

Tissue chemistry of biocrust species along an aridity gradient and comparison to vascular plant leaves

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Abstract

1. Biocrusts are an extensive autotrophic groundcover but are regularly excluded from ecosystem models. One rationale for their exclusion is that their contributions to C and N cycles are negligible in comparison to vascular plants. Here we estimated the magnitude of the biocrust contribution to nutrient cycling in functional terms, comparing tissue chemistry and stoichiometry per ground area with vascular plants per leaf area.
2. We quantified tissue C, N, P and a range of micronutrients in 21 abundant biocrust taxa from an aridity gradient spanning 500 km of Australian drylands.
3. The C, N and P tissue chemistry of biocrust species and vascular plant leaves occupied a similar range, both as ratios and per area. This implies that in functional terms, biocrusts could be considered as a single layer of leaf area spread out across the ground and added to Leaf Area Index (LAI) measurements accordingly.
4. Within biocrust species, the C:N ratio significantly declined with increasing aridity, which was entirely driven by carbon. This finding demonstrates a key functional difference between vascular leaves and biocrusts: C:N ratios in vascular plants are lower in drier environments due to elevated levels of N-rich photosynthetic machinery relating to a trade-off in water-use regulation, while C:N ratios in biocrusts decline with aridity most likely due to carbon shortages relating to their inability to regular water loss (poikilohydry).
5. As global drylands become drier with climate change, our findings suggest that biocrust tissue carbon stocks will decline gradually until the point where carbon budgets become negative and standing biomass is no longer viable.

KEYWORDS

biocrust, bryophyte, C/N ratio, functional traits, lichen, nutrient cycling, stoichiometry, tissue chemistry

1 | INTRODUCTION

A key aspect of the functional and evolutionary strategies of plants can be inferred from the carbon, nitrogen and phosphorus in their tissues (Pérez-Harguindeguy et al., 2013; Sterner & Elser, 2002; Wright et al., 2004). Carbon, fixed by plants during photosynthesis,

forms the basis of all organic molecules within plants and can be strategically allocated to reproductive, growth or defensive functions (Hartmann et al., 2020). Within photosynthetic organisms, nitrogen concentrations are strongly linked to protein construction, particularly rubisco (ribulose-1,5-bisphosphate carboxylase-oxygenase). Similarly, phosphorus can serve as a proxy for ribosome

activity (Niklas, 2008). In water-limited environments, there has long been thought to be a trade-off between nitrogen use and water-use (Field et al., 1983), with N per leaf area a key mediator. Vascular plants living in drier environments often have higher leaf N because the elevated concentration of rubisco allows a greater drawdown of CO₂ and thus stomates can remain closed for longer periods of time (Wright et al., 2003), trading-off N-use efficiency for water-use efficiency.

Biocrusts—soil-dwelling communities of lichens, bryophytes and microbes that cover extensive areas of drylands and tundra (Crittenden, 2000; Maestre et al., 2021)—have been analogised to a vast leaf covering the soil (Concostrina-Zubiri et al., 2018; Mallen-Cooper et al., 2020). It has been estimated that biocrusts account for 5% of carbon fixation and 36% of nitrogen fixation on the global land surface (Elbert et al., 2012). In addition to nutrient cycling, biocrusts perform a wide range of functional roles associated with hydrology (Eldridge et al., 2020), erosion (Chamizo et al., 2017), biotic interactions (Havrilla et al., 2019) and maintaining fine-scale microclimates (Mallen-Cooper et al., 2021). Because of their important roles in ecosystem functioning, there has been growing interest in quantifying the functional traits of biocrust taxa to explain patterns in community ecology (Ellis et al., 2021; Ferrenberg & Reed, 2017; Mallen-Cooper et al., 2018; Soliveres & Eldridge, 2020) and predict the effects of climate change on nutrient cycling (Concostrina-Zubiri et al., 2021; Deane-Coe et al., 2015). Since the biochemical traits of lichens and bryophytes were first expounded by Cornelissen et al. (2007), numerous studies have measured tissue nutrients in biocrust species, particularly those examining anthropogenic nitrogen deposition (Table S1). To our knowledge, only nine studies have measured tissue chemistry in dryland biocrusts, and tissue nutrients have yet to be quantified, at the biocrust species level, in continents other than Europe and North America (Table S1). Similar to foliar nutrients (Elser et al., 2010), tissue nutrients in biocrusts respond to climate variables and can therefore act as indicators of global change (Concostrina-Zubiri et al., 2018).

Often the amount of leaf area in arid sites is measured without considering biocrust (e.g. Xiao & Hu, 2017). This is understandable since biocrusts create an intricate three-dimensional structure on the ground's surface that is decidedly not flat and so cannot be quantified with conventional approaches. In addition, lichen chemistry is fundamentally driven by the dynamics of the symbiosis, and cell wall chemistry is different to vascular plants (Palmqvist et al., 1998), meaning that estimation techniques (e.g. leaf area estimates from hyperspectral sensors; le Maire et al., 2008) developed for vascular plants cannot easily be applied to lichens. On the other hand, biocrust species photosynthesise and transpire water like leaves, although they can only photosynthesise when wet (Raggio et al., 2021), and one might be tempted to consider biocrust in simplified earth system models as a single layer of leaf area spread out across the ground. One key test is whether the chemical and stoichiometric traits of biocrust species are similar to vascular plant leaves within arid regions and across aridity gradients. In other words, if vascular plant leaves and biocrust organisms (including all their leafy and thalloid

microstructures) are broadly equivalent in their nutrient pools per ground area, biocrust nutrient cycling could be approximated as a flat leaf covering the soil surface.

The C:N ratio of a species can vary throughout its range. Along a gradient of increasing aridity, the C:N ratios of biocrust mosses have been shown to decrease, likely because the organisms are unable to access deep subsoil moisture and therefore carbon fixation is tightly coupled with rainfall and other forms of moisture (Delgado-Baquerizo et al., 2018). In other words, low C:N ratios at the arid limit of a biocrust species can reflect an undersupply of carbon rather than an oversupply, or high allocation of, nitrogen, as might be the case of vascular plants optimising CO₂ drawdown (Luo et al., 2017; Wright et al., 2003). However, Delgado-Baquerizo et al. (2018) used pooled moss samples containing a varying composition of three moss taxa, and so their findings do not preclude a compositional turnover effect whereby a low C:N species could have been more abundant at drier sites. Thus, the relationship between biocrust tissue stoichiometry and aridity remains to be tested at the species level.

In our study, we aimed to (a) quantify the tissue chemistry of 21 abundant biocrust taxa in the drylands of south-eastern Australia, (b) compare biocrust tissue chemistry with vascular leaf traits and (c) examine relationships between biocrust tissue nutrients and aridity. Along with environmental factors such as nutrient deposition and climate (Concostrina-Zubiri et al., 2018; Hogan et al., 2010), species identity typically explains a substantial amount of variation in biocrust tissue chemistry (e.g. Concostrina-Zubiri et al., 2021; Torres-Cruz et al., 2018). In general, we anticipated that the distribution of biocrust C, N and P values will be similar to vascular plant leaves, reflecting an underlying functional similarity in the allocation of nutrients to photosynthetic machinery and other cellular functions. We expected biocrusts to contain high amounts of structural C-rich tissue relative to N and P, because according to the leaf economics spectrum, they are analogous to extremely long-lived leaves (Wright et al., 2004). However, we also predicted a decrease in the C:N ratio with increasing aridity in line with the findings of Delgado-Baquerizo et al. (2018). Additionally, as a preliminary exploration of the link between biocrust tissue nutrients and the process of nutrient cycling, we compared tissue nutrients and enzymes that relate to the degradation and recycling of those nutrients.

2 | MATERIALS AND METHODS

Biocrust organisms were collected from nine nature reserves in the drylands of south-eastern Australia in May 2020 (Table S2; Figure S1). Our study only includes the macroscopic components of biocrusts, that is lichens and bryophytes, and none of the included taxa were able to fix nitrogen. Rainfall at the study sites ranges from 284 to 642 mm per year, and mean annual temperatures range from 14.9 to 20.2°C (Table S2). At the humid end of the gradient, biocrust communities are typically dominated by tall mosses (e.g. *Triquetrella papillata*) and large, fruticose or foliose lichens (e.g. *Cladia* spp., *Xanthoparmelia* spp.). At more arid sites, biocrusts largely consisted

of short mosses (e.g. *Didymodon torquatus*) and squamulose lichens (e.g. *Psora decipiens*, *Endocarpon* spp.).

Biocrust organisms were identified to species where possible, and then separated from the soil by carefully brushing and scraping the dry specimens. We selected species that were abundant and relatively large, because the labour time required to separate very small organisms (e.g. *Didymodon torquatus*, *Collema coccophorum*) is exceedingly high. Apart from large crustose lichens, each replicate sample was a patch of multiple organisms, often hundreds of stems or squamules, from the same species and site. The size of the patch varied according to species mass (i.e. large patches up to 15 cm diameter were required for lightweight species such as *Riccia limbata*), and patches sampled at the same site were separated by at least 10 m. Samples were dried for 7 days in an oven at 60°C, and all samples had a minimum dry mass of 0.5 g, which was sufficient for multiple nutrient analyses. There were four replicates for each species except for the liverwort *Asterella drummondii* ($N = 3$ due to limited material) and a few abundant taxa ($N = 5$ for *Endocarpon* spp., *Diploschistes thunbergianus*, *Pseudocrossidium crinitum*; $N = 6$ for *Psora decipiens*; and $N = 8$ for *Barbula calycina*). The exact two-dimensional area of each sample was derived from a photograph taken directly above the sample, which was manually traced using ImageJ software (Abràmoff et al., 2004). For most mosses, which are not self-supporting once detached from the soil, photographs were taken before separation from the soil, in order to accurately characterise the area occupied by the sample.

Dried samples were then crushed to a fine powder using either a ball bearing or a pestle. Several lichen species were brittle enough to be crushed with a steel ball bearing, which was shaken, along with the sample material, inside a sealed test tube. The remaining taxa were crushed using a mortar and pestle. The ball bearing, mortar and pestle were carefully cleaned with 95% ethanol between samples. Powdered samples were analysed for the content of C, N, S (LECO combustion), and P, Ca, Co, Cu, Fe, K, Mg, Mn, Si and Zn (nitric acid digest) by a commercial laboratory (Environmental Analysis Laboratory, Southern Cross University, Lismore, New South Wales, Australia).

We compiled a list of all vascular plant species recorded within a 50-km radius of each collection site using data from the Atlas of Living Australia (<https://www.ala.org.au>). We extracted the area-based leaf N (g/m^2) and P (g/m^2), and biomass-based leaf N (mg/g), P (mg/g) and C (mg/g), of the listed locally occurring vascular plants (comprising 131, 54, 254, 127 and 152 taxa respectively) from the AusTraits database in February 2021 (Falster et al., 2021). Leaf C per area was unavailable in this dataset at the time of extraction. Stoichiometric ratios of vascular plants were calculated using the biomass-based leaf traits, which are paired within AusTraits by site and species but not individual. Plants were grouped into four growth form categories (tree, shrub, grass and herb), and those that could not be easily grouped (e.g. climbers and epiphytes) were excluded for simplicity.

We chose to compare the chemical traits of biocrusts and vascular plants in per area terms for two reasons. First, traits standardised

by area reflect the exchange of nutrients across a surface, which is more relevant to our comparison of nutrient cycling than traits standardised by biomass, which are more closely linked to the allocation of resources per gram of plant tissue (Wright et al., 2004). Second, we observed that it was virtually impossible to completely remove all soil particles from crustose lichens, and therefore traits expressed in per mass terms would be underestimated. The crustose lichens in our study area have thin thalli (approximately 0.5 mm; Mallen-Cooper & Eldridge, 2016) and could therefore not withstand vigorous cleaning. Despite attempting several gentle cleaning strategies, a non-negligible amount of clay- and silt-sized soil particles remained among their hyphae when examined microscopically in cross-section. Indeed, the silicon content of crustose lichen samples was markedly higher than other biocrust taxa, suggesting soil contamination (Figure S2). Per area measurements, on the other hand, are unaffected by the amount of remaining soil, unless the nutrient of interest is a chemical constituent of soil particles.

Biocrust taxa were assigned to morphogroups with similar physical attributes (Eldridge & Rosentreter, 1999). Enzyme trait means associated with N and P cycling were available from the study by Mallen-Cooper and Eldridge (2016) for 15 of the 21 species in our study, and could be compared at the species level with N and P tissue trait means. In brief, the enzymes *N*-acetyl- β -glucosaminidase (NAG) and phosphatase were measured fluorometrically after incubating cleaned biocrust samples for 90 min in fluorescently tagged substrate (Mallen-Cooper & Eldridge, 2016). To calculate the amount of variation explained by species, variance partitioning was conducted in the `LME4` R package by assigning species as a random effect (version 1.1-26; Bates et al., 2015). The `NLME` R package (version 3.1-149; Pinheiro et al., 2021) was used to conduct linear mixed effects models of the relationships between aridity and each of biocrust C, N, P and the C:N ratio. We calculated aridity by extracting the Aridity Index (precipitation/potential evapotranspiration) from the study by Trabucco and Zomer (2018) and then taking the reciprocal such that increasing aridity corresponded to increasing dryness. The models were only conducted on taxa collected from more than three sites, and included a random slope and intercept for each taxon. In all three models, the response variable was log-transformed to satisfy assumptions.

3 | RESULTS

The tissue nutrient contents of biocrusts varied widely among species (Table 1; Tables S3 and S4), with tissue N values ranging from 1.1 to 16.3 g/m^2 , tissue C values ranging from 26.4 to 413.1 g/m^2 and tissue P values ranging from 0.082 to 0.911 g/m^2 . Species explained 62.5%, 64.1% and 56.0% of the variation in C, N and P traits respectively.

Biocrust N values were relatively high compared with vascular plant leaves (Figure 1). The mean biocrust tissue N, 5.24 g/m^2 (± 2.74 SD), represented the 85th percentile of dryland vascular plant species recorded in the vicinity of our collection sites. Similarly, biocrust

TABLE 1 Study species, number of replicate samples and mean quantity (g) of tissue C, N and P per m²

Species	Morphogroup	Reps	C (g/m ²)	N (g/m ²)	P (g/m ²)
<i>Acarospora schleicheri</i>	Crustose lichen	4	168.04 ± 27.82	4.75 ± 0.93	0.38 ± 0.04
<i>Cladia aggregata</i>	Fruticose lichen	4	189.16 ± 41.41	5.72 ± 2.29	0.27 ± 0.08
<i>Cladia beaugleholei</i>	Fruticose lichen	4	207.39 ± 35.90	6.47 ± 0.33	0.36 ± 0.13
<i>Cladia corallaizon</i>	Fruticose lichen	4	228.22 ± 66.11	5.42 ± 1.41	0.31 ± 0.10
<i>Cladia muelleri</i>	Fruticose lichen	4	165.35 ± 60.08	3.87 ± 1.00	0.27 ± 0.04
<i>Circinaria calcarea</i>	Fruticose lichen	4	131.56 ± 12.96	7.69 ± 0.61	0.41 ± 0.09
<i>Diploschistes thunbergianus</i>	Crustose lichen	5	77.18 ± 12.62	5.82 ± 0.69	0.40 ± 0.10
<i>Endocarpon</i> spp.	Squamulose lichen	5	127.51 ± 15.43	12.44 ± 2.17	0.58 ± 0.05
<i>Lecidea ochroleuca</i>	Crustose lichen	4	95.73 ± 41.32	5.40 ± 2.00	0.42 ± 0.08
<i>Psora decipiens</i>	Squamulose lichen	6	98.79 ± 18.00	5.38 ± 0.48	0.35 ± 0.04
<i>Xanthoparmelia pulla</i>	Foliose lichen	4	96.48 ± 47.37	2.69 ± 0.98	0.17 ± 0.08
<i>Xanthoparmelia reptans</i>	Foliose lichen	4	61.29 ± 7.31	1.95 ± 0.34	0.12 ± 0.04
<i>Xanthoparmelia semiviridis</i>	Foliose lichen	4	163.82 ± 6.38	3.52 ± 1.08	0.17 ± 0.00
<i>Xanthoparmelia taractica</i>	Foliose lichen	4	160.27 ± 48.19	4.92 ± 1.97	0.30 ± 0.10
<i>Asterella drummondii</i>	Thallose liverwort	3	63.68 ± 4.06	3.08 ± 0.38	0.46 ± 0.09
<i>Barbula calycina</i>	Short moss	8	98.54 ± 29.62	3.14 ± 1.01	0.22 ± 0.06
<i>Campylopus introflexus</i>	Short moss	4	198.76 ± 34.71	7.19 ± 3.74	0.49 ± 0.32
<i>Pseudocrossidium crinitum</i>	Tall moss	5	248.55 ± 108.91	7.64 ± 3.35	0.70 ± 0.23
<i>Riccia lamellosa</i>	Thallose liverwort	4	81.93 ± 15.02	4.12 ± 0.35	0.40 ± 0.08
<i>Rosulabryum campylothecium</i>	Short moss	4	92.75 ± 10.51	3.88 ± 0.34	0.26 ± 0.04
<i>Triquetrella papillata</i>	Tall moss	4	78.41 ± 36.89	4.00 ± 2.14	0.28 ± 0.15

P values fell in the upper range of leaf P values (Figure S3), with the mean of 0.35 g/m² (±0.17 SD) representing the 98th percentile of leaf values from vascular species recorded near collection sites. The lichen taxon *Endocarpon* was extremely nitrogen rich, with a mean nitrogen content of 12.44 g/m² (±2.17 SD) or 2.46% (±0.49 SD). The next largest mean value of tissue N, 7.69 g/m² (±0.61 SD), was found in the fruticose lichen *Circinaria calcarea*. Foliose lichens in the *Xanthoparmelia* genus were especially low in nitrogen. In percentage terms, and after excluding crustose lichens due to suspected soil contamination, the average lichen in our study was 33.09% C (±7.86 SD), 1.18% N (±0.45 SD) and 0.066% P (±0.020 SD), matching closely with the global biocrust lichen average, calculated from Table S1, of 30.38% C (±8.33 SD), 0.87% N (±0.57 SD) and 0.046% P (±0.014 SD). The average bryophyte in our study was 32.94% C (±4.15 SD), 1.33% N (±0.25 SD) and 0.117% P (±0.047 SD), while the global biocrust bryophyte average was 40.88% C (±6.90 SD), 1.32% N (±0.50 SD) and 0.149% P (±0.074 SD).

The highest C:N ratios were found in large lichens with complex morphological structures (Figure 2). Biocrust C:N values were similar to vascular plant leaves, although values for the lichens *Endocarpon* spp. and *Diploschistes thunbergianus* were below 1 SD of the leaf mean (Figure S5). Biocrust N:P ratios were mostly contained within 1 SD below the leaf mean (Figure 2; Figure S6). Thallose liverworts were particularly nitrogen and phosphorus rich relative to their carbon content. Biocrust C:P ratios were generally in the lower range of leaf values (Figure 2; Figure S7).

Biocrust tissue C:N significantly decreased with aridity (Figure 3; $t = 2.80$, $p = 0.0086$), which was driven by a decrease in C ($t = 2.75$, $p = 0.0099$) but no significant change in N ($t = 0.33$, $p = 0.74$). There was no significant change in biocrust tissue P across the aridity gradient ($t = 0.64$, $p = 0.52$).

There were moderate associations between tissue nutrient traits and corresponding nutrient cycle enzyme activities (Figure 4). Taxa with high N tended to exhibit high activity of the nitrogen cycle enzyme, NAG (Pearson's $r = 0.45$). Similarly, tissue P was positively correlated with phosphatase activity (Pearson's $r = 0.45$). Crustose lichens, *Circinaria calcarea* and the moss *Pseudocrossidium crinitum* were markedly higher than other biocrust taxa in their tissue Ca, Mg and Fe content (Figures S8–S10).

4 | DISCUSSION

Here, we quantified the tissue chemical traits of 21 biocrust taxa from Australian drylands. We found that C, N and P pools in biocrusts and their stoichiometry were similar to vascular leaves, implying that, as nutrient exchange surfaces, biocrusts are functionally analogous to leaves. Biocrust taxa with higher tissue N and P were associated with higher activities of N and P cycle enzymes. There was, however, one important difference from past observations of vascular plant leaves (Wright et al., 2003): the C:N ratios of biocrust taxa significantly decreased with

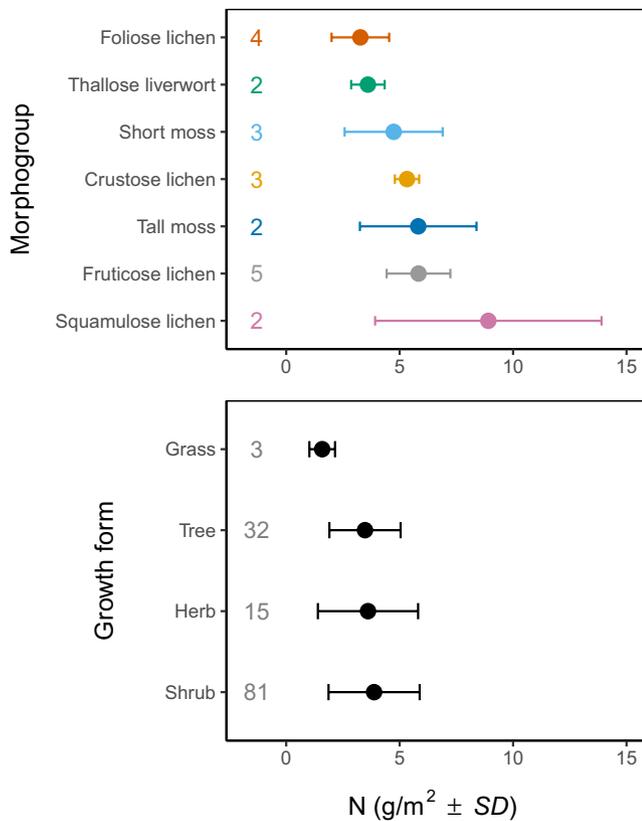


FIGURE 1 Mean tissue nitrogen (g/m^2) among biocrust morphogroups compared to mean leaf nitrogen (g/m^2) among vascular plants recorded within a 50-km radius of biocrust collection sites (left side numbers represent replicate species; for replicate samples of biocrust taxa, see Table 1)

increasing aridity, and this relationship was entirely driven by carbon.

Our findings indicate that while biocrust lichens and bryophytes have similar overall tissue chemistry to vascular leaves, there are key differences. We expected a photosynthetic surface with no stomata and high longevity to be extremely tough according to the leaf economics spectrum (Wright et al., 2004), consisting mostly of structural carbon compounds. However, biocrust tissue N values fell within the upper range of leaf values, and C:N ratios were not especially high relative to leaves. A possible explanation for this finding is that biocrusts can readily absorb nitrogen from the atmosphere and epiphytic N-fixing microbes (Deane-Coe & Sparks, 2016; Gavazov et al., 2010; Gutiérrez-Larruga et al., 2020). It may also be that, due to their small stature, biocrusts do not face the same physical hazards as vascular leaves, and therefore do not need to optimise toughness. Rather than wind shear, rain damage and wilting, the main risks to biocrust survival relate to soil detachment and burial (Chandler et al., 2019; Zaady et al., 2016), which are influenced by traits such as height, rooting depth and ability to grow through layers of deposited sediment (Danin & Ganor, 1991; Mallen-Cooper & Eldridge, 2016). It is also worth noting that our limited set of biocrust species is very unlikely to capture the full extent of tissue N variation and future studies with more species

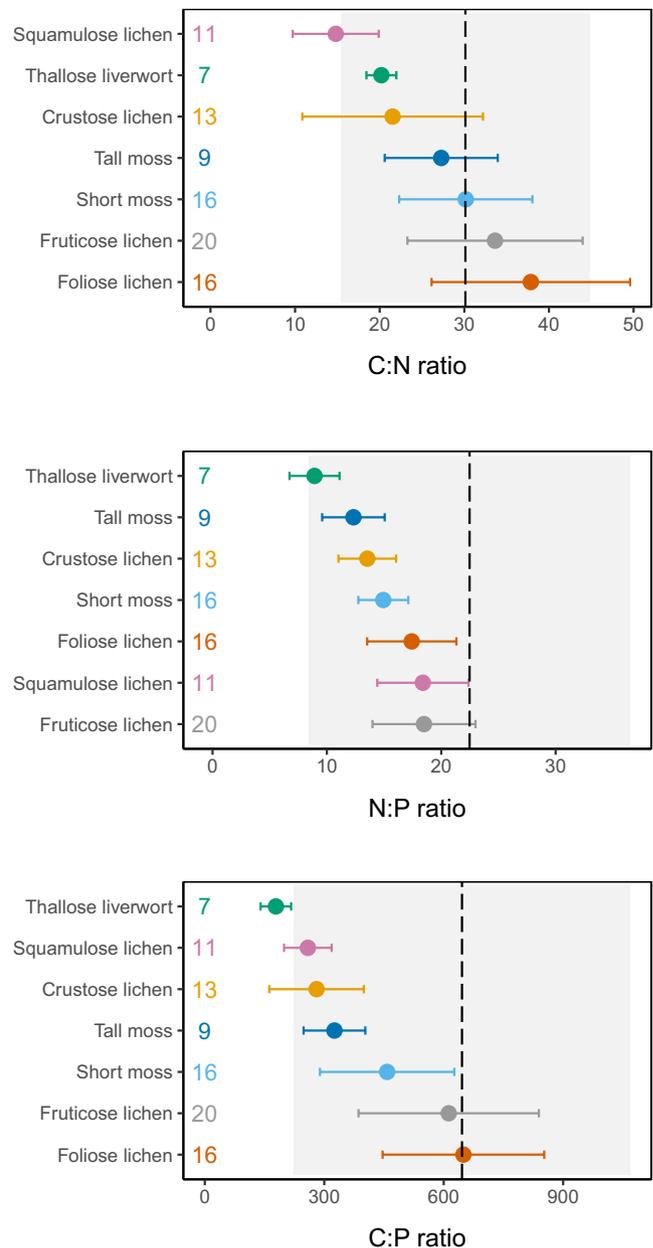
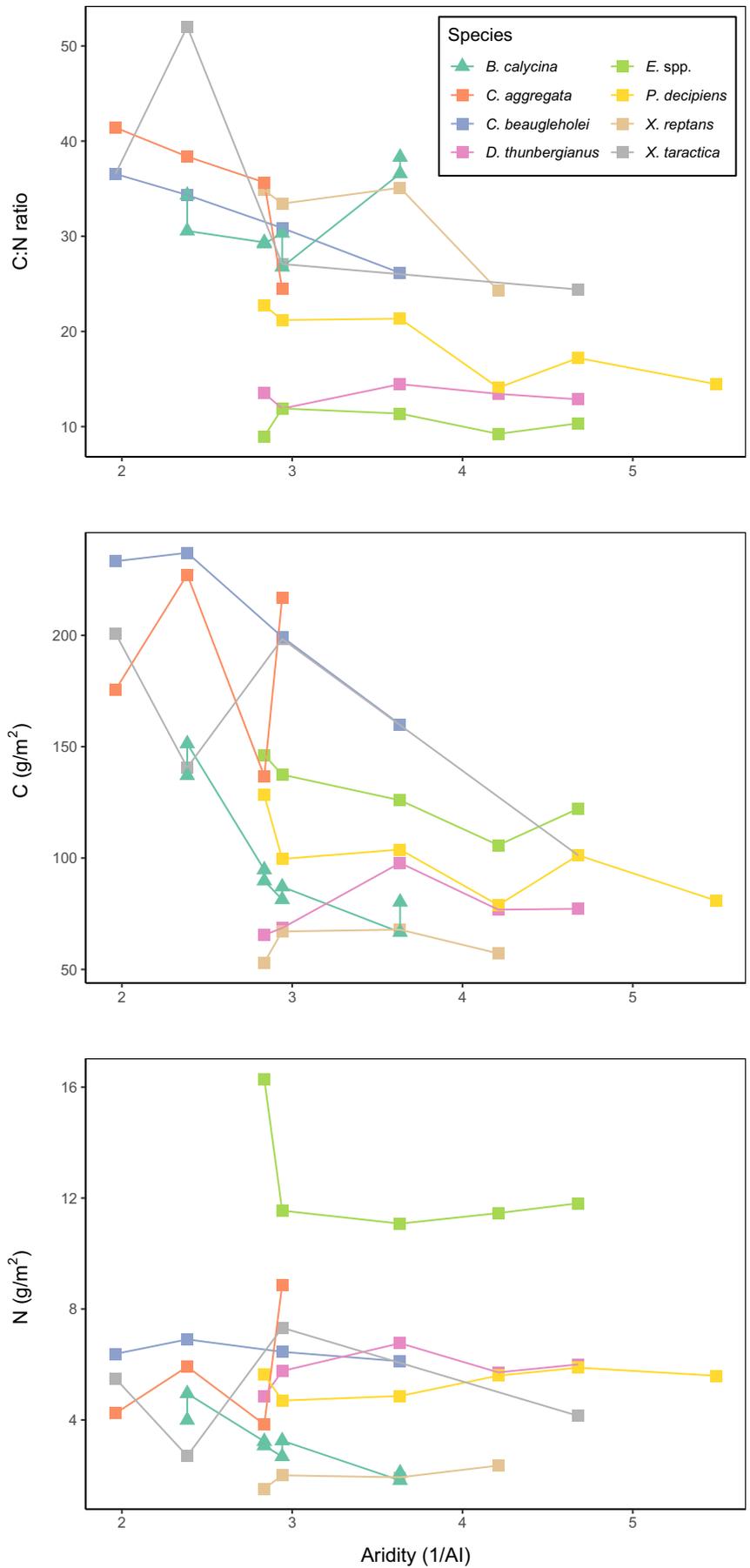


FIGURE 2 Mean tissue C:N, N:P and C:P ratios (\pm SD) among biocrust morphogroups (unlike Figure 1, left side numbers here indicate number of replicates). Dashed lines represent the mean leaf values (sourced from AusTraits) of vascular plants recorded within a 50-km radius of biocrust collection sites, with grey shading showing 1 SD above and below the mean

might find greater overlap among biocrusts and vascular plant leaves.

If tissue nutrient pools are a reasonable proxy for nutrient cycling, our results imply that biocrusts and vascular leaves act as similar nutrient exchange surfaces. There is clear evidence that tissue N, specifically N stored in chlorophyll *a*, is strongly related to carbon fixation in lichens collected from Antarctic, boreal, temperate, subtropical and Arctic biomes (Palmqvist et al., 2002). We found that the activities of N- and P-associated enzymes, which hydrolyse and recycle N- and P-containing compounds, were higher in biocrust taxa

FIGURE 3 Change in biocrust tissue C:N ratio, C and N with aridity (calculated as 1/Aridity Index)



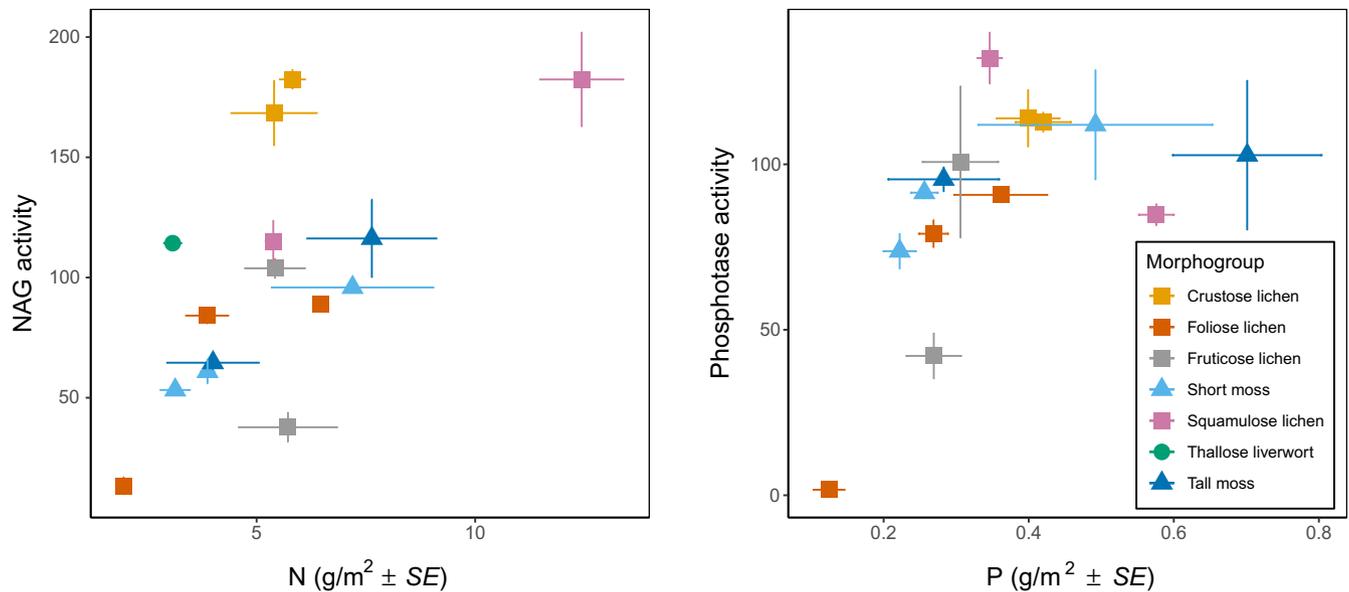


FIGURE 4 Correlation plots of biocrust taxa showing relationships between (a) *N*-acetyl- β -glucosaminidase activity (nmol g⁻¹ hr⁻¹) and tissue N per m² (Pearson's $r = 0.64$), and (b) phosphatase activity (nmol g⁻¹ hr⁻¹) and tissue P per m² (Pearson's $r = 0.47$; enzyme data sourced from Mallen-Cooper & Eldridge, 2016)

that contained higher tissue N and P. In biocrusts, the sugar *N*-acetyl- β -glucosamine is found in fungal cell walls (including lichens) as chitin and in bacterial cell walls as peptidoglycan (Chen et al., 2010). The enzyme NAG can be deployed to attack the cell walls of other organisms, or used to remodel an organism's own cell walls (Gooday et al., 1986). For biocrust lichens, increased NAG activity suggests that N-rich taxa are inducing high amounts of microbial decomposition of their cells, while for bryophytes, which do not contain *N*-acetyl- β -glucosamine, the transfer of N to a NAG-producing microbe would be indirect. Phosphatase is involved in many cellular functions in biocrust lichens, bryophytes and epiphytic microbes and is thus more difficult to attribute to specific pathways (Ariño et al., 2019). Overall these findings, while unsurprising, indicate that tissue chemistry is positively correlated with the rates of nutrient cycling in the immediate vicinity of the organism—the biocrust equivalent of the rhizosphere.

Of course, in productive environments, vascular plants can support multiple layers of leaves, and so maximum nutrients per unit ground area are much higher for vascular plants compared to biocrusts. The leaf mass per area (LMA) of evergreen trees, that is one layer of leaves, averages approximately 100 g/m² (Poorter et al., 2009), and tropical tree species can support >7 complete layers of leaves (e.g. Arias et al., 2007) and thus a total leaf biomass often >700 g/m². By comparison, the biomass per area of biocrusts in our study region ranges from 173 to 734 g/m² in non-crustose taxa (data sourced from Eldridge et al., 2021). However, there are many environments, particularly in drylands and tundra, where biocrust cover far exceeds that of vascular plants (Biasi et al., 2008; Ding & Eldridge, 2020; Remke et al., 2009). Moreover, in these less productive systems, vascular plants generally do not attain one complete layer of leaves (Leaf Area Index <1; Dahlberg et al., 2004; Olsoy et al., 2016), and so their total leaf biomass would fall in the

lower range of, or below, biocrust biomass values per area. Thus, at the landscape scale, biocrust nutrient cycling in these systems may be on par with, or even exceed, vascular plants. Furthermore, our results suggest that the dynamics of biocrust abundance in these environments—largely driven by climate, wildfire, woody plant encroachment and physical disturbances such as livestock grazing and animal diggings (Concostrina-Zubiri et al., 2017; Eldridge et al., 2015; Ferrenberg et al., 2015; Mallen-Cooper et al., 2019; Palmer et al., 2020)—has important ecosystem-level implications for nutrient cycling.

The finding that biocrust C:N ratios decline with increasing aridity demonstrates a key functional difference between vascular plants and biocrusts. There is much empirical evidence that vascular plants inhabiting more arid systems invest in high leaf N, enhancing CO₂ drawdown and allowing plants to keep stomates closed for longer periods of time (Prentice et al., 2011; Wright et al., 2003). Declines in leaf C:N ratios with aridity are therefore driven by nitrogen allocation (Luo et al., 2017). By contrast, the nutrient cycling of biocrusts is intimately linked to their inability to regulate water loss (poikilohydry), resulting in fluctuations between desiccated dormancy and hydrated activity (Raggio et al., 2021). The lack of intraspecific changes in biocrust N along our aridity gradient reinforces the idea that biocrusts do not contend with the vascular plant trade-off between water loss and carbon fixation. Yet the cost of poikilohydry is that carbon fixation is entirely dependent on water availability. Our results, where species were modelled intraspecifically, showed that declining biocrust C:N ratios with aridity were driven by declining carbon content, which implies that biocrust taxa become carbon limited at the dry limit of their range. This finding supports the work of Delgado-Baquerizo et al. (2018) and provides novel evidence of intraspecific declines in biocrust C:N with increasing aridity. It is

possible that biocrusts in wetter regions use the additional carbon to build more structural tissue that can, in turn, retain more water. Another unknown for both vascular plants and biocrusts is the ratio of photosynthetic N to non-photosynthetic N. Both groups of species have similar amounts of N in non-photosynthetic pools (Onoda et al., 2004; Palmqvist, 2000), but whether this proportion shifts with aridity or drought is unknown.

An important facet of climate change is the expansion of global drylands (Huang et al., 2016; Koutroulis, 2019). Because water availability is so closely tied to carbon fixation in poikilohydric organisms (Raggio et al., 2021), the increasing scarcity of water means that biocrust carbon stocks are likely to decline at the global scale. Manipulative experiments and process models concur that a warmer, drier future will generally reduce abundance and the rate of carbon fixation in biocrusts (Baldauf et al., 2021; de Guevara et al., 2014; Reed et al., 2016; Zhang et al., 2018). Our stoichiometry results along an aridity gradient reinforce the carbon fixation results of prior work and agree with a recent mesocosm study, which found that simulated warming and rainfall reduction led to reduced tissue C:N in a biocrust lichen (Concostrina-Zubiri et al., 2021). Changes in biocrust tissue chemistry also have a strong influence on soil C and N cycling through decomposing tissue and the release of nitrogenous compounds (Barger et al., 2016; Berdugo et al., 2021; Delgado-Baquerizo et al., 2015). At the point when biocrust carbon balances become negative, either through reduced water availability or shorter rainfall events that incur a hydration cost (Coe et al., 2012; Reed et al., 2012), areas that previously supported biocrusts will become uninhabitable and there will be a substantial loss of both carbon storage and photosynthetic capacity, with subsequent losses of microbial function and carbon sequestration capacity (Maestre et al., 2013, 2015).

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CONFLICT OF INTEREST

The authors have no conflict of interest.

AUTHORS' CONTRIBUTIONS

The initial idea was conceived by M.M.-C. and developed by both authors; M.M.-C. performed statistical analyses; M.M.-C. wrote the first draft manuscript, and both authors made substantial edits therein.

DATA AVAILABILITY STATEMENT

All data are publicly available on the Open Science Framework <https://osf.io/yf98s/> (Mallen-Cooper & Cornwell, 2021).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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