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RESEARCH ARTICLE

Decomposition of dryland biocrust-forming lichens and mosses contributes to soil nutrient cycling

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Abstract

Background and aims Biocrusts are major contributors to dryland nutrient cycling by regulating C, N and P inputs and fluxes. However, our understanding about how the decomposition of biocrust constituents contributes to soil nutrient cycling in drylands is virtually unknown.

Methods We conducted a microcosm experiment to: i) evaluate the litter decomposition dynamics of two common biocrust-forming species with contrasting tissue chemistry and growth form (the lichen *Cladonia foliacea* and the moss *Syntrichia caninervis*), and ii) their effects on several soil variables related to soil functioning.

Results *Cladonia* litter decomposed gradually with time (92% total mass loss after 342 days), while *Syntrichia* litter decomposed much faster (92% total mass loss after 62 days, with no further losses until the end of the experiment at 342 days). We observed species-specific effects of their litter on dissolved organic N (DON) and NH4+ depending on collection time, which changed the effects of litter decomposition on DON and pH regardless of the biocrust species considered. Overall, biocrust litter had a positive effect on SOC, DON, NH_4^+ and acid phosphatase activity.

Conclusions Our experimental results show that decomposition of biocrust tissues plays an important role in soil nutrient cycling, indicating that this process impacts the fertility and functioning of dryland soils.

Keywords Soil fertility · Microbial activity · Soil pH · *Cladonia foliacea* · *Syntrichia caninervis*

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Introduction

Litter decomposition is a critical ecosystem process with important implications for carbon and nitrogen

storage and release (Berg and Laskowski 2005). However, actual models underestimate decomposition rates in drylands because they were done for mesic to wet ecosystems (Austin 2011). Understanding the potential mechanisms driving litter decomposition in drylands, which store about 32% and 40% of global soil C and total N, respectively, and more than half of total phosphorus (P) (Plaza et al. 2018), is fundamental to better estimate the contribution of drylands to global nutrient cycling.

Biological soil crusts or biocrusts, communities living on the soil surface formed by lichens, mosses, cyanobacteria, liverworts, fungi and other microorganisms, are prevalent in global drylands (Maestre et al. 2021), where they play diverse and key functional roles (Weber et al. 2016). Specifically, they are major contributors to soil nutrient cycling by regulating C, N and P inputs and fluxes (Belnap 2002; Maestre et al. 2013; Delgado-Baquerizo et al. 2014; Concostrina-Zubiri et al. 2021a), and by affecting the abundance, diversity and activity of microbial communities in the first soil centimetres of the soil profile (Maier et al. 2014, 2018). However, our understanding about how biocrusts contribute to soil nutrient cycling in drylands via the decomposition of the tissues of their constituents very limited. For example, how fast and to what extent nutrients are incorporated into the soil, or the effects of biocrust tissue decomposition on soil enzymatic activities have barely been studied so far (Berdugo et al. 2021). As biocrusts are a major feature of global drylands, covering up to 70% of their total surface (Ferrenberg et al. 2017), it is critical to evaluate the impact of their decomposition on dryland soils as they can be potentially very large.

Temperature, soil moisture, UV-radiation and soil-litter mixing are known to regulate the decomposition of plant litter in drylands (Austin et al. 2009). This has also been observed for biocrust-forming lichens in a Mediterranean dryland ecosystem, where increased temperature and rainfall reduction enhanced the decomposition of biocrust-forming lichen litter (Berdugo et al. 2021). However, UV-exposure showed contrasting effects depending on the identity of the lichen species considered (Berdugo et al. 2021). These findings suggest that the attributes of lichen litter, such as their chemical composition, thallus structure (i.e., distribution and proportion of fungal and algal layers), and growth form, may play an important role in their decomposition in drylands. On the other hand, the structure and chemical composition of litter material determines its accessibility and decomposability, which ultimately determine the degree and form at which litter is incorporated into the soil (Cornelissen et al. 1999). For terricolous lichens and mosses, higher nitrogen contents and pH promote lichen and moss decomposition (Limpens and Berendse 2003; Lang et al. 2009), while the concentration of secondary compounds can reduce their decomposability (Glime 2006) and exert an antimicrobial effect (Ranković and Kosanić 2015; Commisso et al. 2021). The type of lichen growth form can also determine how decomposers interact with the litter material (i.e., finely branched lichens are more easily broken and provide higher surface-area ratios for microbial activity (Campbell et al. 2010), further influencing decomposition rates (Asplund and Wardle 2013). However, these issues have been mostly studied in temperate and boreal region and little is known about biocrust decomposition in drylands (Berdugo et al. 2021).

To the best of our knowledge, no previous study has evaluated whether decomposed biocrust litter is effectively incorporated into soil nutrient pools nor whether this process depend on lichen chemistry and decomposition rate (Campbell et al. 2010) in drylands. Therefore, the decomposition process of biocrusts and its effects on soil nutrient cycling remains poorly known in these key ecosystems. To contribute to fill this knowledge gap, we conducted a microcosm experiment involving litter bags to evaluate how the decomposition of the lichen *Cladonia foliacea* and the moss *S. caninervis*, two common biocrust constituents with contrasting morphology and tissue chemistry (Figs. 1 and 2), impacts soil nutrient cycling. Specifically, we simultaneously evaluated changes in lichen and moss litter biomass and multiple variables related to soil functioning (i.e., β-glucosidase and acid phosphatase activity, contents of organic C, dissolved organic N, ammonium and nitrate and pH). We hypothesised that: i) biocrust litter decomposition patterns differ between species; species without secondary metabolites, lower C:N ratio and higher pH will decompose faster and to a greater extent (Limpens and Berendse 2003; Lang et al. 2009), and ii) the decomposition of biocrust litter increases soil nutrient content and enzymatic activities and decreases pH, although these effects are

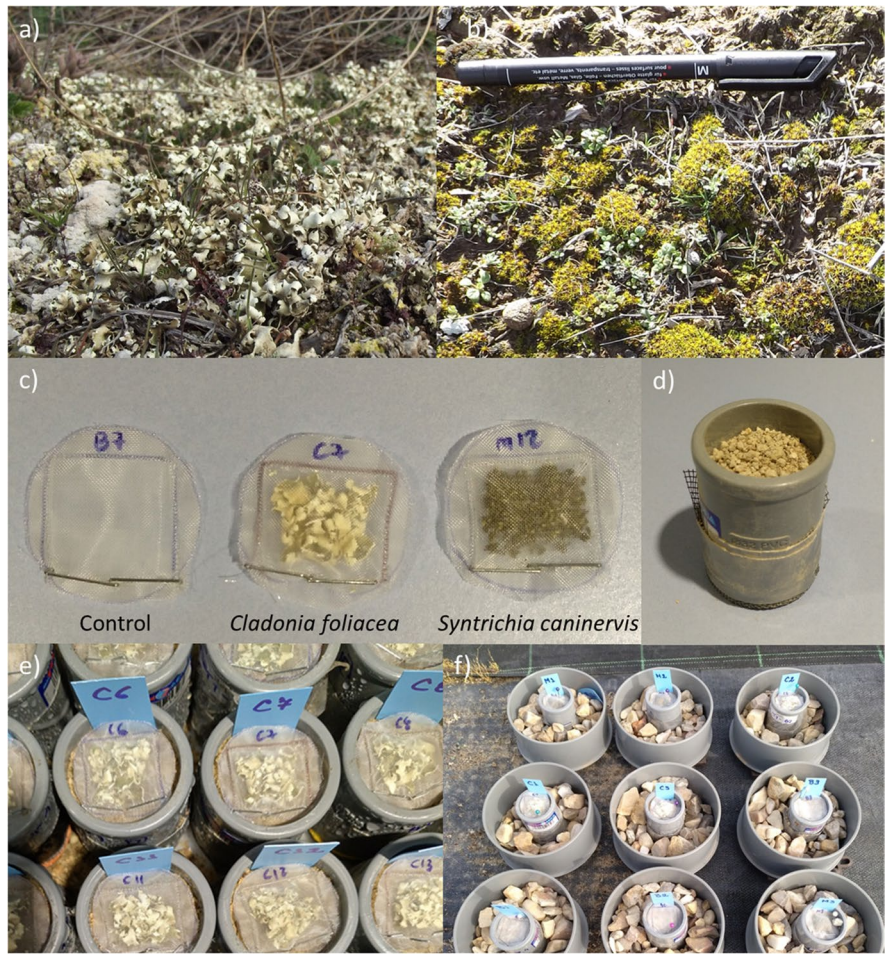

Fig. 1 Biocrust patches dominated by the species of study; **a**) *Cladonia foliacea* and **b**) *Syntrichia caninervis*, and details of **c**) control and biocrust litter bags, **d**) microcosm filled with gypsum soil, **e**) view of biocrust litter bags placed on the top of the microcosms, **f**) view of an experimental block

species-specific due to differences in tissue chemistry and decomposition patterns (Asplund and Wardle 2017). By assessing and quantifying the effects of biocrust litter decomposition on key variables defining soil nutrient cycling, we fill an important gap in our knowledge regarding the role that biocrusts play in dryland biogeochemistry.

Methods

Selection of biocrust species

We selected two biocrust-forming species with contrasting morphology and tissue chemistry: the lichen *Cladonia foliacea* and the moss *Syntrichia caninervis* (Figs. 1 and 2). Both species are common in dryland biocrust communities both in Spain (Maestre et al. 2011; Concostrina-Zubiri et al. 2014) and elsewhere (Weber et al. 2016). *Cladonia* is characterized by a foliose primary thallus, grows in form of cushions barely attached to the soil surface and produces fumarprotocetraric and usnic acids as secondary metabolites (Nimis and Martellos 2004). *Syntrichia* is an acrocarpous moss with an erect habit (stems up to 2 cm) and stems typically growing on dense cushions (Casas 2006). This species produces fatty acids, alcohols and alkanes (Xu et al. 2009).

Biocrust collection, chemical analyses and litter preparation

Individuals and patches of *Cladonia* and *Syntrichia* were collected in February 2018 from gypsum outcrops in the surroundings of Ciempozuelos, in central Spain (40°′11 ‘23”N, 3°36′01”W). All samples were

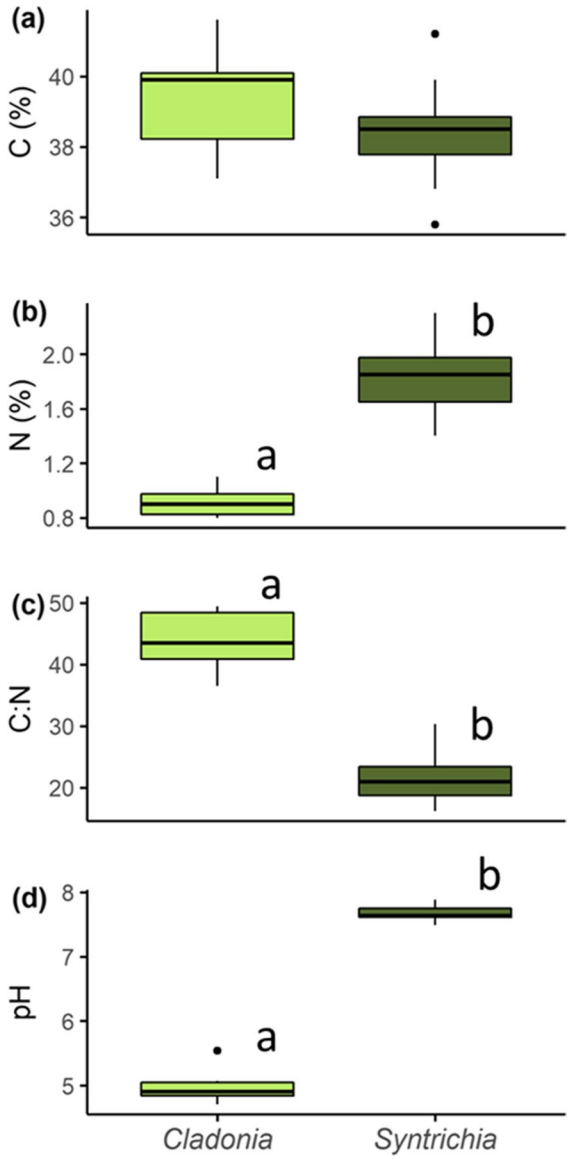

Fig. 2 Biocrust initial tissue chemistry. Boxes show the median, 25th and 75th percentiles; vertical lines show the minimum and maximum values that fall within 1.5 times the height of the box. Different letters above boxes indicate significant ($P < 0.05$) differences between biocrust species (after separate Student's t test, Table S1). *Cladonia*, lichen species *Cladonia foliacea*; *Syntrichia*, moss species *Syntrichia caninervis*

air-dried and stored in the dark until further analysis and preparation. Soil particles and external debris were carefully eliminated from lichen and moss samples. To characterize biocrust initial chemistry, a subsample of ten individuals of *Cladonia* and ten patches of *Syntrichia* were oven-dried (48 h at 60 °C), ground in a homogenizer (Precellys® 24; Bertin Technologies, Montigny-le-Bretonneux, France) and analysed for total C and N on a EuroEA3000 elemental analyser (EuroVector, Pavia, Italy). Tissue pH was determined in ~15 mg of air-dried and clean *Cladonia* and *Syntrichia* material and 1.2 ml of distilled water. The solution was shaken at 200 rpm for 1 h, and then centrifuged for 5 min. The pH of the fluid was measured using a pH-meter (GLP 21, Crison, Barcelona, Spain). Preliminary analyses showed that initial tissue chemistry significantly ($P < 0.05$) differed between biocrust species, except for C concentration ($P = 0.166$, Fig. 2, Online Resource 1, Table S1). Specifically, *Cladonia* had lower N concentration and pH and higher C:N ratio than *Syntrichia* ($P < 0.05$ in all cases, Fig. 2, Online Resource 1, Table S1).

To obtain the litter, we first immersed air-dried and clean *Cladonia* and *Syntrichia* material in liquid N (−196 °C) for 1.5 min (3 cycles, 0.5 s each) and then oven-dried the resulting material at 70 °C for 24 h, following Lang et al. (2009) and Berdugo et al. (2021). Death of lichen and moss tissue was confirmed by assessing the lack of photosynthetic activity using a Plant Efficiency Analyzer (PEA, Handsatech Instruments Ltd., King's Lynn, Norfolk, England) after 1 h of hydration and 15 min dark adaptation.

Experimental design

We conducted a microcosm experiment from July 2019 to June 2020 in the Climate Change Outdoor Laboratory (CCOL) located in central Spain (Rey Juan Carlos University, Móstoles, 40°20′37"N, 3°52′00"W, 650 m a.s.l.). The climate is Mediterranean semi-arid, with mean annual temperature of 14.9 °C, and mean annual precipitation of 427.5 mm (Cuatro Vientos, Madrid, Spain: 40°22′32" N, 3°47′10" O, 690 m a.s.l., 1981–2010, 30-year period; Spanish Meteorological Agency – AEMET). Microcosms were made with 5.5 cm depth plastic pots (diameter 3.3 cm) filled with 5 cm of gypsum soil collected in gypsum outcrops 50 km south of the CCLOL (Fig. 1). We placed nylon litter bags (3 cm diameter, 200 µm mesh size) filled with ~150 mg of *Cladonia* and *Syntrichia* litter on the top of each microcosm in July 2018 (summer) and empty litter bags as controls (Fig. 1). The exact dry weight (oven-dried at 60° for 24 h)

of each sample (control litter bags or biocrust litter + corresponding litter bags due to the small sample weight) was recorded.

The experiment had two factors: i) biocrust species (three levels): empty litter bags without biocrust litter as a control, *Cladonia* litter and *Syntrichia* litter, and ii) collection time: 62, 181, and 342 days (hereafter T1, T2 and T3, respectively). Five replicated microcosms per combination of factors were distributed in five experimental blocks (Fig. 1), resulting in 45 microcosms in total. Microcosms were uncovered and exposed to natural weather conditions throughout the experiment (Fig. 1).

Harvest and analyses

Five microcosms and the corresponding litter bags per biocrust species level were randomly retrieved at each collection time. Litter bags were carefully cleaned with a brush to remove soil particles and external debris accumulated during the experiment. Litter bags were then oven-dried at 60° for 24 h and weighted. Litter decomposition was estimated as the percentage remaining biomass (dry weight) for each collection time.

We evaluated changes in soil properties across factors at T1 and T3. Soil samples (1 cm depth) were harvested in each microcosm (n = 30) after litter bag removal, and then sieved (2 mm mesh), air-dried at room temperature for two weeks and stored in sealed plastic bags in the dark until further analyses (Maestre et al. 2012; Delgado-Baquerizo et al. 2015). In each soil sample, we measured organic C (SOC), dissolved organic N (DON), exchangeable ammonium (NH_4^+) and nitrate (NO_3^-). We also measured two soil enzymatic activities (β-glucosidase and acid phosphatase), which are good indicators of microbial activity and soil pH, an important regulator of microbial activity in drylands (e.g., Sardans et al. 2008; Delgado-Baquerizo et al. 2014; Sinsabaugh et al. 2008). These soil variables were analysed as described in Maestre et al. (2012) except soil pH. Soil pH was determined in a sample consisting of 2.5 g of soil and 2.5 ml of distilled water (1:1). The solution was shaken for 30 min at 150 rpm. The pH of the fluid was measured using a pH-meter (GLP 21, Crison, Barcelona, Spain).

Data analyses

To test our first hypothesis (i.e., biocrust litter decomposition differs between species with contrasting tissue chemistry and with time), we conducted a two-way ANOVA (type III error due to unbalanced design) for biocrust remaining biomass with species (two levels; *Cladonia* and *Syntrichia*) and time (three levels; T1, T2 and T3) as fixed factors, and block and time as random terms to control the variability between experimental blocks with time. When the interaction species x time had a significant effect on biocrust remaining biomass, we conducted Tukey post hoc multiple comparison tests. Values of remaining biomass of three *Syntrichia* litter bags (one in T2, two in T3) were identified as outliers (values >1.5*IQR; where IQR is the inter-quartile range, or distance between the 25th and 75th percentiles). Thus, we discarded these litter bags and the corresponding soil microcosms for further analysis, resulting in a total of 42 experimental units.

To test our second hypothesis (i.e., biocrust litter decomposition increases soil fertility and enzymatic activity and decrease pH in a species-specific manner), we calculated the Relative Interaction Intensity (RII) index (Armas et al. 2004) separately for each biocrust species and time (i.e., T1 and T3). RII was computed as $(S_{bc} - S_{bs})/(S_{bc} + S_{bs})$; where S_{bc} and S_{bs} are the values of a given soil variable under each species and time in biocrust microcosms and in control microcosms (value of the microcosms with a control litter bag for each block and time, n = 3–5). The RII values range from −1 to +1; a value of zero indicates no effects of a given biocrust species on the variable of interest, while positive/negative RII values indicate positive/negative effects on such variable, compared to bare soil. To test whether RII values were significantly different from zero, we computed bootstrapped 95% confidence intervals using the boot R package (Canty and Ripley 2019). Bootstrapped coefficients do not make assumptions on the distribution of its statistic for inferring significance, therefore are less dependent on deviations from classical distributions and are particularly appropriate for small sampling sizes. To evaluate the effects of biocrust species, time and the interaction species x time on RII values, we conducted separate two-way ANOVAs (type III error due to unbalanced design) for each soil variable with species and time as fixed factors. To evaluate

the influence of the variability between replicates in the models, we compared model fit with and without block as a random factor using the AIC (Akaike 1973). When the interaction species x time had a significant effect on RII values in the best-fitting models, we conducted Tukey post hoc multiple comparison tests.

Data (initial tissue chemistry, remaining biomass and soil RIIs) were tested for Student's t test and ANOVA assumptions before analyses. Tissue data (except C values) were log10-transformed to meet Student's t test assumptions. All analyses were performed with R version 3.6.1 (R Core Team 2019) using the "car" package (Fox and Weisberg 2019). Data are available from Figshare (Concostrina-Zubiri et al. 2021b).

Results

Species, time and the interaction species x time had significant effects on biocrust remaining biomass (Online Resource 1, Table S2). The post hoc multiple comparison tests revealed differences between *Cladonia* and *Syntrichia* remaining biomass in T1 and T2, and in *Cladonia* remaining biomass between T1 and the other two collection times (Fig. 3). Specifically, *Cladonia* remaining biomass gradually decreased from 98%, to 94% and 92% in T1, T2 and T3, respectively, while *Syntrichia* remaining biomass was 92% in T2 and remained similar until the end of the experiment (Fig. 3).

Regarding the soil RII indices, both time and the interaction species x time had significant ($P < 0.05$) effects on DON (Online Resource 1, Table S3). The interaction species x time also had a significant effect ($P < 0.05$) on NH_4^+ (Online Resource 1, Table S3). Time alone had a significant effect ($P < 0.05$) on NO_3^- and pH (Online Resource 1, Table S3). In particular, DON decreased under biocrust litter compared to bare soil in T1 and this effect was the opposite in T3 (Fig. 4b, Online Resource 1, Table S3). We also found that biocrust litter had a positive effect on NH_4, compared to bare soil, and that this effect was stronger in T1 than in T3 (Fig. 4c, Online Resource 1, Table S3). Finally, biocrust litter increased soil pH, compared to bare soil, in T1, while decreased it in T3 (Fig. 4g, Online Resource 1, Table S3). Biocrust litter also had an overall positive effect on NH_4^+ in T1

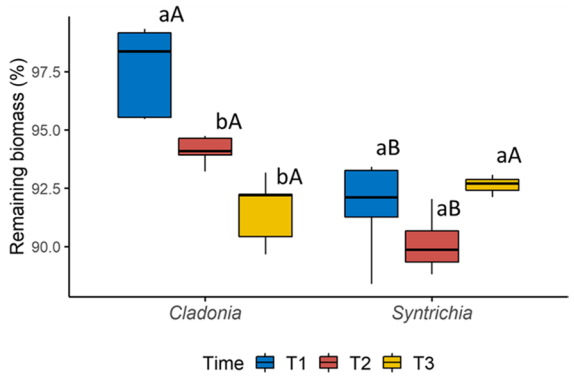

Fig. 3 Remaining biomass (%) of biocrust litter for each species in T1, T2 and T3 (62, 181 and 342 days after the setup of the experiment, respectively). Boxes show the median, 25th and 75th percentiles; vertical lines show the minimum and maximum values that fall within 1.5 times the height of the box. Different lowercase and capital letters indicate significant ($P < 0.05$) differences between collection times for each species and between species for each collection time, respectively. *Cladonia*, lichen species *Cladonia foliacea*; *Syntrichia*, moss species *Syntrichia caninervis*

and T3 (Fig. 4c), and on SOC, DON and the activity of acid phosphatase in T3 (Fig. 4a,b,f) and pH in T1 (Fig. 4g), compared to bare soil. These effects were, however, negative on DON in T1 (Fig. 4b) and pH in T3 (Fig. 4g), compared to bare soil. We did not find significant effects of species alone for any soil variable (Fig. 5, Online Resource 1, Table S3) or that of time or the interaction species x time on SOC and the activity of β-glucosidase and acid phosphatase (Fig. 4a–f, Online Resource 1, Table S3). Nevertheless, *Cladonia* had an overall positive effect on NH_4^+ and the activity of acid phosphatase (Fig. 5c, f), compared to bare soil, throughout the duration of the experiment. Similarly, *Syntrichia* had an overall positive effect on SOC and NH_4^+ (Fig. 5a,c), compared to bare soil.

Discussion

Our study shows that biocrust species with contrasting tissue chemistry decompose differently, particularly during the initial stages of decomposition. We also found that the decomposition of *Cladonia* and *Syntrichia* litter drives changes in soil fertility, microbial activity and pH in a similar manner. Our findings provide novel experimental evidence on the

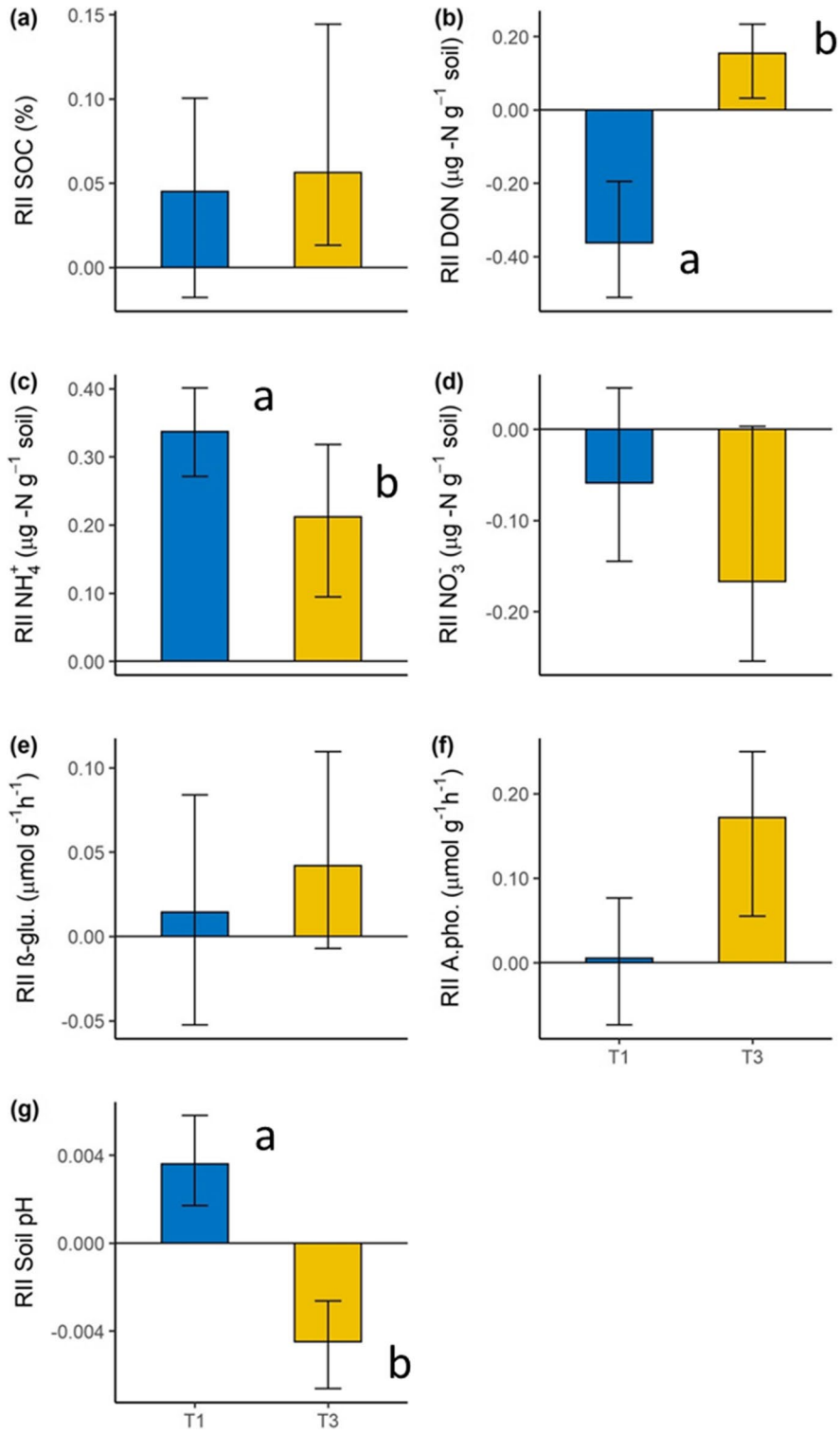

Fig. 4 Effects of time on soil properties, as measured with the Relative Interaction Intensity (RII) index. Panels show RII indices for soil (**a**) organic C content (SOC); (**b**) dissolved organic N (DON); (**c**) exchangeable ammonium concentration $\left(NH_4^+\right)$; (**d**) nitrate concentration $\left(NO_3^-\right)$; (**e**) β-glucosidase activity (β-glu.); (**f**) acid phosphatase activity (A. pho.); and (**g**) pH in T1 and T3 (62 and 342 days after the setup of the experiment, respectively). RII indices and corresponding confidence intervals (CIs) above/below zero indicate a significant ($P < 0.05$) and positive/negative effect of biocrust litter on a given soil property, relative to bare soil. Different letters indicate significant ($P < 0.05$, after two-way ANOVA, Online Resource 1, Table S3) differences between collection times. Data are mean ± 95% bootstrap CIs

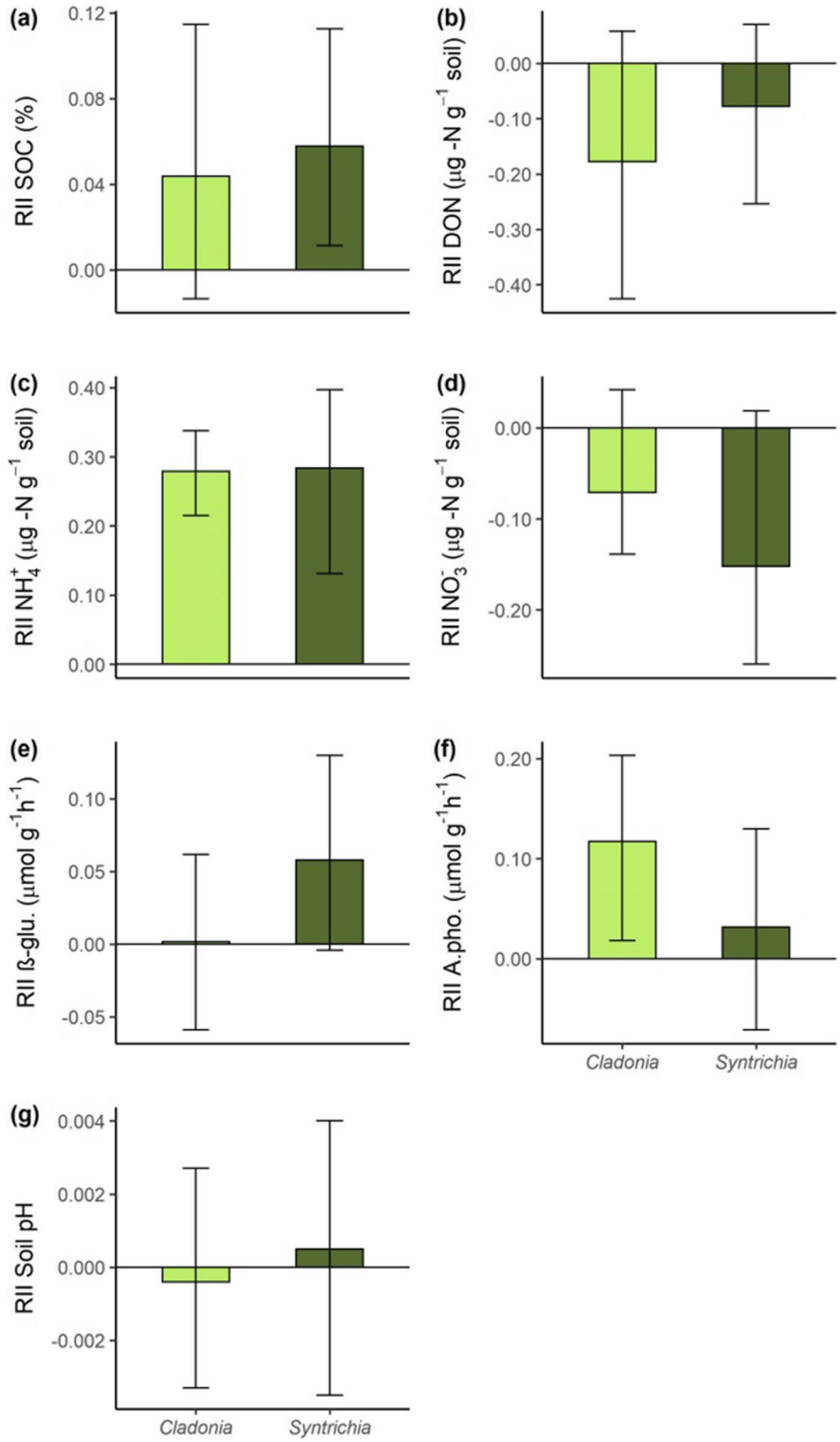

Fig. 5 Effects of *Cladonia* and *Syntrichia* litter on soil properties, as measured with the Relative Interaction Intensity (RII) index. Panels show RII indices for soil (**a**) organic C content (SOC); (**b**) dissolved organic N (DON); (**c**) exchangeable ammonium concentration $\left(NH_4^+\right)$; (**d**) nitrate concentration $\left(NO_3^-\right)$; (**e**) β-glucosidase activity (β-glu.); (**f**) acid phosphatase activity (A. pho.); and (**g**) pH. RII indices and corresponding confidence intervals (CIs) above/below zero indicate a significant ($P < 0.05$) and positive/negative effect of biocrust litter on a given soil property, relative to bare soil. Different letters indicate significant ($P < 0.05$, after two-way ANOVA, Online Resource 1, Table S3) differences between species. Data are mean ± 95% bootstrap CIs. *Cladonia*, lichen species *Cladonia foliacea*; *Syntrichia*, moss species *Syntrichia caninervis*

impacts of biocrust litter decomposition on soil nutrient cycling, and indicate that this process should play an important role in the biogeochemistry of drylands.

Biocrust species decompose differently over time but to a similar degree

As expected, *Syntrichia* showed a greater biomass loss at the initial and short-term stages of decomposition (i.e., T1 and T2) compared to *Cladonia*, although both species reached a similar decomposition degree at the end of the experiment. Generally, higher N content and pH (Limpens and Berendse 2003; Lang et al. 2009) and lower concentration of secondary compounds (Ranković and Kosanić 2015; Commisso et al. 2021), which is the case of *Syntrichia* relative to *Cladonia*, allow for faster decomposition rates in lichens and mosses because these attributes enhance litter decomposability for microbial communities. Indeed, our results suggest that earlier changes in *Syntrichia* litter may have occur before the first collection time, so future research should evaluate moss decomposition in the very short-term scale (e.g., at two weeks after the beginning of the experiment). Also, the presence of secondary compounds with known antimicrobial effects, such as usnic acid (Molnár and Farkas 2010; Maciag-Dorszyńska et al. 2014), may have hampered litter decomposition in *Cladonia* compared to *Syntrichia*, which only produces secondary compounds such as fatty acids, alcohols and alkanes (Wetmore 1982; Xu et al. 2009). In addition, *Syntrichia* differs from *Cladonia* by containing crystalline cellulose (Xu et al. 2009). Future research should also evaluate how the structural characteristics of biocrust tissue affect its decomposition.

Finally, the remarkable differences in growth form between the biocrust species studied may have facilitated a faster microbial consumption in *Syntrichia* (Campbell et al. 2010). For instance, the thallus of *Cladonia* is composed of leaf-like, long squamules which are thicker than *Syntrichia* leaves (Osyczka and Rola 2013; Coe et al. 2019). In addition, *Syntrichia* leaves are also crowded; something that increases the surface-to-volume ratio and the water absorption capacity of *Syntrichia* (Concostrina-Zubiri et al. 2017), further promoting *Syntrichia* decomposition.

At the end of the experiment, both species reached a similar decomposition degree (~92% of remaining biomass). Our results are in agreement to a previous study reporting that the biocrust-forming lichens *C. foliacea* and *Diploschistes diacapsis*, with contrasting tissue chemistry (i.e., *C. foliacea* litter shows almost three times higher C:N ratios relative to *D. diacapsis*) achieved similar decomposition degree (i.e., ~55%) after 2.5 years under natural field conditions, although *C. convoluta* decomposed faster in the first months (Berdugo et al. 2021). The relatively low decomposition showed by both species in our experiment compared to that observed by Berdugo et al. (2021) could be explained by i) a low nutrient and microbial abundance in the initial soil used in our experiment, ii) the lack of living biocrusts and iii) the short-term nature (~1 year) of our study. Indeed, the enzymatic activities registered in our soils are notably lower (~0.8–1.4 and 0.2–1 μmol/g·h for the activity of the β-glucosidase and acid phosphatase enzymes, respectively, Fig. S1) than those reported from a previous microcosm experiment (~5–35 and 20–200 μmol/g·h for the activity of the β-glucosidase and acid phosphatase enzymes, respectively) using living biocrusts and maintained for 4.5 years in the same experimental facility (Concostrina-Zubiri et al. 2021a).

Biocrust litter decomposition affects soil fertility, enzymatic activity and pH

Our results partially supported our second hypothesis; i.e., biocrust litter decomposition increases soil fertility and enzymatic activity and decreases pH in a species-specific way. We found empirical evidence that the decomposition of even small amounts of biocrust litter (i.e., 2–8% of dry weight) exerted important effects on soil fertility, enzymatic activities (i.e., acid phosphatase activity) and pH, although these effects were similar between species. For example, we found that biocrust litter increased SOC at the end of the experiment, compared to bare soil, regardless of the species considered. This result may be explain by the expected losses of biocrust C content via decomposition (Berdugo et al. 2021), which are incorporated into the soil as organic matter or as increases in microbial biomass. Nevertheless, this effect was rather weak (RII ~0.04–0.06; Fig. 4a). It would be interesting to evaluate changes in SOC associated to biocrust decomposition by using labelled biocrust organic C to better understand how biocrust litter is incorporated into the soil. In the case of DON, biocrust litter had an overall negative effect

on DON in T1, compared to bare soil, and effect likely explained by high N consumption requirements of microbes decomposing biocrust litter. This effect was, however, the opposite in T3. We also found that biocrust litter had overall increasing effects on NH_4^+ and that this effect was maintained through the duration of the experiment. These results suggest that during the first year of biocrust litter decomposition, mineralization dominates over nitrification, i.e., a minimum concentration of NH_4^+ has to be produced until nitrification starts, or conversely, that microbial communities are consuming NO_3^-. It would be interesting to test these hypotheses by evaluating the microbial community composition (e.g., ammonifying and nitrifying bacteria) and N-related activity in the soil in the long-term.

The activity of acid phosphatase was higher under *Cladonia* litter compared to bare soil (but not under *Syntrichia* litter). Our results are partially in agreement with those reported by Sedia and Ehrenfeld (2006), who reported higher soil enzymatic activities under lichens compared to mosses. These authors related their results with lower litter quality in lichens limiting the nutrition of microbial communities (Sinsabaugh 1994). However, this study was carried out in a temperate ecosystem, where contrasting climatic conditions operate. Finally, biocrust litter had a relatively weak effect on soil pH compared to bare soil that, however, showed a marked shift with time; i.e., biocrust litter had a positive effect on T1, while this effect changed to negative in T3. The first months of the experiment (July to September 2019) were characterized by moderated precipitation (75 mm) and high temperature (~22–28 °C, Online Resource 1, Fig. S2). It would be expected that biocrust litter would exert a buffering effect (Concostrina-Zubiri et al. 2017), decreasing soil evapotranspiration and allowing higher soil moisture and then, reduced pH values (Zhao et al. 2019). However, we found the opposite, so the initial increase in soil pH under biocrust litter may be conversely due to i) high amounts of NH_3 released under biocrust litter; as expected from the observed NH_4^+ increase, iii) cation (e.g., Na^+, Ca^+, Mg^+, contained in biocrust tissue) transfer from biocrust litter to soil or iii) the increasing short-term effect of organic compound decarboxylation (Yan et al. 1996). In contrast, the progressive incorporation of biocrust organic matter into soil organic matter via decomposition resulted in a pH decrease after almost a year. Since decomposition processes in drylands are highly dependent on water pulses (Austin et al. 2009), it would be interesting to include soil water measurements in future studies when evaluating the effect of biocrust litter on soil functioning.

Conclusions

Our study is the first to experimentally demonstrate that the decomposition of biocrust litter impacts soil nutrient cycling. Specifically, we found that biocrust species with contrasting initial tissue chemistry showed different decomposition patterns, i.e., although both species decomposed to a similar degree, moss litter decomposed faster. We also found that, irrespective of the species considered and despite their low degree of decomposition, biocrust litter increased SOC, DON, NH_4^+ and acid phosphatase activity and decreased pH after almost a year. Our results highlight the contribution of biocrusts to nutrient cycling in dryland soils. They also open new research avenues for further exploring the importance of this process in dryland ecosystems and highlight the importance of incorporating biocrust-forming lichens and mosses into biogeochemical and C cycling models to refine their predictions. Future work should evaluate biocrust decomposition in the long-term and its impact on microbial community composition and N-related activity in the soil to better understand their contribution to dryland ecosystem functioning.

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Authors' contributions LCZ planned and designed the experiment, LCZ, BJM and EV set up and maintained the experiment and conducted laboratory analyses, LCZ and MB processed and analysed data, LCZ, MB, EV and FTM wrote the manuscript and all authors contributed to the final review.

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Data availability Data are available from Figshare, https://doi.org/10.6084/m9.figshare.14680560.

Declarations

Competing interests The authors declare no conflict of interests.

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