually measured via sophisticated spatial models such as species distribution models, which both require a large amount of data and make a large number of assumptions (Elith & Leathwick, 2009). Historical resurveys tend to be data-limited and generally report an annual rate of movement according to the range mean, optimum, centroid or margin (e.g. Auld et al., 2022; Lättman et al., 2009; Lenoir et al., 2008). This calculation is more difficult for climate gradients that are not closely linked to an easily measurable proxy like altitude or latitude. Further, the range mean is a surrogate of the range optimum, which is often not located at the climatic centre of a species range (Sagarin et al., 2006).

Here, we resurveyed the 25-year-old biocrust sites of Eldridge and Tozer (1997) in south-eastern Australia. Since Eldridge and Tozer (1997) recorded geographic coordinates, abundances and absences, the data are remarkably robust to many of the obstacles that frequently plague historical resurveys (Tingley et al., 2009). Additionally, most biocrust taxa, particularly lichens, are long-lived and are therefore unlikely to exhibit high inter-annual variability and bias the comparison of temporal snapshots (Stuble et al., 2021). Using a quadratic niche approach along gradients of temperature and moisture, we compared the abundances of 28 biocrust species between surveys, as well as community-level attributes such as cover and richness. Currently, we lack any knowledge of how the ranges of dryland biocrust species have responded to recent climate change. Our aim was to assess whether the biocrust community and individual biocrust species have shifted their ranges in the past quarter century. In view of evidence suggesting that dryland biocrust species rarely disperse over long distances and establish but may be vulnerable to altered temperature and precipitation regimes at their arid range edge, we hypothesised that species have contracted from their arid range edges but have not expanded into newly suitable area at their cool range edges (Figure 1, Hypothesis ii). We also examined the extent to which livestock and kangaroo grazing intensity has moderated shifts in biocrust abundance and richness. We expected that high recent grazing pressure would be more likely to

be associated with a decline in biocrust cover and richness than an increase but only for livestock, whose hard hooves are known to trample biocrusts and destabilise the soil surface (Mallen-Cooper et al., 2018; Wu et al., 2023).

## 2 | METHODS

### 2.1 | Study region

Our study was conducted across a large region of south-eastern Australia, approximately 400,000 km<sup>2</sup> (Figure 2). The extensive dryland study area largely consists of pastoral land where grazing of sheep and cattle is the predominant land-use. Across the study area, the Aridity Index—an index of dryness (the ratio of annual precipitation to potential evapotranspiration) where values <0.65 are considered dryland—ranges from 0.07–0.24 (Trabucco & Zomer, 2018). Smaller areas of nature reserves and isolated dryland cropping occur across the study area. Mean annual temperatures in this region range from about 12°C in the south-east to 21°C in the north-west, with average January maximum temperatures ranging from 30 to 36°C and average July minimum temperatures ranging from 1 to 6°C. Mean annual precipitation ranges from 446 mm year<sup>-1</sup> in the east to 226 mm year<sup>-1</sup> in the north-west. Elevation in the study region rarely exceeds 300 m a.s.l., although there are ridgelines in the south-east that reach a maximum of 574 m a.s.l.

Increasing aridity in a north-westerly direction across the study region is associated with a change in vegetation community type from dry sclerophyll forest dominated by *Eucalyptus* spp. to semi-arid woodlands dominated by *Eucalyptus* spp. and *Allocasuarina* spp., to arid shrublands characterised by *Dodonaea* spp., *Eremophila* spp. and chenopod shrubs (Keith, 2004). Common plant species across the gradient were *Dodonaea*, *Senna* and *Eremophila* in the midstorey (shrub) layer, and annual forbs and perennial grasses such as *Aristida*, *Austrostipa* and *Enterpogon* in the groundstorey. In semi-arid

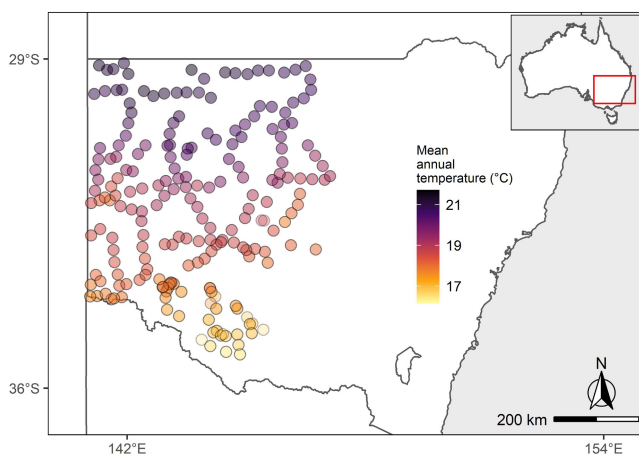


FIGURE 2 Map of the study region in south-eastern Australia, with study sites represented by coloured circles (N=204) and state boundaries shown as solid black lines.

sites with low grazing intensity, biocrust can cover >70% of the soil surface, and comprise a rich community with >20 species of lichens and bryophytes (Eldridge, 1996). In the arid north-west corner of the study region, however, biocrusts typically occur as small patches of squamulose or gelatinous lichens, typically covering <5% of the soil surface (Eldridge, 1996). Soil texture ranged from clay loams in dry subhumid and semi-arid areas, to loams and loamy sands in arid areas. Dryland soils in the study region ranged from slightly acidic in dry subhumid environments (pH 5–6; Ding et al., 2021) to calcareous in arid areas (pH 7–8).

### 2.2 | Site selection and relocation

From the original 282 sites of Eldridge and Tozer (1997), we re-sampled 204 sites based on optimal spatial coverage. For example, if multiple sites occurred within a radius of 2 km, only one was selected. Each site consisted of a single transect of ten 0.5 m<sup>2</sup> (0.707 × 0.707 m) plots, each separated by 10 m. Most of the sites were grazed by livestock at varying intensities, although some sites (N=17) occurred within protected reserves. The original sites were selected randomly, and placed at least 100 m from roads and vehicle tracks (for details, see Eldridge & Delgado-Baquerizo, 2019). Sites from Eldridge and Tozer (1997) were relocated using original GPS coordinates, but relocation accuracy was limited to about 20 m since only the coordinates of the first plot were recorded at each site. Vegetation resurveys are typically robust to approximate site relocations (Kopecký & Macek, 2015). Surveys by Eldridge and Tozer (1997) and the present study were conducted across a range of years, that is 1992–96, and 2019–21, respectively. Consequently, a resurvey site could have been revisited after 23–29 years. For simplicity, we refer to the resurvey interval as 25 years.

### 2.3 | Survey methods

Our methods were based on those of the previous survey. First, we placed a 100 m transect perpendicular to, and 50 m away from, the nearest road, although in a few cases it was only feasible to place a parallel transect next to the road. Along this transect, we recorded the occurrence of biocrust species in 10 quadrats (sensu Eldridge & Tozer, 1997). Abundance was determined as the number of quadrats in which a species occurred (1–10) because estimating percentage cover at the species level is not feasible for organisms that are often smaller than 1 mm and unable to be identified with the naked eye. When species could not be identified with a 40× hand lens in the field, samples were taken and identified under a compound microscope. We identified all lichens and bryophytes to the species level, unless their taxonomy was uncertain or had changed since the original survey, in which case organisms were recorded at the genus level. In each quadrat, we also recorded total biocrust cover (comprising lichens, bryophytes and visible cyanobacteria) and vascular plant cover, although the latter cannot

be reliably compared with historical plant cover data, which was recorded as coarse ordinal integers. Finally, we recorded the number of sheep, goat, cow, rabbit and kangaroo dung in each quadrat. We then derived a value of dry mass for the dung of each animal using average values reported in Eldridge et al. (2017), who studied the same region of south-eastern Australia. No formal permission was required for this fieldwork.

## 2.4 | Climate data

Climate data (i.e. maximum daily temperature and daily precipitation) at each site were extracted from the Australian Gridded Climate Data at 5 km<sup>2</sup> resolution (Jones et al., 2009). Climate statistics were averaged across the 30 years preceding each survey, that is 1964–1994 and 1989–2019. Aggregating climate data over a shorter time period (e.g. 10 years) would be strongly influenced by decadal patterns of climate variability such as the Pacific Decadal Oscillation and the El Niño Southern Oscillation, yet longer periods are unlikely to accurately represent the conditions that led to the distributions of biocrust taxa at the time of surveying.

From daily climate data, we derived nine climate variables. Three variables related to temperature: (1) summer maximum temperature, derived from the average daily maximum temperature during the three summer months (November, December, January), (2) maximum temperature, derived from the average daily maximum temperature across the entire year, and (3) annual temperature, calculated as the mean of average daily maximum and minimum temperatures. High temperatures are likely to limit biocrust taxa at their arid range edge by enhancing evaporation, thereby restricting the ability of biocrust organisms to fix carbon. In addition, two global studies have shown that temperature is often the dominant control of the ranges of biocrust communities and species (Mallen-Cooper et al., 2023; Rodriguez-Caballero et al., 2018). We also derived six variables related to moisture availability: (1) annual rainfall, (2) summer rainfall, (3) non-summer rainfall, calculated as the total rainfall from March to November, (4) the number of days where rainfall exceeded 1 mm, (5) the mean number of consecutive days between rainfall events >1 mm and (6) the number of days with >1 mm rainfall and maximum temperature >30°C. Summer rainfall, days between rainfall events, and rain days with high temperatures are expected to be associated with mortality events at the arid edge of species ranges, due to rehydration costs and thermal damage (Coe et al., 2012; Oukarroum et al., 2012). Moisture variables relating to total rainfall are intended to capture the limit beyond which biocrust carbon budgets become negative, and possibly the cool-edge limit where vascular plant competition becomes too strong. We selected an arbitrary threshold of 1 mm to capture rainfall events because the interpolated climate data rarely estimated exactly 0 mm of rainfall and very small rainfall events are often photosynthetically unproductive for biocrust organisms (Ladrón de Guevara & Maestre, 2022).

## 2.5 | Data analysis

Following classical niche theory (Chase & Leibold, 2003), a quadratic model is useful for capturing species abundance patterns, which often reach a maximum at a certain climate and decline away from this optimum (but see Dallas et al., 2017). In our study, we conduct a quadratic version of the models of Lenoir et al. (2008) that can be applied to any climate gradient and explicitly tests whether species niche optima and/or breadths differ between surveys. We fitted quadratic models with abundance or richness as the response variable, site as a random effect, and one climate variable as a predictor interacting with time. All models were fitted in the *glmmTMB* R package (version 1.1.3; Brooks et al., 2017) and assessed for spatial autocorrelation using the *variogram* function in the *gstat* R package (version 2.0-9; Gräler et al., 2016), yet finding no autocorrelation signal for any species, we did not include a spatial covariance structure in our models. For each model, we chose the error distribution (quasi-poisson, poisson-gamma negative-binomial or tweedie) that produced the model that best met assumptions, which were checked using the *DHARMA* R package (version 0.4.5; Hartig, 2020).

To limit our analyses to one temperature and one rainfall variable, we followed a variable selection process using the Akaike information criterion (AIC). That is, we compared AIC values across climate variables within a species or community attribute, and selected the two variables that produced the top models (lowest AIC) for the most number of species or attributes.

Using the estimated coefficients from the model and standard algebra, we calculated the optima (parabola vertex) and a relative measure of climatic, or spatial, breadth (parabola focal width) at each time point. We then computed 95% bootstrap confidence intervals (CIs) for optima and breadths, using the mean and variance-covariance matrix of the original model to simulate new values. We considered there to be strong evidence for a change in the niche optimum or breadth when CIs were non-overlapping among time points.

Since dung counts were not recorded in the past survey, we were unable to quantitatively assess the extent to which changes in grazing intensity moderated biocrust range shifts. However, using recent dung counts as a proxy, we explored whether recent grazing intensity was associated with changes in biocrust cover and species richness. To this end, we used univariate linear models with t-distributed errors, where the response variables were biocrust attributes and the predictors were either log-transformed livestock (cow, sheep, goat) dung mass or log-transformed kangaroo dung mass.

All analysis code and climate data extraction code are available on the Open Science Framework ([https://osf.io/q7yjf/?view\\_only=d4ace109e4944758848028ff391b28c3](https://osf.io/q7yjf/?view_only=d4ace109e4944758848028ff391b28c3)).

## 3 | RESULTS

Of all climatic predictors, the distributions of biocrust species and community attributes were generally best explained by mean

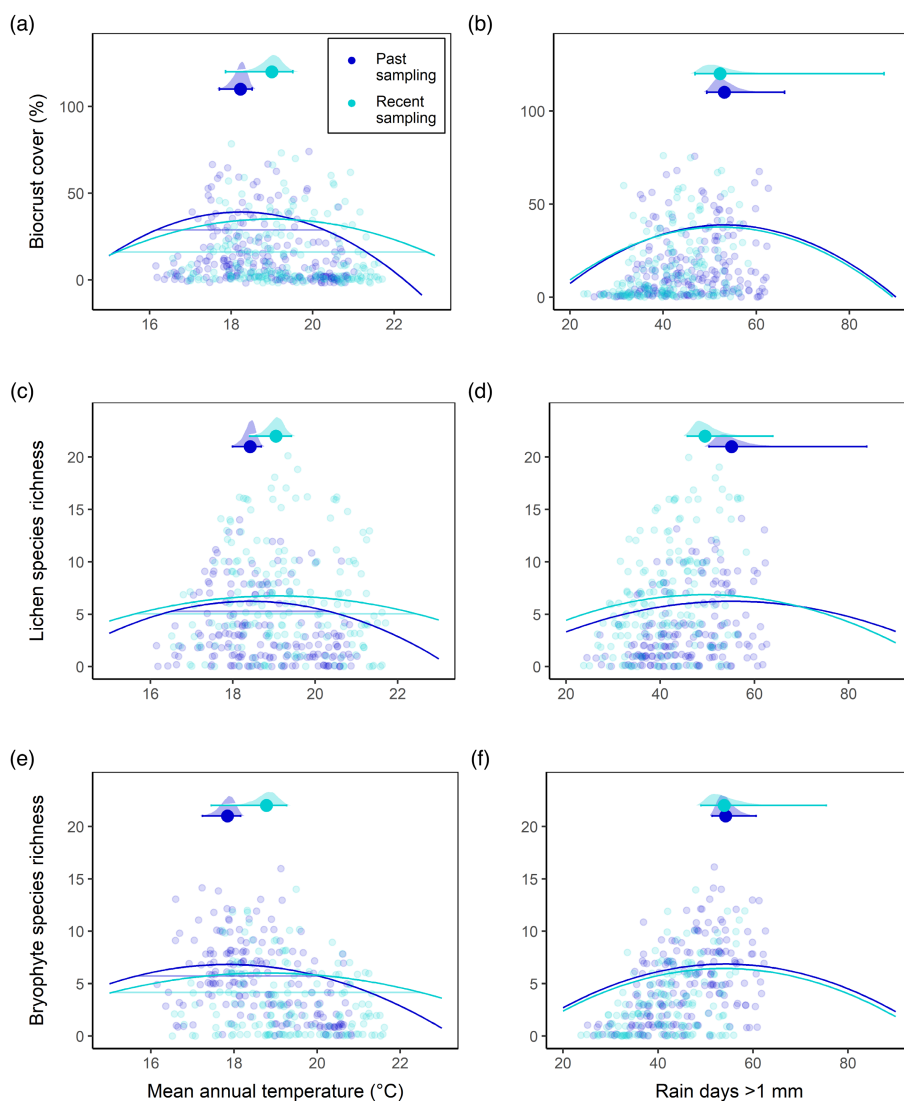
annual temperature and the number of rain days >1 mm (Figure S1). However, temperature variables were very highly correlated (Spearman  $|\rho| > 0.95$ ), while moisture variables varied widely in their intercorrelations ( $|\rho| = 0.03\text{--}0.98$ ).

From 1995 to 2020, mean annual temperatures at our sites rose, on average, by  $0.52^\circ\text{C}$  ( $\pm 0.14$ ; Figure S2a), while the number of rain days >1 mm declined, on average, by  $4.1\text{ days year}^{-1}$  ( $\pm 2.1$  SD; Figure S2b). As an indication of long-term temporal variability, Figure S3 shows the long-term climate record from a weather station in the centre of the study region.

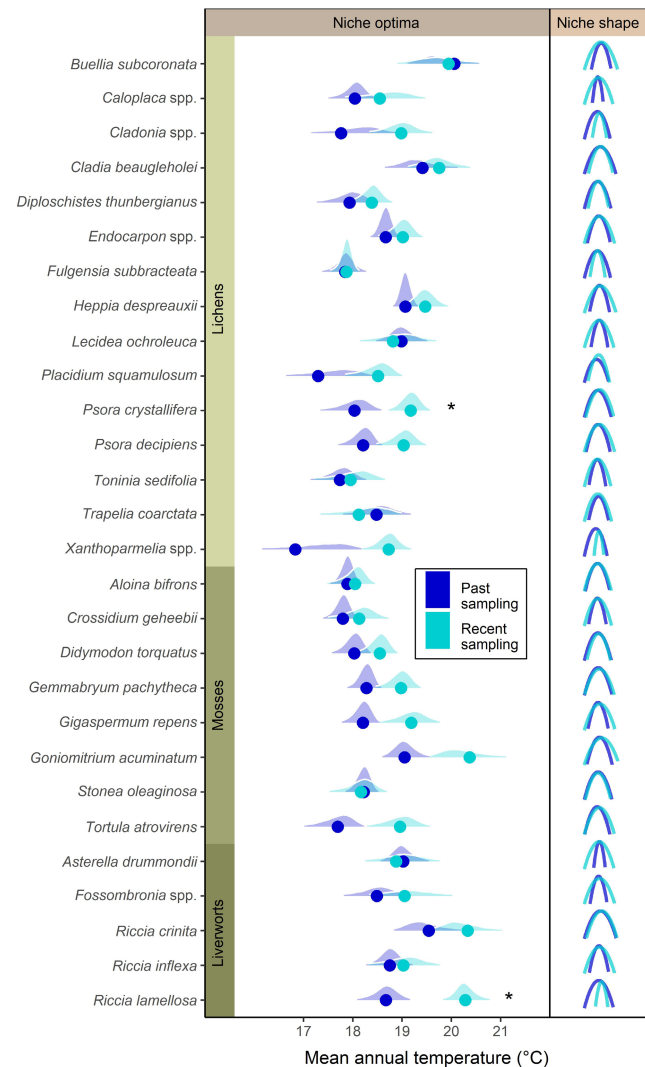
The highest biocrust cover we observed at any site was 76.9% during recent sampling and 74.5% during past sampling. Our climate niche model indicated that biocrust cover in south-eastern Australia currently reaches a peak at  $19.0^\circ\text{C}$  (17.9–19.5 bootstrap CI) mean annual temperature, while historically peaking at  $18.2^\circ\text{C}$  (17.7–18.5

bootstrap CI; Figure 3a). Although these optima were not strongly different according to 95% bootstrapped CIs, 95.8% of bootstrap simulations derived a lower value for the historical optimum, providing some evidence that the observed biocrust niche has become hotter. Similarly, there was some evidence that lichen and bryophyte species richness now peaks in a hotter environment (Figure 3), however, a lack of high-rainfall sites resulted in uncertain and strongly overlapping distributions across the rainfall gradient. It is also worth noting that at the leading (cool) range edge, the decline of biocrust cover coincided with a marked increase in plant cover (Figure S4).

We found strong evidence that the observed temperature niches of the lichen *Psora crystallifera* and the liverwort *Riccia lamellosa* have become hotter in the last 25 years (Figure 4). In the case of *Psora crystallifera*, the change appears to be consistent with geographic stasis, where the species has remained in the same geographic space while



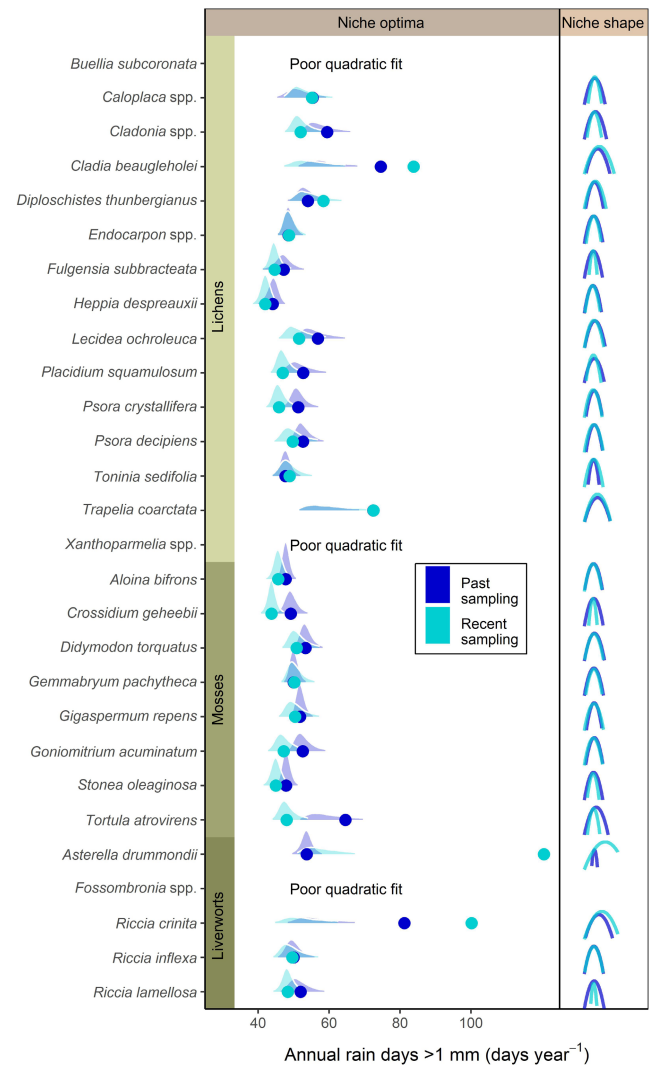
**FIGURE 3** Quadratic models of biocrust cover (a, b), lichen species richness (c, d) and bryophyte species richness (e, f) along gradients of mean annual temperature (a, c, e) and the number of rain days >1 mm (b, d, f). Temperature niche breadths (focal widths) are shown as horizontal bars across fitted parabolas (rain niche breadths were too broad to depict here), raw data are shown as background points, and estimated niche optima are shown above the raw data, with error bars representing 95% bootstrap confidence intervals and density curves representing the distribution of bootstrapped values.



**FIGURE 4** Temperature niche optima for all biocrust taxa extracted from quadratic models of abundance, with points representing the fitted optimum, density curves representing the distribution of bootstrapped optima values, and (\*) highlighting species in which 95% bootstrap confidence intervals do not overlap among sampling times. The panel on the right shows the shape of the entire fitted quadratic niches for each sampling time.

ambient temperatures have increased (Figure 1, Hypothesis i; Figure 4). By contrast, the change in distribution of *Riccia lamellosa* most likely represents a range contraction at the arid range edge (Figure 1, Hypothesis ii; Figure 4). Our models generally indicate that most other species are inhabiting both a hotter and drier climate (Figures 4 and 5), consistent with geographic stasis, although model estimates were more uncertain. Shifts in *Cladonia* spp. and *Xanthoparmelia* spp., however, were more consistent with a range contraction response.

The focal widths of species niches were extremely broad for rainfall, mostly  $>50$  days year<sup>-1</sup>, but narrower for temperature (0.09–14.88°C; Table S1). According to the estimated focal widths, the lichen *Fulgensia substracteata* and the mosses *Aloina bifrons* and *Crossidium geheebii* showed relatively narrow temperature niches, while lichens such as *Placidium squamulosum* and *Claviscidium laniculatum* exhibited



**FIGURE 5** Rainfall niche optima for all biocrust taxa extracted from quadratic models of abundance, with points representing the fitted optimum, and density curves representing the distribution of bootstrapped optima values. The panel on the right shows the shape of the entire fitted quadratic niches for each sampling time.

relatively broad temperature niches (Table S1). However, focal widths were highly variable among bootstrap simulations and showed no clear differences among species or sampling times (Tables S1 and S2).

Finally, sites with high recent grazing intensity by livestock were less likely to have increased in biocrust cover ( $z = -2.33$ ,  $p = 0.02$ ) and lichen richness ( $z = -2.64$ ,  $p = 0.01$ ) since the past survey (Figure S5; Table S3). We detected no significant effects of recent kangaroo grazing on biocrust community attributes. In addition, recent grazing intensity by livestock or kangaroos had no strong correlations with any climate variable (Spearman  $|\rho| < 0.16$ ).

## 4 | DISCUSSION

We found strong empirical evidence that biocrust communities and most species have not shifted their ranges geographically in

the past 25 years and are now inhabiting a hotter environment. Contrary to our hypothesis of widespread range contractions, these findings largely align with a geographic stasis response (Figure 1), and this suggests that range shifting in these species may now be lagging behind the changing temperature. As the climate continues to warm (Koutroulis, 2019), these results imply that biocrust ranges will be or will soon be, out of climatic equilibrium for the foreseeable future.

Our results suggest that biocrust taxa are likely to be experiencing a mortality lag at their trailing range edges (Jackson & Sax, 2010; Svenning & Sandel, 2013), with the exception of the liverwort *Riccia lamellosa* and possibly lichens in the genera *Cladonia* and *Xanthoparmelia*. One explanation for a mortality lag is that extensive long-term climate variability in our study system (Figure S3; Dey et al., 2019; Min et al., 2013; Nicholls et al., 1997) is likely to have selected for the ability to withstand multi-year warm periods as long as there is an eventual return to mean conditions. This notion of a variability-derived historical contingency is founded on the climate variability hypothesis (Stevens, 1989; Sunday et al., 2015) and implies that mortality will only start to occur as unfavourable years become more frequent and biocrust carbon balances become untenable (Coe et al., 2014; Jackson et al., 2009). Reinforcing this explanation, there is considerable palaeoecological evidence that plant and animal taxa can tolerate conditions well beyond the average climate they typically inhabit, for as long as several centuries (see Loehle, 2018 for a review). Interestingly, species of *Riccia*, *Cladonia* and *Xanthoparmelia* tend to be associated with regions that have become wetter in the last 20,000 years and may be particularly sensitive to dry conditions due to the high surface area of their thalli (Eldridge & Delgado-Baquerizo, 2019). This sensitivity could explain why we found evidence of contraction at the trailing edges of these particular taxa.

There are two key traits of biocrust lichens and bryophytes that suggest that their trailing-edge mortality will be characterised by slow individual carbon starvation rather than intermittent pulses of mortality and recovery in the population (Allen et al., 2010; Loehle, 2018). First, the ability of biocrust organisms to enter a state of dormancy between hydration events gives them a major advantage in withstanding long periods without moisture (Coe et al., 2014). In particular, rising temperatures and enhanced evaporation mean that many small rainfall events will soon become photosynthetically unproductive, and even deadly, while effective periods of desiccation will lengthen (Coe et al., 2012; Ladrón de Guevara & Maestre, 2022; Reed et al., 2012). Second, many biocrust taxa have a remarkable capacity to regenerate from vegetative tissues (de la Torre Noetzel et al., 2020; Stark et al., 2017). As such, even when extreme events cause drastic losses of biomass (e.g. Barker et al., 2005), the individuals may still retain the capacity to recover. With historical climate variation and these tolerance traits, many biocrust species could potentially persist in a landscape for many decades as climate relicts (Jackson & Sax, 2010; Woolbright et al., 2014).

On the cool side of species ranges, disequilibrium occurs as an expansion lag, which could relate to dispersal or establishment

(Alexander et al., 2018). The most likely driver of an establishment lag in biocrusts is a delay in the mortality of resident vascular plant species and/or the persistence of vascular plant litter. Vascular plants are well-known to suppress biocrusts through shading and litter fall (Ding & Eldridge, 2020; Zhang et al., 2016). Moreover, there is a point along a gradient of increasing moisture where vegetation cover starts to regularly exceed 50% (Berdugo et al., 2020) and this point corresponds closely to the decline of biocrust cover (Figure S4; Chen et al., 2020). While other factors could play a role in limiting the leading range edges of biocrust taxa, such as minimum temperature or invertebrate herbivory, overwhelming evidence suggests that competition with vascular plants is the key factor (Chen et al., 2020; Corbin & Thiet, 2020; Ding & Eldridge, 2020; Zhang et al., 2016). This type of niche limit fits into a common pattern of stress on one margin and competition on the other (Normand et al., 2009). Another consideration is that CO<sub>2</sub> fertilisation could further delay the mortality of trees (Bond & Midgley, 2012), which have the strongest suppressive effects on biocrusts relative to shrubs and grasses (Ding & Eldridge, 2020).

An establishment lag could also be driven by human land use, since the leading edges of many biocrust ranges in our study region coincide with an area of intense ongoing sheep and wheat production (Sherren et al., 2012). Numerous restoration studies suggest that biocrusts rarely recover naturally after intense agricultural disturbance, largely due to unstable or compacted soils (Chandler et al., 2019; Fick et al., 2020; Weber et al., 2016). Indeed, studies of the recovery of the lichen *Psora crenata* after complete surface removal suggest that half a century may be required for disturbed sites to approach undisturbed sites (Eldridge & Ferris, 1999). Dispersal may also play a role in hindering colonisation since much of the vast agricultural matrix is not close to a source of biocrust propagules (Bowker, 2007). Finally, even when small populations of biocrust taxa are able to disperse and establish beyond the leading range edge, there is likely to be a series of localised extinction and recolonisation events over long timescales due to demographic stochasticity and/or the effects of climate variability on vascular plant competition (Bennie et al., 2013; Holt, 2009).

Two other, less likely, explanations relating to rainfall and microclimate may have contributed to the geographic stasis we observed in many biocrust taxa. Firstly, annual rainfall across our study region is highly variable and there has only been a slight decline in average rainfall in the past few decades, largely in autumn and winter (Dey et al., 2019). Therefore, if rainfall alone is the key determinant of biocrust ranges, there has been limited opportunity for mortality at the trailing range edge, expansion at the leading range edge, and/or a shift in abundance (Lenoir & Svenning, 2015). However, temperature regulates hydration time through evaporation and is strongly associated with moss and lichen declines in manipulative studies (Escolar et al., 2012; Phillips et al., 2022), so the explanation that temperature is entirely unimportant to biocrust range limits seems unlikely. The lack of range contraction at the trailing edge could also be explained by biocrusts retreating to suitable microclimates within the same sites,



for example, under the shade of shrubs or in the shelter of a steep slope (Gutiérrez, 2018; Rodríguez-Caballero et al., 2019). Yet, this also seems improbable, since the same microclimatic features were available at both survey time points, and there was no clear change in trailing-edge abundance.

We found strong evidence that a high intensity of recent livestock grazing was associated with reduced biocrust cover and richness since the previous survey. The trampling effect of livestock is well known to inhibit biocrusts, as organisms are physically crushed, sheared or buried by loose sediment (Wu et al., 2023; Zaady et al., 2016). Not only does trampling directly reduce biocrust cover but also species richness by excluding species that are particularly susceptible to crushing and shearing forces such as fruticose lichens and tall mosses (Concostrina-Zubiri et al., 2017; Read et al., 2014). On the other hand, recent kangaroo grazing did not moderate changes in biocrust cover and richness, aligning with previous work suggesting that their much lighter foot pressure has minimal effects on the soil surface (Eldridge et al., 2017). It is likely that changes in livestock grazing intensity in the last quarter century have had localised effects on biocrust cover and richness at our survey sites. However, livestock grazing intensity was not correlated with climate variables and was therefore unlikely to confound our climatic niche results. It is also worth noting that the protection of some sites within nature reserves may have had localised effects on biocrust cover and the persistence of disturbance-sensitive species, yet it is unlikely to have affected broader climatic responses.

Our method of using parabolic vertices and focal widths to characterise niche optima and breadths has advantages and disadvantages. Focal widths were highly variable among bootstrapped simulations and did not allow clear comparisons among sampling times. We therefore cannot recommend their use in identifying changes in relative niche breadth unless variance can be quantified more precisely. On the other hand, niche optima were estimated with greater precision and enabled clear comparisons among sampling times. The advantage of the niche optimum approach over a simple average is that it accounts for species with non-centred abundance distributions (Dallas et al., 2017; Sagarin et al., 2006). Of course, range shifting can be quantified in a more multidimensional way using sophisticated distribution models (e.g. Grenouillet & Comte, 2014) but these approaches also come with drawbacks such as the large amount of data required (Elith & Leathwick, 2009).

## 5 | CONCLUSIONS

Our results indicate that most biocrust species have not yet shifted their distributions in space, despite the changing climate and the arid range edge populations of these species are good candidates for climate relicts (Woolbright et al., 2014). Our findings are an important contribution to the knowledge of range-shifting in understudied

taxa (Lenoir et al., 2020; Pecl et al., 2017). As we continue to monitor biocrust ranges in the future, new remote sensing techniques will be pivotal in enhancing the spatial and temporal resolution of surveys (Baxter et al., 2021). Manipulative experiments suggest that the contraction of the biocrust community will be a gradual collapse of lichen and bryophytes species, followed by cyanobacteria, after about 2–4°C of additional warming (Antoninka et al., 2022; Ladrón de Guevara et al., 2018; Phillips et al., 2022). Another long-term experiment testing smaller temperature increases (0.5 and 1°C above ambient) found that mosses, but not lichens, declined (Li et al., 2021). As the community disassembles, important ecosystem functions such as erosion control and productivity will decline, with wide-reaching consequences for dryland functioning and climate change feedbacks (Phillips et al., 2022; Rodríguez-Caballero et al., 2018; Rodríguez-Caballero et al., 2022). Many more experiments are required to evaluate the relationship between niche limits and range limits in biocrusts (Hargreaves et al., 2014), and no experiments thus far have transplanted biocrust taxa beyond their current climatic ranges (Mallen-Cooper & Cornwell, 2020). The potential for active management of species living beyond their niche limits is small, although restoring disturbed landscapes could enhance population sizes, thereby creating more opportunities for adaptation (Gaston, 2009), and influence microclimate availability (Shriver et al., 2018). The more feasible option is to facilitate the expanding range edge and create dispersal pathways (Robillard et al., 2015), ensuring that biocrust taxa can continue to fulfil their functional roles across the entirety of their niche.

## AUTHOR CONTRIBUTIONS

Max Mallen-Cooper conceived the study. Max Mallen-Cooper designed the study, with support from William K. Cornwell and David J. Eldridge. Manon E. B. Sabot extracted climate data. Max Mallen-Cooper and Eve Slavich conducted statistical modelling. Max Mallen-Cooper and Zoe A. Xirocostas contributed to data presentation. Max Mallen-Cooper wrote the first draft manuscript and all authors contributed substantially to edits therein.

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## CONFLICT OF INTEREST STATEMENT

The authors have no conflicts of interest to declare.

## PEER REVIEW

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## DATA AVAILABILITY STATEMENT

All data and code associated with the results of this study are available on the Open Science Framework: <https://osf.io/q7yjf/> (Mallen-Cooper et al., 2023).

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## SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

**Table S1.** Focal widths (proxy of relative niche breadth) of fitted quadratic temperature niches, and 95% bootstrap confidence intervals.

**Table S2.** Focal widths (proxy of relative niche breadth) of fitted quadratic rainfall niches, and 95% bootstrap confidence intervals.

**Table S3.** Results of linear models of the relationship between recent livestock grazing intensity (approximated by log-transformed dung mass) and biocrust cover or richness.

**Figure S1.** Akaike information criterion ( $\Delta$ AIC) values for models of species abundance across climatic predictors, as compared to the top model (lowest AIC) for either temperature or rainfall predictors ( $\Delta$ AIC > 2 shown in white).

**Figure S2.** Comparison of (a) mean annual temperature and (b) the number of rain days >1mm at study sites among historical (1964–1994) and recent (1989–2019) climates.

**Figure S3.** Change in (a) mean annual temperature and (b) the number of rain days >1mm since 1888 at Wilcannia (weather station 046043, data available at <http://www.bom.gov.au/climate/data/stations/>) near the centre of the study region, with dark blue shading showing the 30-year climate preceding the past survey and turquoise shading for the recent survey.

**Figure S4.** Relationships, using only recent sampling data, between (a) cover types and mean annual temperature, fit with cubic regression splines (penalised by the integral of the square of the second derivative), and (b) cover types paired at the site level.

**Figure S5.** Relationships between recent livestock grazing intensity (using log-transformed livestock dung as a proxy) and (a) change in biocrust cover or (b) change in lichen richness since the original survey 25 years prior, with the fitted regression lines and standard errors shown in purple.

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