Received: 10 May 2023 | Accepted: 5 July 2023

DOI: 10.1111/1365-2745.14169

Journal of Ecology

BRITISH ECOLOGICAL SOCIETY

RESEARCH ARTICLE

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

Max Mallen-Cooper[1,2] | William K. Cornwell[1] | Eve Slavich[3] | Manon E. B. Sabot[4,5] | Zoe A. Xirocostas[1] | David J. Eldridge[1,2]

[1]Ecology and Evolution Research Centre, School of Biological, Earth and Environmental Sciences, University of New South Wales, Sydney, New South Wales, Australia

[2]Centre for Ecosystem Science, School of Biological, Earth and Environmental Sciences, University of New South Wales, Sydney, New South Wales, Australia

[3]School of Mathematics and Statistics, University of New South Wales, Sydney, New South Wales, Australia

[4]Climate Change Research Centre, University of New South Wales, Sydney, New South Wales, Australia

[5]ARC Centre of Excellence for Climate Extremes, Sydney, New South Wales, Australia

**Correspondence**

Max Mallen-Cooper

Email: maxmallencooper@gmail.com

**Funding information**

Holsworth Wildlife Research Endowment; Australian National University

**Handling Editor:** Peter Bellingham

## 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 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

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 m year$^{-1}$. Critically, no studies have assessed historical biocrust range shifts in drylands, where biocrusts are most dominant (Rodriguez-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-Higgens 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-Higgens 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 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).

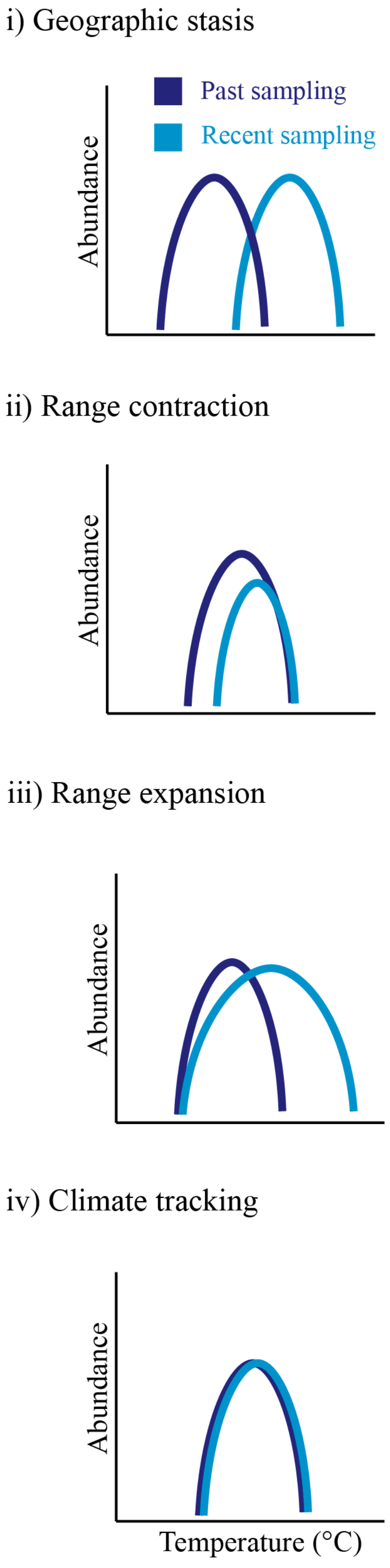

**FIGURE 1** Four responses of species ranges to climate change, shown along a gradient of increasing temperature: (i) geographic stasis, where a species occupies the same spatial position, and the observed temperature niche has become hotter over time; (ii) range contraction, where a species retains 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.

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$^2$ (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$^{-1}$ in the east to 226 mm year$^{-1}$ 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 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).

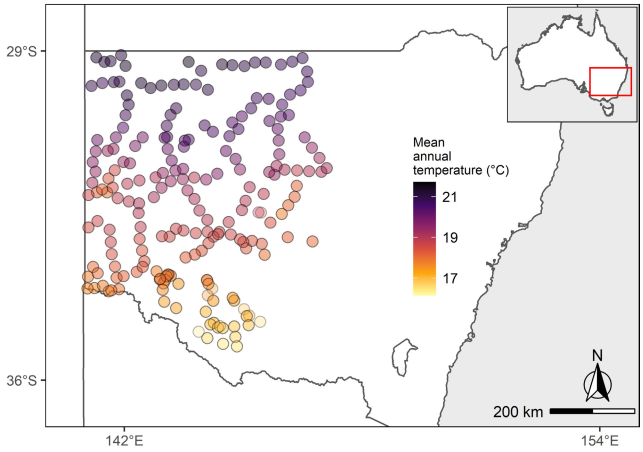

**FIGURE 2** Map of the study region in south-eastern Australia, with study sites represented by coloured circles ($N = 204$) and state boundaries shown as solid black lines.

### 2.2 | Site selection and relocation

From the original 282 sites of Eldridge and Tozer (1997), we resampled 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$^2$ (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$^2$ 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).

## 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 ($|\rho| = 0.03–0.98$).

From 1995 to 2020, mean annual temperatures at our sites rose, on average, by 0.52°C (±0.14; Figure S2a), while the number of rain days >1 mm declined, on average, by 4.1 days year$^{-1}$ (±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°C (17.9–19.5 bootstrap CI) mean annual temperature, while historically peaking at 18.2°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

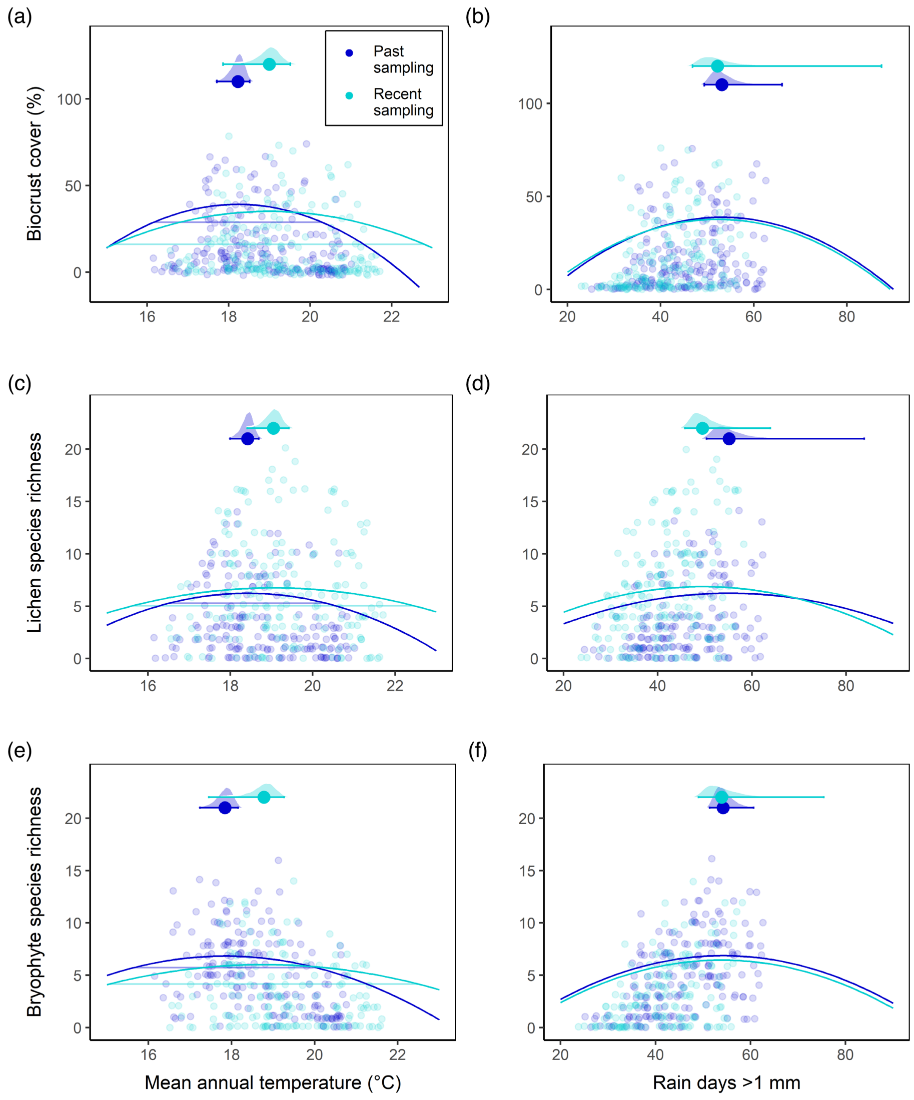

FIGURE 3 Quadratic models of biocrust cover (a, b), lichen species richness (c, d) and bryophyte species richness (e, f) along gradients of mean annual temperature (a, c, e) and the number of rain days >1 mm (b, d, f). Temperature niche breadths (focal widths) are shown as horizontal bars across fitted 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.

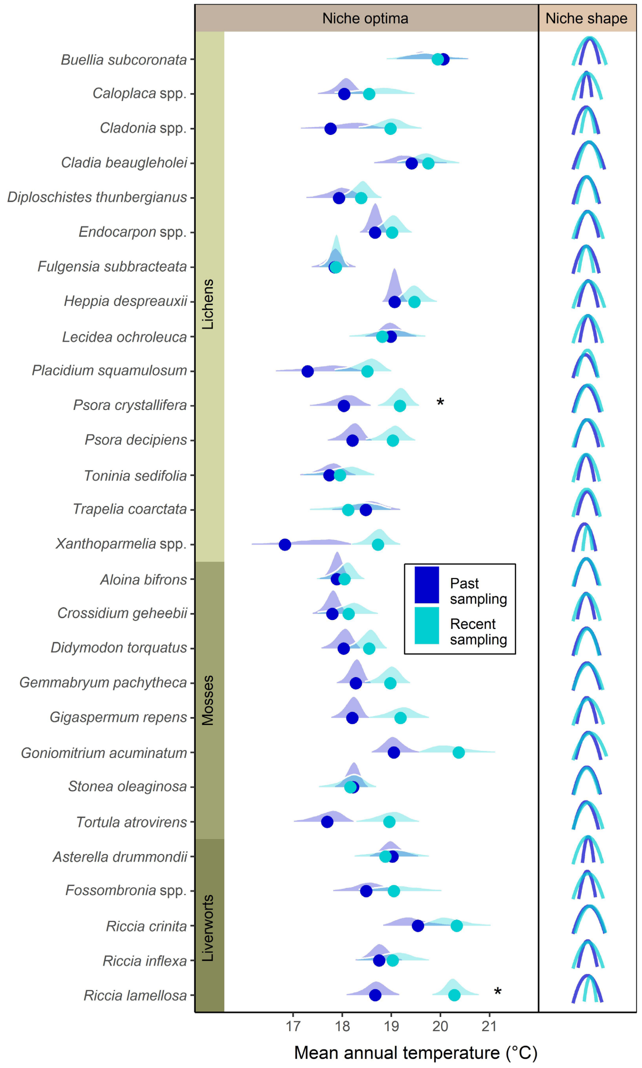

**FIGURE 4** Temperature niche optima for all biocrust taxa extracted from quadratic models of abundance, with points representing the fitted optimum, density curves representing the distribution of bootstrapped optima values, and (*) highlighting species in which 95% bootstrap confidence intervals do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

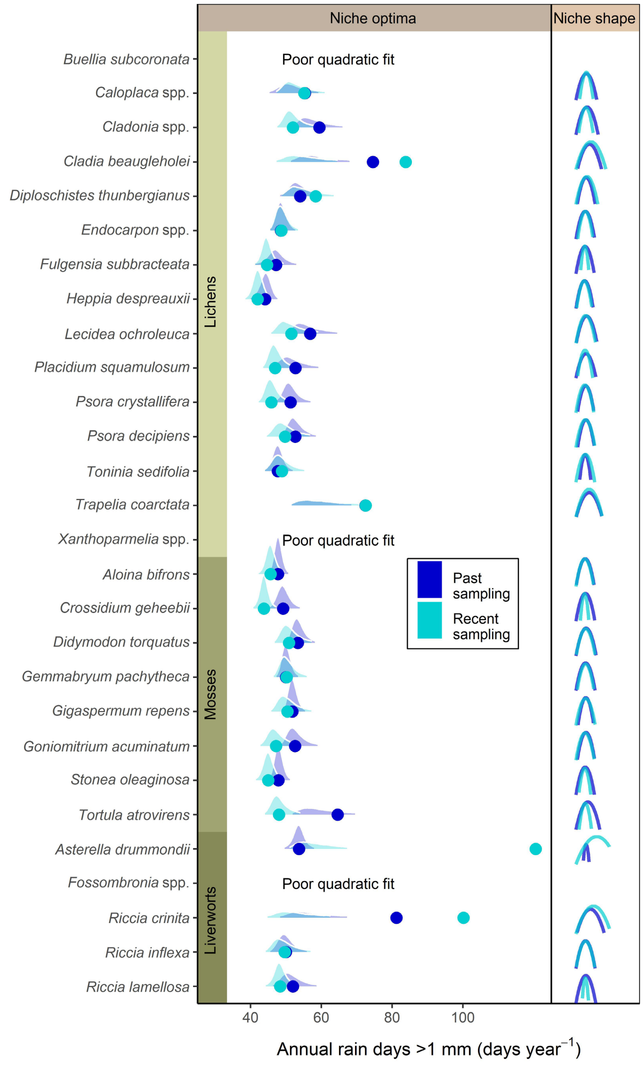

**FIGURE 5** Rainfall niche optima for all biocrust taxa extracted from quadratic models of abundance, with points representing the fitted optimum, and density curves representing the distribution of bootstrapped optima values. The panel on the right shows the shape of the entire fitted quadratic niches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

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$^{-1}$, but narrower for temperature (0.09–14.88°C; Table S1). According to the estimated focal widths, the lichen *Fulgensia subbtracteata* and the mosses *Aloina bifrons* and *Crossidium geheebii* showed relatively narrow temperature niches, while lichens such as *Placidium squamulosum* and *Claviscidium laninculatum* exhibited 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 $CO_2$ 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; Rodriguez-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.

## ACKNOWLEDGEMENTS

We acknowledge the First Nations peoples on whose country we conducted fieldwork, and the support of the Holsworth Wildlife Research Endowment. We are also grateful for the fieldwork assistance of Jingyi Ding, Samantha Travers, Georgie Fleming, Julia Chabros, Gillian Kowalick and Aya Miller, and we thank the National Computational Infrastructure at the Australian National University, an initiative of the Australian Government, for access to supercomputer resources. Open access publishing facilitated by University of New South Wales, as part of the Wiley - University of New South Wales agreement via the Council of Australian University Librarians.

## CONFLICT OF INTEREST STATEMENT

The authors have no conflicts of interest to declare.

## PEER REVIEW

The peer review history for this article is available at https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/1365-2745.14169.

## 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).

## ORCID

*Max Mallen-Cooper* https://orcid.org/0000-0002-8799-8728
*William K. Cornwell* https://orcid.org/0000-0003-4080-4073
*Eve Slavich* https://orcid.org/0000-0002-6520-6195
*Manon E. B. Sabot* https://orcid.org/0000-0002-9440-4553
*Zoe A. Xirocostas* https://orcid.org/0000-0001-7103-5153
*David J. Eldridge* https://orcid.org/0000-0002-2191-486X

## REFERENCES

Alexander, J. M., Chalmandrier, L., Lenoir, J., Burgess, T. I., Essl, F., Haider, S., Kueffer, C., McDougall, K., Milbau, A., Nuñez, M. A., Pauchard, A., Rabitsch, W., Rew, L. J., Sanders, N. J., & Pellissier, L. (2018). Lags in the response of mountain plant communities to climate change. *Global Change Biology*, *24*(2), 563–579. https://doi.org/10.1111/gcb.13976

Allen, C. D., Macalady, A. K., Chenchouni, H., Bachelet, D., McDowell, N., Vennetier, M., Kitzberger, T., Rigling, A., Breshears, D. D., (Ted) Hogg, E. H., Gonzalez, P., Fensham, R., Zhang, Z., Castro, J., Demidova, N., Lim, J.-H., Allard, G., Running, S. W., Semerci, A., & Cobb, N. (2010). A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *Forest Ecology and Management*, *259*(4), 660–684. https://doi.org/10.1016/j.foreco.2009.09.001

Antoninka, A., Chuckran, P. F., Mau, R. L., Slate, M. L., Mishler, B. D., Oliver, M. J., Coe, K. K., Stark, L. R., Fisher, K. M., & Bowker, M. A. (2022). Responses of biocrust and associated soil bacteria to novel climates are not tightly coupled. *Frontiers in Microbiology*, *13*, 821860. https://doi.org/10.3389/fmicb.2022.821860

Auld, J., Everingham, S. E., Hemmings, F. A., & Moles, A. T. (2022). Alpine plants are on the move: Quantifying distribution shifts of Australian alpine plants through time. *Diversity and Distributions*, *28*(5), 943–955. https://doi.org/10.1111/ddi.13494

Bailey, R. H. (1966). Studies on the dispersal of lichen soredia. *Journal of the Linnean Society of London, Botany*, *59*(380), 479–490. https://doi.org/10.1111/j.1095-8339.1966.tb00074.x

Barker, D. H., Stark, L. R., Zimpfer, J. F., Mcletchie, N. D., & Smith, S. D. (2005). Evidence of drought-induced stress on biotic crust moss in the Mojave Desert. *Plant, Cell & Environment*, *28*(7), 939–947. https://doi.org/10.1111/j.1365-3040.2005.01346.x

Baxter, C., Mallen-Cooper, M., Lyons, M. B., & Cornwell, W. K. (2021). Measuring reflectance of tiny organisms: The promise of species level biocrust remote sensing. *Methods in Ecology and Evolution*, *12*(11), 2174–2183. https://doi.org/10.1111/2041-210X.13690

Bennie, J., Hodgson, J. A., Lawson, C. R., Holloway, C. T. R., Roy, D. B., Brereton, T., Thomas, C. D., & Wilson, R. J. (2013). Range expansion through fragmented landscapes under a variable climate. *Ecology Letters*, *16*(7), 921–929. https://doi.org/10.1111/ele.12129

Berdugo, M., Delgado-Baquerizo, M., Soliveres, S., Hernández-Clemente, R., Zhao, Y., Gaitán, J. J., Gross, N., Saiz, H., Maire, V., Lehmann, A., Rillig, M. C., Solé, R. V., & Maestre, F. T. (2020). Global ecosystem thresholds driven by aridity. *Science*, *367*(6479), 787–790. https://doi.org/10.1126/science.aay5958

Bergamini, A., Ungricht, S., & Hofmann, H. (2009). An elevational shift of cryophilous bryophytes in the last century—An effect of climate warming? *Diversity and Distributions*, *15*(5), 871–879. https://doi.org/10.1111/j.1472-4642.2009.00595.x

Bond, W. J., & Midgley, G. F. (2012). Carbon dioxide and the uneasy interactions of trees and savannah grasses. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, *367*(1588), 601–612. https://doi.org/10.1098/rstb.2011.0182

Bowker, M. A. (2007). Biological soil crust rehabilitation in theory and practice: An underexploited opportunity. *Restoration Ecology*, *15*(1), 13–23. https://doi.org/10.1111/j.1526-100X.2006.00185.x

Bowker, M. A., Belnap, J., Büdel, B., Sannier, C., Pietrasiak, N., Eldridge, D. J., & Rivera-Aguilar, V. (2016). Controls on distribution patterns of biological soil crusts at micro-to global scales. In B. Weber, B. Büdel, & J. Belnap (Eds.), *Biological soil crusts: An organizing principle in drylands* (Vol. *226*, pp. 173–197). Springer International Publishing. https://doi.org/10.1007/978-3-319-30214-0_10

Breshears, D. D., Nyhan, J. W., Heil, C. E., & Wilcox, B. P. (1998). Effects of woody plants on microclimate in a semiarid woodland: Soil temperature and evaporation in canopy and intercanopy patches. *International Journal of Plant Sciences*, *159*(6), 1010–1017.

Brooks, M. E., Kristensen, K., Van Benthem, K. J., Magnusson, A., Berg, C. W., Nielsen, A., Skaug, H. J., Machler, M., & Bolker, B. M. (2017). GlmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *The R Journal*, *9*(2), 378–400.

Catullo, R. A., Ferrier, S., & Hoffmann, A. A. (2015). Extending spatial modelling of climate change responses beyond the realized niche: Estimating, and accommodating, physiological limits and adaptive evolution: Incorporating adaptive capacity into climate change models. *Global Ecology and Biogeography*, *24*(10), 1192–1202. https://doi.org/10.1111/geb.12344

Chamizo, S., Belnap, J., Eldridge, D. J., Cantón, Y., & Malam Issa, O. (2016). The role of biocrusts in arid land hydrology. In B. Weber, B. Büdel, & J. Belnap (Eds.), *Biological soil crusts: An organizing principle in drylands* (Vol. *226*, pp. 321–346). Springer International Publishing. https://doi.org/10.1007/978-3-319-30214-0_17

Chamizo, S., Rodríguez-Caballero, E., Moro, M. J., & Cantón, Y. (2021). Non-rainfall water inputs: A key water source for biocrust carbon fixation. *Science of the Total Environment*, *792*, 148299. https://doi.org/10.1016/j.scitotenv.2021.148299

Chandler, D. G., Day, N., Madsen, M. D., & Belnap, J. (2019). Amendments fail to hasten biocrust recovery or soil stability at a disturbed dryland sandy site. *Restoration Ecology*, *27*(2), 289–297. https://doi.org/10.1111/rec.12870

Chase, J. M., & Leibold, M. A. (2003). *Ecological niches: Linking classical and contemporary approaches*. University of Chicago Press.

Chen, N., Yu, K., Jia, R., Teng, J., & Zhao, C. (2020). Biocrust as one of multiple stable states in global drylands. *Science Advances*, *6*(39), eaay3763. https://doi.org/10.1126/sciadv.aay3763

Coe, K. K., Belnap, J., & Sparks, J. P. (2012). Precipitation-driven carbon balance controls survivorship of desert biocrust mosses. *Ecology*, *93*(7), 1626–1636. https://doi.org/10.1890/11-2247.1

Coe, K. K., Sparks, J. P., & Belnap, J. (2014). Physiological ecology of dryland biocrust mosses. In D. T. Hanson & S. K. Rice (Eds.), *Photosynthesis in bryophytes and early land plants* (Vol. *37*, pp. 291–308). Springer. https://doi.org/10.1007/978-94-007-6988-5_16

Concostrina-Zubiri, L., Molla, I., Velizarova, E., & Branquinho, C. (2017). Grazing or not grazing: Implications for ecosystem services provided by biocrusts in Mediterranean cork oak woodlands.

*Land Degradation & Development*, *28*(4), 1345–1353. https://doi.org/10.1002/ldr.2573

Corbin, J. D., & Thiet, R. K. (2020). Temperate biocrusts: Mesic counterparts to their better-known dryland cousins. *Frontiers in Ecology and the Environment*, *18*(8), 456–464. https://doi.org/10.1002/fee.2234

Crimmins, S. M., Dobrowski, S. Z., Greenberg, J. A., Abatzoglou, J. T., & Mynsberge, A. R. (2011). Changes in climatic water balance drive downhill shifts in plant species' optimum elevations. *Science*, *331*(6015), 324–327. https://doi.org/10.1126/science.1199040

Dallas, T., Decker, R. R., & Hastings, A. (2017). Species are not most abundant in the centre of their geographic range or climatic niche. *Ecology Letters*, *20*(12), 1526–1533. https://doi.org/10.1111/ele.12860

Damialis, A., Kaimakamis, E., Konoglou, M., Akritidis, I., Traidl-Hoffmann, C., & Gioulekas, D. (2017). Estimating the abundance of airborne pollen and fungal spores at variable elevations using an aircraft: How high can they fly? *Scientific Reports*, *7*(1), 44535. https://doi.org/10.1038/srep44535

Darby, B. J., & Neher, D. A. (2016). Microfauna within biological soil crusts. In B. Weber, B. Büdel, & J. Belnap (Eds.), *Biological soil crusts: An organizing principle in drylands* (Vol. *226*, pp. 139–157). Springer International Publishing. https://doi.org/10.1007/978-3-319-30214-0_8

Darrouzet-Nardi, A., Reed, S. C., Grote, E. E., & Belnap, J. (2015). Observations of net soil exchange of CO2 in a dryland show experimental warming increases carbon losses in biocrust soils. *Biogeochemistry*, *126*, 363–78. https://doi.org/10.1007/s10533-015-0163-7

de la Torre Noetzel, R., Ortega García, M. V., Miller, A. Z., Bassy, O., Granja, C., Cubero, B., Jordão, L., Martínez Frías, J., Rabbow, E., Backhaus, T., Ott, S., García Sancho, L., & de Vera, J.-P. P. (2020). Lichen vitality after a space flight on board the expose-R2 facility outside the international space station: Results of the biology and Mars experiment. *Astrobiology*, *20*(5), 583–600. https://doi.org/10.1089/ast.2018.1959

Dey, R., Lewis, S. C., Arblaster, J. M., & Abram, N. J. (2019). A review of past and projected changes in Australia's rainfall. *Wiley Interdisciplinary Reviews: Climate Change*, *10*(3), e577. https://doi.org/10.1002/wcc.577

Ding, J., Delgado-Baquerizo, M., Wang, J., & Eldridge, D. J. (2021). Ecosystem functions are related to tree diversity in forests but soil biodiversity in open woodlands and shrublands. *Journal of Ecology*, *109*(12), 4158–4170. https://doi.org/10.1111/1365-2745.13788

Ding, J., & Eldridge, D. J. (2020). Biotic and abiotic effects on biocrust cover vary with microsite along an extensive aridity gradient. *Plant and Soil*, *450*(1–2), 429–441. https://doi.org/10.1007/s11104-020-04517-0

Elbert, W., Weber, B., Burrows, S., Steinkamp, J., Büdel, B., Andreae, M. O., & Pöschl, U. (2012). Contribution of cryptogamic covers to the global cycles of carbon and nitrogen. *Nature Geoscience*, *5*(7), 459–462. https://doi.org/10.1038/ngeo1486

Eldridge, D. J. (1996). Distribution and floristics of terricolous lichens in soil crusts in arid and semi-arid New South Wales, Australia. *Australian Journal of Botany*, *44*(5), 581. https://doi.org/10.1071/BT9960581

Eldridge, D. J., & Delgado-Baquerizo, M. (2019). The influence of climatic legacies on the distribution of dryland biocrust communities. *Global Change Biology*, *25*(1), 327–336. https://doi.org/10.1111/gcb.14506

Eldridge, D. J., Delgado-Baquerizo, M., Travers, S. K., Val, J., & Oliver, I. (2017). Do grazing intensity and herbivore type affect soil health? Insights from a semi-arid productivity gradient. *Journal of Applied Ecology*, *54*(3), 976–985. https://doi.org/10.1111/1365-2664.12834

Eldridge, D. J., & Ferris, J. M. (1999). Recovery of populations of the soil lichen *Psora crenata* after disturbance in arid South Australia. *The Rangeland Journal*, *21*(2), 194. https://doi.org/10.1071/RJ9990194

Eldridge, D. J., Mallen-Cooper, M., & Ding, J. (2021). Biocrust functional traits reinforce runon-runoff patchiness in drylands. *Geoderma*, *400*, 115152. https://doi.org/10.1016/j.geoderma.2021.115152

Eldridge, D. J., & Tozer, M. E. (1997). Environmental factors relating to the distribution of terricolous bryophytes and lichens in semi-arid eastern Australia. *The Bryologist*, *100*(1), 28. https://doi.org/10.2307/3244384

Elith, J., & Leathwick, J. R. (2009). Species distribution models: Ecological explanation and prediction across space and time. *Annual Review of Ecology, Evolution, and Systematics*, *40*(1), 677–697. https://doi.org/10.1146/annurev.ecolsys.110308.120159

Escolar, C., Martínez, I., Bowker, M. A., & Maestre, F. T. (2012). Warming reduces the growth and diversity of biological soil crusts in a semi-arid environment: Implications for ecosystem structure and functioning. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, *367*(1606), 3087–3099. https://doi.org/10.1098/rstb.2011.0344

Faist, A. M., Antoninka, A. J., Belnap, J., Bowker, M. A., Duniway, M. C., Garcia-Pichel, F., Nelson, C., Reed, S. C., Giraldo-Silva, A., Velasco-Ayuso, S., & Barger, N. N. (2020). Inoculation and habitat amelioration efforts in biological soil crust recovery vary by desert and soil texture. *Restoration Ecology*, *28*(S2), S96–S105. https://doi.org/10.1111/rec.13087

Ferrenberg, S., Reed, S. C., & Belnap, J. (2015). Climate change and physical disturbance cause similar community shifts in biological soil crusts. *Proceedings of the National Academy of Sciences of the United States of America*, *112*(39), 12116–12121. https://doi.org/10.1073/pnas.1509150112

Fick, S. E., Day, N., Duniway, M. C., Hoy-Skubik, S., & Barger, N. N. (2020). Microsite enhancements for soil stabilization and rapid biocrust colonization in degraded drylands. *Restoration Ecology*, *28*(S2), S139–S149. https://doi.org/10.1111/rec.13071

Finger-Higgens, R., Duniway, M. C., Fick, S., Geiger, E. L., Hoover, D. L., Pfennigwerth, A. A., Van Scoyoc, M. W., & Belnap, J. (2022). Decline in biological soil crust N-fixing lichens linked to increasing summertime temperatures. *Proceedings of the National Academy of Sciences of the United States of America*, *119*(16), e2120975119. https://doi.org/10.1073/pnas.2120975119

Gaston, K. J. (2009). Geographic range limits: Achieving synthesis. *Proceedings of the Royal Society B: Biological Sciences*, *276*(1661), 1395–1406. https://doi.org/10.1098/rspb.2008.1480

Germain, S. J., & Lutz, J. A. (2020). Climate extremes may be more important than climate means when predicting species range shifts. *Climatic Change*, *163*(1), 579–598. https://doi.org/10.1007/s10584-020-02868-2

Gräler, B., Pebesma, E. J., & Heuvelink, G. B. (2016). Spatio-temporal interpolation using gstat. *The R Journal*, *8*(1), 204.

Grenouillet, G., & Comte, L. (2014). Illuminating geographical patterns in species' range shifts. *Global Change Biology*, *20*(10), 3080–3091. https://doi.org/10.1111/gcb.12570

Gutiérrez, M. (2018). Non-random distribution of biocrust in a natural arid environment in the northern Mexican Plateau. *Applied Ecology and Environmental Research*, *16*(3), 2441–2451. https://doi.org/10.15666/aeer/1603_24412451

Hargreaves, A. L., Samis, K. E., & Eckert, C. G. (2014). Are species' range limits simply niche limits writ large? A review of transplant experiments beyond the range. *The American Naturalist*, *183*(2), 157–173. https://doi.org/10.1086/674525

Hartig, F. (2020). *DHARMa: Residual diagnostics for hierarchical (multi-level/mixed) regression models*. R package version 0.3.3.0. https://CRAN.R-project.org/package=DHARMa

Holt, R. D. (2009). Bringing the Hutchinsonian niche into the 21st century: Ecological and evolutionary perspectives. *Proceedings of the National Academy of Sciences of the United States of America*, *106*(Suppl 2), 19659–19665. https://doi.org/10.1073/pnas.0905137106

Jackson, S. T., Betancourt, J. L., Booth, R. K., & Gray, S. T. (2009). Ecology and the ratchet of events: Climate variability, niche dimensions, and species distributions. *Proceedings of the National Academy of Sciences of the United States of America*, *106*(Suppl 2), 19685–19692. https://doi.org/10.1073/pnas.0901644106

Jackson, S. T., & Sax, D. F. (2010). Balancing biodiversity in a changing environment: Extinction debt, immigration credit and species turnover. *Trends in Ecology & Evolution*, *25*(3), 153–160. https://doi.org/10.1016/j.tree.2009.10.001

Jones, D., Wang, W., & Fawcett, R. (2009). High-quality spatial climate data-sets for Australia. *Australian Meteorological and Oceanographic Journal*, *58*(4), 233–248. https://doi.org/10.22499/2.5804.003

Keith, D. A. (2004). *Ocean shores to desert dunes: The native vegetation of New South Wales and the ACT*. Department of Environment and Conservation (NSW).

Kopecký, M., & Macek, M. (2015). Vegetation resurvey is robust to plot location uncertainty. *Diversity and Distributions*, *21*(3), 322–330. https://doi.org/10.1111/ddi.12299

Koutroulis, A. G. (2019). Dryland changes under different levels of global warming. *Science of the Total Environment*, *655*, 482–511. https://doi.org/10.1016/j.scitotenv.2018.11.215

Ladrón de Guevara, M., Gozalo, B., Raggio, J., Lafuente, A., Prieto, M., & Maestre, F. T. (2018). Warming reduces the cover, richness and evenness of lichen-dominated biocrusts but promotes moss growth: Insights from an 8 yr experiment. *New Phytologist*, *220*(3), 811–823. https://doi.org/10.1111/nph.15000

Ladrón de Guevara, M., & Maestre, F. T. (2022). Ecology and responses to climate change of biocrust-forming mosses in drylands. *Journal of Experimental Botany*, *73*, 4380–4395. https://doi.org/10.1093/jxb/erac183

Lättman, H., Milberg, P., Palmer, M. W., & Mattsson, J.-E. (2009). Changes in the distributions of epiphytic lichens in southern Sweden using a new statistical method. *Nordic Journal of Botany*, *27*(5), 413–418. https://doi.org/10.1111/j.1756-1051.2009.00425.x

Lenoir, J., Bertrand, R., Comte, L., Bourgeaud, L., Hattab, T., Murienne, J., & Grenouillet, G. (2020). Species better track climate warming in the oceans than on land. *Nature Ecology & Evolution*, *4*(8), 1044–1059. https://doi.org/10.1038/s41559-020-1198-2

Lenoir, J., Gégout, J.-C., Guisan, A., Vittoz, P., Wohlgemuth, T., Zimmermann, N. E., Dullinger, S., Pauli, H., Willner, W., & Svenning, J.-C. (2010). Going against the flow: Potential mechanisms for unexpected downslope range shifts in a warming climate. *Ecography*, *33*(1), 295–303. https://doi.org/10.1111/j.1600-0587.2010.06279.x

Lenoir, J., Gégout, J. C., Marquet, P. A., de Ruffray, P., & Brisse, H. (2008). A significant upward shift in plant species optimum elevation during the 20th century. *Science*, *320*(5884), 1768–1771. https://doi.org/10.1126/science.1156831

Lenoir, J., & Svenning, J.-C. (2015). Climate-related range shifts—A global multidimensional synthesis and new research directions. *Ecography*, *38*(1), 15–28. https://doi.org/10.1111/ecog.00967

Lewis, L. R., Rozzi, R., & Goffinet, B. (2014). Direct long-distance dispersal shapes a New World amphitropical disjunction in the dispersal-limited dung moss *Tetraplodon* (Bryopsida: Splachnaceae). *Journal of Biogeography*, *41*(12), 2385–2395. https://doi.org/10.1111/jbi.12385

Li, X., Hui, R., Zhang, P., & Song, N. (2021). Divergent responses of moss- and lichen-dominated biocrusts to warming and increased drought in arid desert regions. *Agricultural and Forest Meteorology*, *303*, 108387. https://doi.org/10.1016/j.agrformet.2021.108387

Li, X.-R., He, M.-Z., Zerbe, S., Li, X.-J., & Liu, L.-C. (2010). Micro-geomorphology determines community structure of biological soil crusts at small scales. *Earth Surface Processes and Landforms*, *35*(8), 932–940. https://doi.org/10.1002/esp.1963

Loehle, C. (2018). Disequilibrium and relaxation times for species responses to climate change. *Ecological Modelling*, *384*, 23–29. https://doi.org/10.1016/j.ecolmodel.2018.06.004

Mallen-Cooper, M., Cornwell, W. K., Slavich, E., Sabot, M. E. B., Xirocostas, Z. A., & Eldridge, D. J. (2023). Limited range shifting in biocrusts despite climate warming: A 25-year resurvey. *Dryad Digital Repository*.

Mallen-Cooper, M., Bowker, M. A., Antoninka, A. J., & Eldridge, D. J. (2020). A practical guide to measuring functional indicators and traits in biocrusts. *Restoration Ecology*, *28*(S2), S56–S66. https://doi.org/10.1111/rec.12974

Mallen-Cooper, M., & Cornwell, W. K. (2020). A systematic review of transplant experiments in lichens and bryophytes. *The Bryologist*, *123*(3), 444–454. https://doi.org/10.1639/0007-2745-123.3.443

Mallen-Cooper, M., & Cornwell, W. K. (2021). Tissue chemistry of biocrust species along an aridity gradient and comparison to vascular plant leaves. *Functional Ecology*, *35*(11), 2604–2614. https://doi.org/10.1111/1365-2435.13903

Mallen-Cooper, M., Ding, J., & Eldridge, D. J. (2022). Contrasting effects of vegetation cover and site condition on biocrust communities in subhumid drylands. *Journal of Vegetation Science*, *33*(6), e13161. https://doi.org/10.1111/jvs.13161

Mallen-Cooper, M., Eldridge, D. J., & Delgado-Baquerizo, M. (2018). Livestock grazing and aridity reduce the functional diversity of biocrusts. *Plant and Soil*, *429*(1–2), 175–185. https://doi.org/10.1007/s11104-017-3388-5

Mallen-Cooper, M., Graae, B. J., & Cornwell, W. K. (2021). Lichens buffer tundra microclimate more than the expanding shrub *Betula nana*. *Annals of Botany*, *128*(4), 407–418. https://doi.org/10.1093/aob/mcab041

Mallen-Cooper, M., Rodríguez-Caballero, E., Eldridge, D. J., Weber, B., Büdel, B., Höhne, H., & Cornwell, W. K. (2023). Towards an understanding of future range shifts in lichens and mosses under climate change. *Journal of Biogeography*, *50*(2), 406–417. https://doi.org/10.1111/jbi.14542

Min, S.-K., Cai, W., & Whetton, P. (2013). Influence of climate variability on seasonal extremes over Australia. *Journal of Geophysical Research: Atmospheres*, *118*(2), 643–654. https://doi.org/10.1002/jgrd.50164

Morueta-Holme, N., Engemann, K., Sandoval-Acuña, P., Jonas, J. D., Segnitz, R. M., & Svenning, J.-C. (2015). Strong upslope shifts in Chimborazo's vegetation over two centuries since Humboldt. *Proceedings of the National Academy of Sciences of the United States of America*, *112*(41), 12741–12745. https://doi.org/10.1073/pnas.1509938112

Nicholls, N., Drosdowsky, W., & Lavery, B. (1997). Australian rainfall variability and change. *Weather*, *52*(3), 66–72. https://doi.org/10.1002/j.1477-8696.1997.tb06274.x

Normand, S., Treier, U. A., Randin, C., Vittoz, P., Guisan, A., & Svenning, J.-C. (2009). Importance of abiotic stress as a range-limit determinant for European plants: Insights from species responses to climatic gradients. *Global Ecology and Biogeography*, *18*(4), 437–449. https://doi.org/10.1111/j.1466-8238.2009.00451.x

Nörr, M. (1974). Trockenresistenz bei Moosen. *Flora*, *163*(5), 371–387.

Oukarroum, A., Strasser, R. J., & Schansker, G. (2012). Heat stress and the photosynthetic electron transport chain of the lichen *Parmelina tiliacea* (Hoffm.) Ach. in the dry and the wet state: Differences and similarities with the heat stress response of higher plants. *Photosynthesis Research*, *111*(3), 303–314. https://doi.org/10.1007/s11120-012-9728-7

Pecl, G. T., Araújo, M. B., Bell, J. D., Blanchard, J., Bonebrake, T. C., Chen, I.-C., Clark, T. D., Colwell, R. K., Danielsen, F., Evengård, B., Falconi, L., Ferrier, S., Frusher, S., Garcia, R. A., Griffis, R. B., Hobday, A. J., Janion-Scheepers, C., Jarzyna, M. A., Jennings, S., … Williams, S. E. (2017). Biodiversity redistribution under climate change: Impacts on ecosystems and human well-being. *Science*, *355*(6332), eaai9214. https://doi.org/10.1126/science.aai9214

Phillips, M. L., McNellis, B. E., Howell, A., Lauria, C. M., Belnap, J., & Reed, S. C. (2022). Biocrusts mediate a new mechanism for land degradation under a changing climate. *Nature Climate Change*, *12*(1), 71–76. https://doi.org/10.1038/s41558-021-01249-6

Raggio, J., Green, A., Pintado, A., Sancho, L. G., & Büdel, B. (2021). Functional performance of biocrusts across Europe and its implications for drylands. *Journal of Arid Environments*, *186*, 104402. https://doi.org/10.1016/j.jaridenv.2020.104402

Rapacciuolo, G., Maher, S. P., Schneider, A. C., Hammond, T. T., Jabis, M. D., Walsh, R. E., Iknayan, K. J., Walden, G. K., Oldfather, M. F., Ackerly, D. D., & Beissinger, S. R. (2014). Beyond a warming fingerprint: Individualistic biogeographic responses to heterogeneous climate change in California. *Global Change Biology*, *20*(9), 2841–2855. https://doi.org/10.1111/gcb.12638

Read, C. F., Duncan, D. H., Vesk, P. A., & Elith, J. (2014). Biocrust morphogroups provide an effective and rapid assessment tool for drylands. *Journal of Applied Ecology*, *51*(6), 1740–1749. https://doi.org/10.1111/1365-2664.12336

Reed, S. C., Coe, K. K., Sparks, J. P., Housman, D. C., Zelikova, T. J., & Belnap, J. (2012). Changes to dryland rainfall result in rapid moss mortality and altered soil fertility. *Nature Climate Change*, *2*(10), 752–755. https://doi.org/10.1038/nclimate1596

Robillard, C. M., Coristine, L. E., Soares, R. N., & Kerr, J. T. (2015). Facilitating climate-change-induced range shifts across continental land-use barriers: Conserving habitat for range shifts. *Conservation Biology*, *29*(6), 1586–1595. https://doi.org/10.1111/cobi.12556

Rodriguez-Caballero, E., Belnap, J., Büdel, B., Crutzen, P. J., Andreae, M. O., Pöschl, U., & Weber, B. (2018). Dryland photoautotrophic soil surface communities endangered by global change. *Nature Geoscience*, *11*(3), 185–189. https://doi.org/10.1038/s41561-018-0072-1

Rodríguez-Caballero, E., Castro, A. J., Chamizo, S., Quintas-Soriano, C., Garcia-Llorente, M., Cantón, Y., & Weber, B. (2018). Ecosystem services provided by biocrusts: From ecosystem functions to social values. *Journal of Arid Environments*, *159*, 45–53. https://doi.org/10.1016/j.jaridenv.2017.09.005

Rodríguez-Caballero, E., Román, J. R., Chamizo, S., Roncero Ramos, B., & Cantón, Y. (2019). Biocrust landscape-scale spatial distribution is strongly controlled by terrain attributes: Topographic thresholds for colonization in a semiarid badland system. *Earth Surface Processes and Landforms*, *44*(14), 2771–2779. https://doi.org/10.1002/esp.4706

Rodriguez-Caballero, E., Stanelle, T., Egerer, S., Cheng, Y., Su, H., Canton, Y., Belnap, J., Andreae, M. O., Tegen, I., Reick, C. H., Pöschl, U., & Weber, B. (2022). Global cycling and climate effects of aeolian dust controlled by biological soil crusts. *Nature Geoscience*, *15*(6), 458–463. https://doi.org/10.1038/s41561-022-00942-1

Sagarin, R. D., Gaines, S. D., & Gaylord, B. (2006). Moving beyond assumptions to understand abundance distributions across the ranges of species. *Trends in Ecology & Evolution*, *21*(9), 524–530. https://doi.org/10.1016/j.tree.2006.06.008

Sancho, L. G., Belnap, J., Colesie, C., Raggio, J., & Weber, B. (2016). Carbon budgets of biological soil crusts at micro-, meso-, and global scales. In B. Weber, B. Büdel, & J. Belnap (Eds.), *Biological soil crusts: an organizing principle in drylands* (Vol. *226*, pp. 287–304). Springer International Publishing. https://doi.org/10.1007/978-3-319-30214-0_15

Sax, D. F., Early, R., & Bellemare, J. (2013). Niche syndromes, species extinction risks, and management under climate change. *Trends in Ecology & Evolution*, *28*(9), 517–523. https://doi.org/10.1016/j.tree.2013.05.010

Sexton, J. P., McIntyre, P. J., Angert, A. L., & Rice, K. J. (2009). Evolution and ecology of species range limits. *Annual Review of Ecology, Evolution, and Systematics*, *40*(1), 415–436. https://doi.org/10.1146/annurev.ecolsys.110308.120317

Sherren, K., Fischer, J., & Fazey, I. (2012). Managing the grazing landscape: Insights for agricultural adaptation from a mid-drought photo-elicitation study in the Australian sheep-wheat belt. *Agricultural Systems*, *106*(1), 72–83. https://doi.org/10.1016/j.agsy.2011.11.001

Shriver, R. K., Andrews, C. M., Pilliod, D. S., Arkle, R. S., Welty, J. L., Germino, M. J., Duniway, M. C., Pyke, D. A., & Bradford, J. B. (2018). Adapting management to a changing world: Warm temperatures, dry soil, and interannual variability limit restoration success of a dominant woody shrub in temperate drylands. *Global Change Biology*, *24*(10), 4972–4982. https://doi.org/10.1111/gcb.14374

Stark, L. R. (2005). Phenology of patch hydration, patch temperature and sexual reproductive output over a four-year period in the desert moss Crossidium crassinerve. *Journal of Bryology*, *27*(3), 231–240. https://doi.org/10.1179/174328205X69977

Stark, L. R., Greenwood, J. L., & Brinda, J. C. (2017). Desiccated *Syntrichia ruralis* shoots regenerate after 20 years in the herbarium. *Journal of Bryology*, *39*(1), 85–93. https://doi.org/10.1080/03736687.2016.1176307

Stevens, G. C. (1989). The latitudinal gradient in geographical range: How so many species coexist in the tropics. *The American Naturalist*, *133*(2), 240–256. https://doi.org/10.1086/284913

Stuble, K. L., Bewick, S., Fisher, M., Forister, M. L., Harrison, S. P., Shapiro, A. M., Latimer, A. M., & Fox, L. R. (2021). The promise and the perils of resurveying to understand global change impacts. *Ecological Monographs*, *91*(2), e01435. https://doi.org/10.1002/ecm.1435.

Sunday, J. M., Pecl, G. T., Frusher, S., Hobday, A. J., Hill, N., Holbrook, N. J., Edgar, G. J., Stuart-Smith, R., Barrett, N., Wernberg, T., Watson, R. A., Smale, D. A., Fulton, E. A., Slawinski, D., Feng, M., Radford, B. T., Thompson, P. A., & Bates, A. E. (2015). Species traits and climate velocity explain geographic range shifts in an ocean-warming hotspot. *Ecology Letters*, *18*(9), 944–953. https://doi.org/10.1111/ele.12474

Svenning, J.-C., & Sandel, B. (2013). Disequilibrium vegetation dynamics under future climate change. *American Journal of Botany*, *100*(7), 1266–1286. https://doi.org/10.3732/ajb.1200469

Tingley, M. W., Monahan, W. B., Beissinger, S. R., & Moritz, C. (2009). Birds track their Grinnellian niche through a century of climate change. *Proceedings of the National Academy of Sciences of the United States of America*, *106*, 19637–19643. https://doi.org/10.1073/pnas.0901562106

Trabucco, A., & Zomer, R. J. (2018). Global aridity index and potential evapo-transpiration (ET0) climate database v2. *CGIAR Consortium Spatial Information*, *10*, m9.

Virtanen, R., Luoto, M., Rämä, T., Mikkola, K., Hjort, J., Grytnes, J.-A., & Birks, H. J. B. (2010). Recent vegetation changes at the high-latitude tree line ecotone are controlled by geomorphological disturbance, productivity and diversity: Drivers of vegetation change at high latitudes. *Global Ecology and Biogeography*, *19*(6), 810–821. https://doi.org/10.1111/j.1466-8238.2010.00570.x

Wang, T., Kou, X., Xiong, Y., Mou, P., Wu, J., & Ge, J. (2010). Temporal and spatial patterns of NDVI and their relationship to precipitation in the Loess Plateau of China. *International Journal of Remote Sensing*, *31*(7), 1943–1958. https://doi.org/10.1080/01431160902929263

Warren, S. D., Clair, L. L., Stark, L. R., Lewis, L. A., Pombubpa, N., Kurbessoian, T., Stajich, J. E., & Aanderud, Z. T. (2019). Reproduction and dispersal of biological soil crust organisms. *Frontiers in Ecology and Evolution*, *7*, 344. https://doi.org/10.3389/fevo.2019.00344

Weber, B., Belnap, J., Büdel, B., Antoninka, A. J., Barger, N. N., Chaudhary, V. B., Darrouzet-Nardi, A., Eldridge, D. J., Faist, A. M., Ferrenberg, S., Havrilla, C. A., Huber-Sannwald, E., Malam Issa, O., Maestre, F. T., Reed, S. C., Rodriguez-Caballero, E., Tucker, C., Young, K. E., Zhang, Y., … Bowker, M. A. (2022). What is a biocrust? A refined, contemporary definition for a broadening research community. *Biological Reviews*, *97*, 1768–1785. https://doi.org/10.1111/brv.12862

Weber, B., Bowker, M., Zhang, Y., & Belnap, J. (2016). Natural recovery of biological soil crusts after disturbance. In B. Weber, B. Büdel, & J. Belnap (Eds.), *Biological soil crusts: An organizing principle in drylands*

(Vol. *226*, pp. 479–498). Springer International Publishing. https://doi.org/10.1007/978-3-319-30214-0_23

Woolbright, S. A., Whitham, T. G., Gehring, C. A., Allan, G. J., & Bailey, J. K. (2014). Climate relicts and their associated communities as natural ecology and evolution laboratories. *Trends in Ecology & Evolution*, *29*(7), 406–416. https://doi.org/10.1016/j.tree.2014.05.003

Wu, Y.-S., Li, X.-R., Jia, R.-L., Yin, R.-P., & Liu, T.-J. (2023). Livestock trampling regulates the soil carbon exchange by mediating surface roughness and biocrust cover. *Geoderma*, *429*, 116275. https://doi.org/10.1016/j.geoderma.2022.116275

Yalcin, S., & Leroux, S. J. (2017). Diversity and suitability of existing methods and metrics for quantifying species range shifts. *Global Ecology and Biogeography*, *26*(6), 609–624. https://doi.org/10.1111/geb.12579

Zaady, E., Eldridge, D. J., & Bowker, M. A. (2016). Effects of local-scale disturbance on biocrusts. In B. Weber, B. Büdel, & J. Belnap (Eds.), *Biological soil crusts: An organizing principle in drylands* (Vol. *226*, pp. 429–449). Springer International Publishing. https://doi.org/10.1007/978-3-319-30214-0_21

Zhang, Y., Aradottir, A. L., Serpe, M., & Boeken, B. (2016). Interactions of biological soil crusts with vascular plants. In B. Weber, B. Büdel, & J. Belnap (Eds.), *Biological soil crusts: An organizing principle in drylands* (Vol. *226*, pp. 385–406). Springer International Publishing. https://doi.org/10.1007/978-3-319-30214-0_19

Zhu, K., Woodall, C. W., & Clark, J. S. (2012). Failure to migrate: Lack of tree range expansion in response to climate change. *Global Change Biology*, *18*(3), 1042–1052. https://doi.org/10.1111/j.1365-2486.2011.02571.x

## 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 (ΔAIC) values for models of species abundance across climatic predictors, as compared to the top model (lowest AIC) for either temperature or rainfall predictors (ΔAIC > 2 shown in white).

**Figure S2.** Comparison of (a) mean annual temperature and (b) the number of rain days >1 mm 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 >1 mm 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.

**How to cite this article:** Mallen-Cooper, M., Cornwell, W. K., Slavich, E., Sabot, M. E. B., Xirocostas, Z. A., & Eldridge, D. J. (2023). Limited range shifting in biocrusts despite climate warming: A 25-year resurvey. *Journal of Ecology*, *111*, 2194–2207. https://doi.org/10.1111/1365-2745.14169