Fruticose lichens shape multiple soil functions in a protected Mediterranean dryland

Tadeo Sáez-Sandino[1*], Laura García-Velázquez[2], Enrique Muñoz-Ulecia[3,4], Noelia Serrano-Prieto[2], Ana López[1], Antonio Gallardo[2*]

[1]Hawkesbury Institute for the Environment, Western Sydney University, Penrith, NSW, Australia.

[2]Departamento de Sistemas Físicos, Químicos y Naturales, Universidad Pablo de Olavide, 41013 Sevilla, Spain.

[3]Centro de Investigación y Tecnología Alimentaria de Aragón (CITA), Zaragoza, Spain.
[4]Instituto Agroalimentario de Aragón (IA2), Universidad de Zaragoza, Spain

Corresponding author: tadeosaez@gmail.com; agallardo@upo.es

Impact Statement:

Dryland ecosystems cover vast areas of the Earth and play a critical role in global carbon and nitrogen cycling, yet many of their key biological components remain underappreciated. This study highlights the important ecological role of fruticose lichens, specifically *Cladonia rangiformis*, as ecosystem engineers in coastal drylands. We show that the loss of these lichens can rapidly disrupt soil functioning and increase carbon dioxide emissions. This has significant implications under ongoing climate change, which is expected to reduce lichen cover in many dryland regions worldwide. Our results suggest that such declines could weaken the capacity of these ecosystems to store carbon and maintain soil fertility, potentially accelerating land degradation. Recognizing and conserving fruticose lichens should be considered a nature-based solution to sustain the functioning of vulnerable dryland ecosystems.

Abstract

The ecological role of fruticose lichens with three-dimensional thalli remains poorly understood. Here, we investigated how the fruticose lichen *Cladonia rangiformis* influences carbon and nitrogen cycling in stabilized coastal dunes of Doñana National Park (Spain). We conducted an in-situ field transplant experiment across four microsites: soils under intact lichen cover, adjacent bare soils, bare soils with lichen addition, and soils with lichen removal. Upright lichen thalli acted as both physical and biochemical ecosystem engineers, reducing wind-driven erosion, buffering soil temperature, and contributing to greater organic matter accumulation and moisture retention. Accordingly, soils under lichens showed higher levels of phenolic and aromatic compounds, microbial biomass carbon, nitrate, ammonium, and dissolved organic nitrogen than bare soils. Lichen addition rapidly reproduced these patterns within two months, whereas removal caused significant declines in soil functions. Despite differences in microclimate

This is an Open Access article, distributed under the terms of the Creative Commons Attribution-NonCommercial-NoDerivatives licence (http://creativecommons.org/licenses/by-nc-nd/4.0/), which permits non-commercial re-use, distribution, and reproduction in any medium, provided the original work is unaltered and is properly cited. The written permission of Cambridge University Press must be obtained for commercial re-use or in order to create a derivative work.

This peer-reviewed article has been accepted for publication but not yet copyedited or typeset, and so may be subject to change during the production process. The article is considered published and may be cited using its DOI.

10.1017/dry.2026.10058

Downloaded from https://www.cambridge.org/core. UNIVERSIDAD AUTONOMA METROPOLITANA, on 17 Nov 2026 at 22:47:38, subject to the Cambridge Core terms of use, available at https://www.cambridge.org/core/terms. https://doi.org/10.1017/dry.2026.10058

conditions, soil respiration did not differ between lichens and bare soils. However, lichen removal significantly increased soil respiration, with effects persisting for at least 70 days. Declines in lichen cover under climate change may therefore reduce several soil functions related to carbon and nitrogen cycling while increasing CO_2 emissions. Conserving fruticose lichens could be thus essential for maintaining soil functioning in Doñana National Park.

Keywords:

Lichen, fruticose, *Cladonia rangiformis*; soil carbon; soil nitrogen, dryland ecosystems, Doñana.

1. Introduction

Biological soil crusts (BSCs) are widespread communities of soil-surface organisms that contribute to the functioning of dryland ecosystems (Bowker, 2007). They comprise diverse assemblages of cyanobacteria, algae, lichens, mosses and associated microorganisms, which can influence soil stability, nutrient cycling, and carbon exchange (Asplund & Wardle, 2017). For instance, these communities can regulate the temporal dynamics of soil CO_2 flux and fix substantial amounts of atmospheric CO_2, estimated at more than 2.6 Pg C yr^{-1} globally (Díaz-Martínez et al., 2022; Maestre et al., 2013). Lichens are of particular interest because they form symbiotic associations between a fungus and a photosynthetic partner, allowing them to tolerate prolonged periods of desiccation and rapidly resume metabolic activity when moisture becomes available (Canali et al., 2025). Most research on lichen-dominated BSCs has focused on crustose and squamulose lichens that grow in close contact with the soil surface (Havrilla et al., 2019; Miralles et al., 2012), potentially because of their close interactions with surface soils (Blanco-Sacristán et al., 2025). However, the effects of fruticose lichens, which develop three-dimensional thalli that extend above the soil surface and can cover substantial portions of dryland soils (Rodríguez-Peñate et al., 2019), on soil properties and biogeochemical processes remain poorly characterized. This distinction is important because differences in thallus morphology may lead to different interactions with the soil environment and, consequently, different effects on soil processes.

A further limitation of current knowledge is the scarcity of in situ experimental studies examining how lichen cover influences soil processes under natural conditions. Experimental research has often been conducted under controlled laboratory conditions(Havrilla et al., 2019; López-Rodríguez et al., 2020), whereas field experiments manipulating lichen cover to examine its addition or removal remain uncommon (Ballesteros et al., 2017; Lalley & Viles, 2008). Such experiments are particularly relevant in drylands, where lichen cover can modify the soil surface and where changes in temperature and precipitation may drastically reduce lichen cover (Maestre et al., 2013). Coastal drylands provide a useful setting in which to examine these interactions. For instance, Doñana National Park in southwestern Spain is a protected Mediterranean ecosystem internationally recognized for its biodiversity and conservation value (Muñoz-Reinoso, 2018). The coastal dunes are characterized by stabilized sandy soils, where lichen and biological soil crust communities are adapted to water limitation and high irradiance (Zunzunegui et al., 2022). Moreover, organic carbon and nutrients are concentrated largely in the uppermost soil layers, highlighting the potential importance of surface-dwelling organisms for biogeochemical processes. In situ experiments examining how fruticose lichens shape soil functions are therefore critical for predicting ecosystem responses to environmental change and informing the management of coastal dryland ecosystems.

Downloaded from https://www.cambridge.org/core. UNIVERSIDAD AUTONOMA METROPOLITANA, on 17 Nov 2026 at 22:47:38, subject to the Cambridge Core terms of use, available at https://www.cambridge.org/core/terms. https://doi.org/10.1017/dry.2026.10058

Here, we investigated the role of the lichen *Cladonia rangiformis* in shaping nutrient dynamics in the surface soil layers of Doñana National Park. This fruticose lichen is common in stabilized Mediterranean dune systems but falls outside the classical definition of biological soil crusts because most of its biomass extends above the soil surface (Belnap, 2003). Specifically, we conducted an in-situ transplant experiment manipulating lichen cover across four microsites: under intact lichen cover, adjacent bare soils without lichens (BS), bare soils where lichens were experimentally added, and soils where lichens were removed (see Figure 1 for the experimental design). This experimental design allowed us to examine three contrasting ecological scenarios: (i) lichen-covered versus adjacent bare soils, representing the ecological role of existing lichen cover; (ii) lichen addition versus bare soils, representing a potential restoration scenario involving the re-establishment of lichen cover; and (iii) lichen removal versus intact lichen-covered soils, representing the potential loss of lichen cover following environmental disturbance. We first quantified differences in soil variables associated with carbon (aromatic and phenolic compounds, dissolved organic carbon, microbial biomass carbon, and pentose-to-hexose ratio) and nitrogen (dissolved organic nitrogen, microbial biomass nitrogen, ammonium, nitrate, and mineralization) cycling. We then examined the temporal dynamics of soil respiration over a two-month period to evaluate its role in soil carbon exchange. We hypothesized that *Cladonia rangiformis* influences soil carbon and nitrogen cycling through changes in near-surface microclimatic conditions and soil organic matter. For instance, we expected lichen cover to buffer soil temperature and act as a barrier to wind erosion, resulting in greater accumulation of organic matter beneath the thalli.

2. Methods

Study site

This study was conducted in the surroundings of Doñana National Park in southwestern Spain (Fig. S1), a protected Mediterranean coastal ecosystem characterized by extensive stabilized dune systems. This arid region is characterized by a mean annual temperature of 17 °C and annual precipitation of approximately 575 mm. Soils are classified as Arenosols developed over coarse siliceous sands and are characterized by acidic pH, high permeability, and low water and nutrient retention capacity. These edaphic conditions, together with water limitation and high irradiance, favor the development of well-established lichen communities typical of Mediterranean dune ecosystems (Muñoz-Reinoso, 2018). The study area hosts abundant terricolous lichen communities dominated by squamulose (*Cladonia foliacea*) and fruticose lichens (*Cladonia rangiformis*) (Gallego Fernández & Díaz Barradas, 2014). *Cladonia rangiformis* is a fruticose lichen that lacks true rhizines or roots. Instead, its thalli form dense, interconnected mats that rest directly on the soil surface and are attached through their basal parts without penetrating deeply into the mineral soil. The large size of the colonies (20–30 cm in diameter) and their interlocking structure provided sufficient natural stability to withstand wind and water displacement in this dune environment.

Experimental design

A field transplant experiment was established in March 2015. Lichens were removed intact from selected patches and transplanted to nearby bare soils lacking lichen or vascular vegetation. Transplanted *Cladonia rangiformis* colonies remained intact and viable during the experiment, showing no visible signs of damage or stress attributable to the transplantation procedure. To minimize variability related to patch size, entire *Cladonia rangiformis* colonies measuring 20–30 cm in diameter were transferred and placed directly on the soil surface at the transplant location. This size range was used to standardize lichen patches across experimental treatments. Lichen-covered and bare

Downloaded from https://www.cambridge.org/core. UNIVERSIDAD AUTONOMA METROPOLITANA, on 17 Nov 2026 at 22:47:38, subject to the Cambridge Core terms of use, available at https://www.cambridge.org/core/terms. https://doi.org/10.1017/dry.2026.10058

soil patches did not exhibit a structured spatial arrangement across the study area. Instead, they occurred in an apparently random distribution within a relatively homogeneous dune surface. This lack of spatial pattern reduces the likelihood that differences between microsites are driven by underlying environmental gradients, supporting their use as comparable experimental units. Five experimental blocks were established within the study area. Each block contained five replicates of each microsite, resulting in a total of 25 soil samples per microsite. Soil samples were collected using stainless steel cylinders (5 cm diameter × 2 cm depth), targeting the uppermost soil layer where lichen–soil interactions occur. Lichen thalli were carefully removed prior to sampling to avoid contamination of the soil material. Soil sampling was performed two months after the completion of the transplant experiment. All soil samples were transported to the laboratory and stored at 4 °C until analysis. Soil samples were sieved (2 mm mesh) to remove coarse fragments, roots, and organic litter. Soil temperature fluctuations were recorded in situ using dataloggers (Fourtec – Fourier Technologies) buried beneath two lichen-covered and two adjacent bare soil microsites for approximately one month (34 days) (Figure 2B).

The transplant experiment was repeated in March 2017 to quantify soil respiration rates. Three experimental blocks were established, and one soil sample was collected from each microsite within each block, resulting in three independent samples per microsite. Soil respiration was measured hourly from sunrise to sunset (ca. 08:00–20:00) using a portable infrared gas analyser (EGM-4 IRGA, PP Systems) equipped with a closed dynamic chamber. The chamber was inserted ~1 cm into the soil surface, and the increase in CO_2 concentration over 1 min was used to calculate soil respiration, expressed as g CO_2 m^{-2} h^{-1}. For measurements under lichen cover, thalli were gently displaced to allow the chamber to form a consistent seal with the soil surface. Thalli were immediately returned to their original position after each measurement to minimize disturbance. The thalli were resting on the soil surface and were not embedded in the soil, and no soil was intentionally removed or disturbed during this process. The exposed surface therefore corresponded to the same soil surface that had been covered by the lichen, rather than a deeper or newly exposed soil layer. Measurements were conducted at the start of the experiment (day 0), 20 days later, approximately one month (34 days), and two months (70 days) following the experimental manipulation.

Laboratory analyses

Soil water content was determined gravimetrically by oven-drying approximately 2 g of fresh soil at 80 °C for 48 h (Allen, 1989). Organic matter content was determined by gravimetric combustion: dried samples were pre-ashed at 200 °C for 1 h with partial oxygen influx, then combusted at 500 °C for 2 h. Soil pH was measured in 1:2.5 suspensions of dry soil to deionized water. These variables were measured to characterize the physicochemical environment under intact lichen cover and adjacent bare soils. In addition, to assess how *Cladonia rangiformis* is associated with multiple soil indicators related to carbon and nitrogen cycling, we measured the following variables: dissolved organic carbon (DOC), microbial biomass carbon (MBC), soluble carbohydrates (pentoses and hexoses), aromatic and phenolic compounds, nitrate and ammonium, microbial biomass nitrogen (MBN), dissolved organic nitrogen (DON), and mineralization rates. For these analyses, 3 g of soil were extracted with 15 mL of 0.5 M K_2SO_4 (1:5 ratio) at 20 °C on a shaker at 200 rpm for 1 h and filtered through 0.45 µm Millipore filters. The resulting extracts were analysed following established colorimetric procedures (Chantigny et al., 2008).

Aromatic compounds were read at 254 nm in quartz cuvettes. Phenols were assayed using 0.7 mL of extract with 50 µL Folin-Ciocalteu reagent, incubated 3 min at room temperature, followed by addition of 100 µL saturated Na_2CO_3 solution, and read

Downloaded from https://www.cambridge.org/core. UNIVERSIDAD AUTONOMA METROPOLITANA, on 17 Nov 2026 at 22:47:38, subject to the Cambridge Core terms of use, available at https://www.cambridge.org/core/terms. https://doi.org/10.1017/dry.2026.10058

at 725 nm after 20 min. Soluble hexoses and pentoses were assayed using anthrone-sulfuric acid and orcinol-$FeCl_3$ reagents, respectively, following standard colorimetric procedures. MBC was determined by chloroform fumigation-extraction (Vance et al., 1987). For both MBC and DOC, 0.6 mL of sample was mixed with 0.2 mL 1 N $K_2Cr_2O_7$ and 0.3 mL concentrated H_2SO_4, digested at 150 °C for 15 min, cooled to room temperature, and 0.25 mL transferred to microplates for absorbance reading at 590 nm. DOC was measured in non-fumigated extracts, while MBC was calculated as the difference between fumigated and non-fumigated samples, divided by a correction factor Kc = 0.45.

Nitrate and ammonium concentrations were quantified colorimetrically from soil extracts (Sims et al., 1995). Briefly, 100 µL of soil extract was incubated with Devarda's alloy and 0.1 M H_2SO_4 for nitrate determination, and 75 µL of extract was incubated with potassium sulfate, citrate-salicylate, and hypochlorite reagents for ammonium, with absorbance measured at 650 nm. Potential net ammonification, nitrification, and mineralization rates were determined following Allen, Grimshaw & Rowland (1986). Dry soil samples were adjusted to 70% of field capacity and incubated at 30 °C for 14 days. Potential net rates were calculated based on the difference between initial and final concentrations over the incubation period. A detailed description of the protocol is available at https://zenodo.org/records/10354902. MBN and DON were determined using the fumigation-extraction method (Brookes et al., 1985). All samples were subjected to identical fumigation and extraction conditions. Briefly, 10 g of fresh soil was fumigated with chloroform or left unfumigated for 5 days before extraction. Both fumigated and non-fumigated soils were extracted with 0.5 M K_2SO_4, filtered, and nitrate and ammonium were quantified as described above. MBN was calculated as the difference between fumigated and non-fumigated samples using a correction factor (Kc = 0.54), while DON was obtained from the non-fumigated extracts.

Statistical analysis

To assess the effects of microsite type on soil properties (pH, organic matter, and moisture), we fitted linear mixed-effects models using the *lmerTest* R package (Kuznetsova et al., 2017). Each soil variable was modeled as a response with microsite type (UL and BS) as a fixed effect, and block was included as a random intercept to account for spatial replication. Significance of fixed effects was evaluated using Satterthwaite's method for degrees of freedom. Pairwise comparisons between microsites were performed using estimated marginal means (*emmeans*) with Tukey-adjusted p-values ($p < 0.05$ considered statistically significant). Linear mixed-effects models were also used to evaluate the effects of lichen addition or removal on soil respiration within each day. Models were fitted separately for each day, with hour included as a fixed covariate and block as a random effect. This modeling framework accounts for the dependence of repeated hourly measurements and adjusts for variation between blocks, thereby avoiding pseudoreplication. All analyses were performed in R using the *lme4* and *emmeans* packages (Bates et al., 2015).

To quantify the effects of lichens on soil functions, we calculated the Relative Interaction Index (RII) for each soil variable (Armas et al., 2004; Eldridge et al., 2023). RII values were calculated as

$$RII=(X_m\text{-}X_b)/(X_m\text{+}X_b),$$

where X_m and X_b represent the value of a given variable in the two microsites of interest. Three contrasts were considered: (i) UL versus BS, to quantify the effect of existing lichen cover; (ii) LA versus BS, to evaluate the effect of introducing lichen cover; and (iii) LR versus UL, to assess the effect of lichen removal. The index is bounded

Downloaded from https://www.cambridge.org/core. UNIVERSIDAD AUTONOMA METROPOLITANA, on 17 Nov 2026 at 22:47:38, subject to the Cambridge Core terms of use, available at https://www.cambridge.org/core/terms. https://doi.org/10.1017/dry.2026.10058

between −1 and 1, with positive values indicating higher levels of the variable in the first microsite of the contrast, and negative values indicating lower levels. Confidence intervals (95% CI) for RII were calculated using the standard error across blocks, and statistical significance was determined using one-sample t-tests against zero (results were considered significant when the CI did not cross zero). This approach allowed us to quantify both individual and combined effects on key soil functional attributes.

3. Results

Soils under intact lichen cover exhibited higher organic matter and moisture content than adjacent bare soils, while showing lower pH values (Figure 2A). The linear mixed-effects model for organic matter returned a singular fit, indicating that the variance associated with the random effect (block) was effectively zero. Pairwise comparisons revealed that organic matter was significantly higher in UL compared to BS (3.30 ± 1.40, t = 2.35, p = 0.023), confirming strong microsite effects despite the negligible random effect variance. The singular fit arose because differences in OM among microsites were very large relative to variation between blocks (Table S1). Soil temperatures were consistently higher in bare soils compared to under lichen, with differences peaking at ~10 °C during maximum solar radiation (Figure 2B).

We then found that lichen presence exerted a strong and positive influence on soil carbon and nitrogen cycling. Specifically, soils under intact lichen cover had significantly higher concentrations of phenolic and aromatic compounds, as well as increased microbial biomass carbon (Figure 3A). In the nitrogen cycle, the most pronounced increases were observed for nitrate, ammonium, and dissolved organic nitrogen (DON) (Figure 3B). After just two months, the experimental addition of lichens led to comparable increases in the same set of variables. Conversely, the removal of lichen cover resulted in a widespread and substantial decline in soil functions, with negative and significant RII values for most variables (Figure 3C). The only exception was the pentose-to-hexose ratio, which showed a positive but nonsignificant trend.

Linear mixed-effects models revealed no significant differences in soil respiration between under intact lichen and bare soils on most measurement days. The only exception was at day 0, when respiration under intact lichen cover was slightly higher (under lichen: 0.478 ± 0.035; bare soil: 0.446 ± 0.035 g CO_2 m^{-2} h^{-1}). Initial lichen removal or addition did not significantly affect respiration relative to bare soils on day 0. However, in all subsequent measurements (days 20, 34, and 70), soils where lichens were added exhibited significantly lower respiration rates than bare soils ($P < 0.01$), with bare soils reaching 0.469 ± 0.008 g CO_2 m^{-2} h^{-1} compared to 0.420 ± 0.008 g CO_2 m^{-2} h^{-1} under added lichens at day 70. Similarly, removal of lichens consistently led to higher respiration rates than soils under intact lichen cover across the same time points. For instance, at day 20, respiration under intact lichen measured 0.344 ± 0.024 g CO_2 m^{-2} h^{-1}, whereas soils from which lichens were removed showed 0.391 ± 0.024 g CO_2 m^{-2} h^{-1}.

4. Discussion

Drylands cover approximately 41% of Earth's land surface and support more than 38% of the global population, making them one of the most extensive and socio-ecologically important terrestrial biomes (Reynolds et al., 2007). Here, we found that fruticose lichens in Doñana National Park substantially modified soil microclimatic conditions, with higher soil moisture and organic matter and greater buffering of temperature fluctuations compared with adjacent bare soils. Differences in soil conditions associated with lichen presence may contribute to the higher values observed for most soil variables related to carbon and nitrogen cycling. Conversely, lichen removal led to widespread declines in

Downloaded from https://www.cambridge.org/core. UNIVERSIDAD AUTONOMA METROPOLITANA, on 17 Nov 2026 at 22:47:38, subject to the Cambridge Core terms of use, available at https://www.cambridge.org/core/terms. https://doi.org/10.1017/dry.2026.10058

soil functional attributes and increased soil respiration, highlighting the critical role of these symbiotic organisms. Given the ongoing decline in lichen cover reported in recent assessments (Ferrenberg et al., 2015), our findings underscore the vulnerability of soils on stabilized coastal dunes in a warmer world. Moreover, our findings highlight the need for restoration strategies that preserve lichen communities and sustain soil health in this vital ecosystem.

The upright thalli of fruticose lichens likely reduce wind-driven erosion (Belnap & Gillette, 1998; Eldridge & Greene, 1994), potentially contributing to greater organic matter accumulation beneath the lichen canopy. Their structure may also buffer soil temperature and contribute to higher soil moisture. For instance, higher temperatures in bare soils could increase evaporation rates, potentially contributing to the lower water content observed in these microsites. Positive RII values for aromatic and phenolic compounds under intact lichen cover also suggest a protective effect against UV-driven photodegradation (Austin & Vivanco, 2006), further stabilizing organic substrates. Consequently, higher soil moisture and greater availability of organic substrates including aromatic and phenolic compounds, may contribute to the higher microbial biomass observed under intact lichen cover. The lack of a significant response in dissolved organic carbon may reflect the high capacity to degrade recalcitrant compounds in arid soils (Dou et al., 2025; Shi et al., 2025). Moreover, the addition of lichens to bare soil reproduced the same effects within two months, indicating a rapid response in carbon cycling. Together, our results indicate that fruticose lichens influence soil carbon cycling by acting as both physical and biochemical modulators.

In terms of nitrogen cycling, lichen presence promoted higher levels of ammonium and nitrate, suggesting greater nitrogen availability under intact lichen cover. Although mineralization rates were not statistically significant, they showed a slightly positive trend. Higher soil moisture under intact lichen cover may favor nitrification and ammonification, as low soil moisture can limit microbial activity in dryland environments (Delgado-Baquerizo et al., 2017). These findings suggest that fruticose lichens may facilitate nitrogen transformations and contribute to greater nitrogen availability in this ecosystem. Moreover, the rapid recovery of ammonium and nitrate following lichen addition to previously bare soils supports this interpretation. Despite these differences, microbial nitrogen biomass did not differ significantly between microsites, which may indicate that microorganisms preferentially retain available inorganic nitrogen under the low nitrogen availability typical of these systems. For instance, previous studies have documented strong competition for dissolved organic nitrogen between plants and soil microorganisms in dryland ecosystems (Kaye & Hart, 1997)..

While differences in soil conditions under lichens, including higher soil moisture and organic matter, could be expected to influence CO_2 fluxes, soil respiration did not differ significantly from adjacent bare soils. This apparent decoupling likely reflects opposing mechanisms operating across microsites. In bare soils, microbial respiration may be constrained by lower soil moisture (Maestre et al., 2015), whereas lower daytime soil temperatures and potential allelopathic interactions may limit microbial activity under lichen. Indeed, previous work on *Cladonia rangiformis* has reported inhibitory effects on soil bacterial communities under natural conditions (Akpinar et al., 2009). Consistent with this idea, the addition of lichens to previously bare soils suppressed respiration rates, suggesting that lichen traits may modulate microbial activity through chemical interactions (e.g., see Figure 2A, which shows slightly more acidic pH under lichen) helping buffer soil carbon losses. In contrast, lichen removal significantly increased soil respiration in comparison to under lichen. The loss of lichen cover may expose soils to higher temperatures and greater solar radiation, potentially increasing microbial metabolism and abiotic processes such as photodegradation (Austin & Vivanco, 2006). Notably, respiration remained higher in removal plots even 70 days after the

Downloaded from https://www.cambridge.org/core. UNIVERSIDAD AUTONOMA METROPOLITANA, on 17 Nov 2026 at 22:47:38, subject to the Cambridge Core terms of use, available at https://www.cambridge.org/core/terms. https://doi.org/10.1017/dry.2026.10058

manipulation, suggesting that declines in lichen cover may lead to sustained increases in soil CO_2 emissions over the medium term.

As with any ecological study, our study has some limitations that should be considered when interpreting the results. First, the seasonal timing of the experiment may influence the magnitude of lichen effects on soil processes. Because the experimental manipulation was initiated in March and soil properties were evaluated approximately two months later, our results primarily reflect responses during the spring period. Whether these effects persist, weaken or change in magnitude across seasons remains to be tested through longer-term experiments. Second, future experiments could include a mechanical control treatment, in which lichen thalli are removed and then returned to their original position. This design would help account for potential effects of the removal procedure. Finally, lichen addition or removal may alter microbial community composition (Maier et al., 2018), which could contribute to the observed changes in soil processes. Further studies combining experimental manipulation with omics approaches could test this possibility.

Conclusion

Understanding how fruticose lichens influence soil functioning in drylands is essential for predicting ecosystem responses to climate change. Overall, our findings demonstrate that fruticose lichens act as key modulators of soil carbon and nitrogen cycling, while stabilizing soil respiration dynamics. Through their upright thalli, fruticose lichens likely operate as both physical and biochemical ecosystem engineers, reducing erosion and photodegradation while promoting organic matter accumulation and moisture retention. Conversely, experimental lichen loss caused widespread declines in soil functions and increased soil respiration, indicating that reductions in lichen cover may rapidly destabilize soil biogeochemical processes. The message for scientists, policymakers and concerned organizations is therefore clear: we need policies that monitor and conserve these organisms in stabilized coastal dune ecosystems such as Doñana National Park.

Author Contribution statement:

T.S.-S., and A.G. conceptualized the project. T.S.-S., L, G.-G, E.M.-U., N. S.-P., and A.L conducted laboratory analyses. T.S.-S. wrote the paper with all authors contributing to the drafts.

Financial Support:

T.S-S is supported by Australian Research Council (DP230101448).

Conflict of Interest statement:

The authors declare no conflicts of interest.

Data Availability statement: The supplementary material for this article can be

found at https://figshare.com/s/25df18e7e4a59c5c7ba7

Acknowledgements:

The authors acknowledge the use of the Grok AI tool to generate the illustration presented in Graphical Abstract and Figure 1.

Downloaded from https://www.cambridge.org/core. UNIVERSIDAD AUTONOMA METROPOLITANA, on 17 Nov 2026 at 22:47:38, subject to the Cambridge Core terms of use, available at https://www.cambridge.org/core/terms. https://doi.org/10.1017/dry.2026.10058

References

Akpinar, A. U., Ozturk, S., & Sinirtas, M. (2009). Effects of some terricolous lichens [Cladonia rangiformis Hoffm., Peltigera neckerii Hepp ex Müll. Arg., Peltigera rufescens (Weiss) Humb.] on soil bacteria in natural conditions. *Https://Pse.Agriculturejournals.Cz/Doi/10.17221/1616-PSE.Html*, *55*(4), 154–158. https://doi.org/10.17221/1616-pse

Allen, S.E., Grimshaw, H.M. & Rowland, A.P., 1986. Chemical Analysis. Methods in Plant Ecology. Blackwell Scientific, Oxford, UK.

Armas, C., Ordiales, R., & Pugnaire, F. I. (2004). Measuring plant interactions: A new comparative index. *Ecology*, *85*(10), 2682–2686. https://doi.org/10.1890/03-0650;WEBSITE:WEBSITE:ESAJOURNALS;REQUESTEDJOURNAL:JOURNAL:19399170;JOURNAL:JOURNAL:19399170;WGROUP:STRING:PUBLICATION

Asplund, J., & Wardle, D. A. (2017). How lichens impact on terrestrial community and ecosystem properties. *Biological Reviews*, *92*(3), 1720–1738. https://doi.org/10.1111/brv.12305

Austin, A. T., & Vivanco, L. (2006). Plant litter decomposition in a semi-arid ecosystem controlled by photodegradation. *Nature 2006 442:7102*, *442*(7102), 555–558. https://doi.org/10.1038/nature05038

Ballesteros, M., Ayerbe, J., Casares, M., Cañadas, E. M., & Lorite, J. (2017). Successful lichen translocation on disturbed gypsum areas: A test with adhesives to promote the recovery of biological soil crusts. *Scientific Reports 2017 7:1*, *7*(1), 45606-. https://doi.org/10.1038/srep45606

Bates, D., Mächler, M., Bolker, B. M., & Walker, S. C. (2015). Fitting Linear Mixed-Effects Models Using lme4. *Journal of Statistical Software*, *67*(1), 1–48. https://doi.org/10.18637/jss.v067.i01

Belnap, J. (2003). *Biological Soil Crusts: Structure, Function, and Management* (J. Belnap & O. L. Lange, Eds.; Vol. 150). Springer Berlin Heidelberg. https://doi.org/10.1007/978-3-642-56475-8

Belnap, J., & Gillette, D. A. (1998). Vulnerability of desert biological soil crusts to wind erosion: the influences of crust development, soil texture, and disturbance. *Journal of Arid Environments*, *39*(2), 133–142. https://doi.org/10.1006/jare.1998.0388

Blanco-Sacristán, J., Nelson, C., Corrochano-Monsalve, M., & Maestre, F. T. (2025). Biological soil crusts in the Arabian Peninsula: Ecological functions, current knowledge and research gaps. *Cambridge Prisms: Drylands*, *2*, e13. https://doi.org/10.1017/dry.2025.10007

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

Brookes, P. C., Landman, A., Pruden, G., & Jenkinson, D. S. (1985). Chloroform fumigation and the release of soil nitrogen: A rapid direct extraction method to measure microbial biomass nitrogen in soil. *Soil Biology and Biochemistry*, *17*(6), 837–842. https://doi.org/10.1016/0038-0717(85)90144-0

Canali, G., Hurtado, P., Giordani, P., & Ellis, C. (2025). Lichen hydration, moisture dynamics and climate change: A synthesis of established methods and potential new directions. *Fungal Biology Reviews*, *52*(5), 100417. https://doi.org/10.1016/j.fbr.2025.100417

Delgado-Baquerizo, M., Eldridge, D. J., Ochoa, V., Gozalo, B., Singh, B. K., & Maestre, F. T. (2017). Soil microbial communities drive the resistance of ecosystem multifunctionality to global change in drylands across the globe. *Ecology Letters*, *20*(10), 1295–1305. https://doi.org/10.1111/ele.12826

Downloaded from https://www.cambridge.org/core. UNIVERSIDAD AUTONOMA METROPOLITANA, on 17 Nov 2026 at 22:47:38, subject to the Cambridge Core terms of use, available at https://www.cambridge.org/core/terms. https://doi.org/10.1017/dry.2026.10058

Díaz-Martínez, P., Panettieri, M., García-Palacios, P., Moreno, E., Plaza, C., & Maestre, F. T. (2022). Biocrusts Modulate Climate Change Effects on Soil Organic Carbon Pools: Insights From a 9-Year Experiment. *Ecosystems 2022 26:3*, *26*(3), 585–596. https://doi.org/10.1007/s10021-022-00779-0

Dou, W., Xiao, B., Saez-Sandino, T., & Delgado-Baquerizo, M. (2025). Coexistence of vascular plants and biocrusts under changing climates and their influence on ecosystem carbon fluxes. *Agricultural and Forest Meteorology*, *360*, 110298. https://doi.org/10.1016/j.agrformet.2024.110298

Eldridge, D. J., & Greene, R. S. B. (1994). Microbiotic Soil Crusts: A Review of their Roles in Soil and Ecological Processes in the Rangelands of Australia. *Aust. J. Soil Res*, *32*, 389–415.

Eldridge, D. J., Guirado, E., Reich, P. B., Ochoa-Hueso, R., Berdugo, M., Sáez-Sandino, T., Blanco-Pastor, J. L., Tedersoo, L., Plaza, C., Ding, J., Sun, W., Mamet, S., Cui, H., He, J.-Z., Hu, H.-W., Sokoya, B., Abades, S., Alfaro, F., Bamigboye, A. R., … Delgado-Baquerizo, M. (2023). The global contribution of soil mosses to ecosystem services. *Nature Geoscience*, *16*(5), 430–438. https://doi.org/10.1038/s41561-023-01170-x

Ferrenberg, S., Reed, S. C., Belnap, J., & Schlesinger, W. H. (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

Gallego Fernández, J. B., & Díaz Barradas, M. C. (2014). Lichens as indicators of a perturbation/stability gradient in the Asperillo dunes, SW spain. *Journal of Coastal Conservation 1997 3:1*, *3*(1), 113–118. https://doi.org/10.1007/BF02908186

Havrilla, C. A., Chaudhary, V. B., Ferrenberg, S., Antoninka, A. J., Belnap, J., Bowker, M. A., Eldridge, D. J., Faist, A. M., Huber-Sannwald, E., Leslie, A. D., Rodriguez-Caballero, E., Zhang, Y., & Barger, N. N. (2019). Towards a predictive framework for biocrust mediation of plant performance: A meta-analysis. *Journal of Ecology*, *107*(6), 2789–2807. https://doi.org/10.1111/1365-2745.13269

Kaye, J. P., & Hart, S. C. (1997). Competition for nitrogen between plants and soil microorganisms. *Trends in Ecology & Evolution*, *12*(4), 139–143. https://doi.org/10.1016/S0169-5347(97)01001-X

Kuznetsova, A., Brockhoff, P. B., & Christensen, R. H. B. (2017). lmerTest Package: Tests in Linear Mixed Effects Models. *Journal of Statistical Software*, *82*(13), 1–26. https://doi.org/10.18637/JSS.V082.I13

Lalley, J. S., & Viles, H. A. (2008). Recovery of lichen-dominated soil crusts in a hyper-arid desert. *Biodivers. Conserv.*, *17*(1), 1–20. https://doi.org/10.1007/s10531-007-9153-y

López-Rodríguez, M. D., Chamizo, S., Cantón, Y., & Rodriguez-Caballero, E. (2020). Identifying social-ecological gaps to promote biocrust conservation actions. *Web Ecology*, *20*(2), 117–132. https://doi.org/10.5194/we-20-117-2020

Maestre, F. T., Delgado-Baquerizo, M., Jeffries, T. C., Eldridge, D. J., Ochoa, V., Gozalo, B., Quero, J. L., García-Gómez, M., Gallardo, A., Ulrich, W., Bowker, M. A., Arredondo, T., Barraza-Zepeda, C., Bran, D., Florentino, A., Gaitán, J., Gutiérrez, J. R., Huber-Sannwald, E., Jankju, M., … Singh, B. K. (2015). Increasing aridity reduces soil microbial diversity and abundance in global drylands. *Proceedings of the National Academy of Sciences*, *112*(51), 15684–15689. https://doi.org/10.1073/pnas.1516684112

Maestre, F. T., Escolar, C., de Guevara, M. L., Quero, J. L., Lázaro, R., Delgado-Baquerizo, M., Ochoa, V., Berdugo, M., Gozalo, B., & Gallardo, A. (2013). Changes in biocrust cover drive carbon cycle responses to climate change in drylands. *Global Change Biology*, *19*(12), 3835–3847. https://doi.org/10.1111/gcb.12306

Downloaded from https://www.cambridge.org/core. UNIVERSIDAD AUTONOMA METROPOLITANA, on 17 Nov 2026 at 22:47:38, subject to the Cambridge Core terms of use, available at https://www.cambridge.org/core/terms. https://doi.org/10.1017/dry.2026.10058

Maier, S., Tamm, A., Wu, D., Caesar, J., Grube, M., & Weber, B. (2018). Photoautotrophic organisms control microbial abundance, diversity, and physiology in different types of biological soil crusts. *The ISME Journal*, *12*(4), 1032–1046. https://doi.org/10.1038/S41396-018-0062-8

Miralles, I., Domingo, F., García-Campos, E., Trasar-Cepeda, C., Leirós, M. C., & Gil-Sotres, F. (2012). Biological and microbial activity in biological soil crusts from the Tabernas desert, a sub-arid zone in SE Spain. *Soil Biology and Biochemistry*, *55*, 113–121. https://doi.org/10.1016/j.soilbio.2012.06.017

Muñoz-Reinoso, J. C. (2018). Doñana mobile dunes: what is the vegetation pattern telling us? *Journal of Coastal Conservation 2018 22:4*, *22*(4), 605–614. https://doi.org/10.1007/s11852-018-0594-0

Reynolds, J. F., Smith, D. M. S., Lambin, E. F., Turner, B. L., Mortimore, M., Batterbury, S. P. J., Downing, T. E., Dowlatabadi, H., Fernández, R. J., Herrick, J. E., Huber-Sannwald, E., Jiang, H., Leemans, R., Lynam, T., Maestre, F. T., Ayarza, M., & Walker, B. (2007). Global Desertification: Building a Science for Dryland Development. *Science*, *316*(5826), 847–851. https://doi.org/10.1126/science.1131634

Rodríguez-Peñate, A. E., Escudero, A., Martínez, I., & Madrigal-González, J. (2019). Unveiling annual growth chronologies from inter-nodal branch elongations in a fruticose lichen in southern Europe. *Fungal Biology*, *123*(11), 824–829. https://doi.org/10.1016/J.FUNBIO.2019.08.008

Shi, J., Tao, J., Peng, Y., Wang, J., & Wang, X. (2025). Biocrusts benefit soil carbon sequestration via increasing the stability of soil dissolved organic carbon in dryland ecosystem. *Journal of Environmental Management*, *375*, 124304. https://doi.org/10.1016/j.jenvman.2025.124304

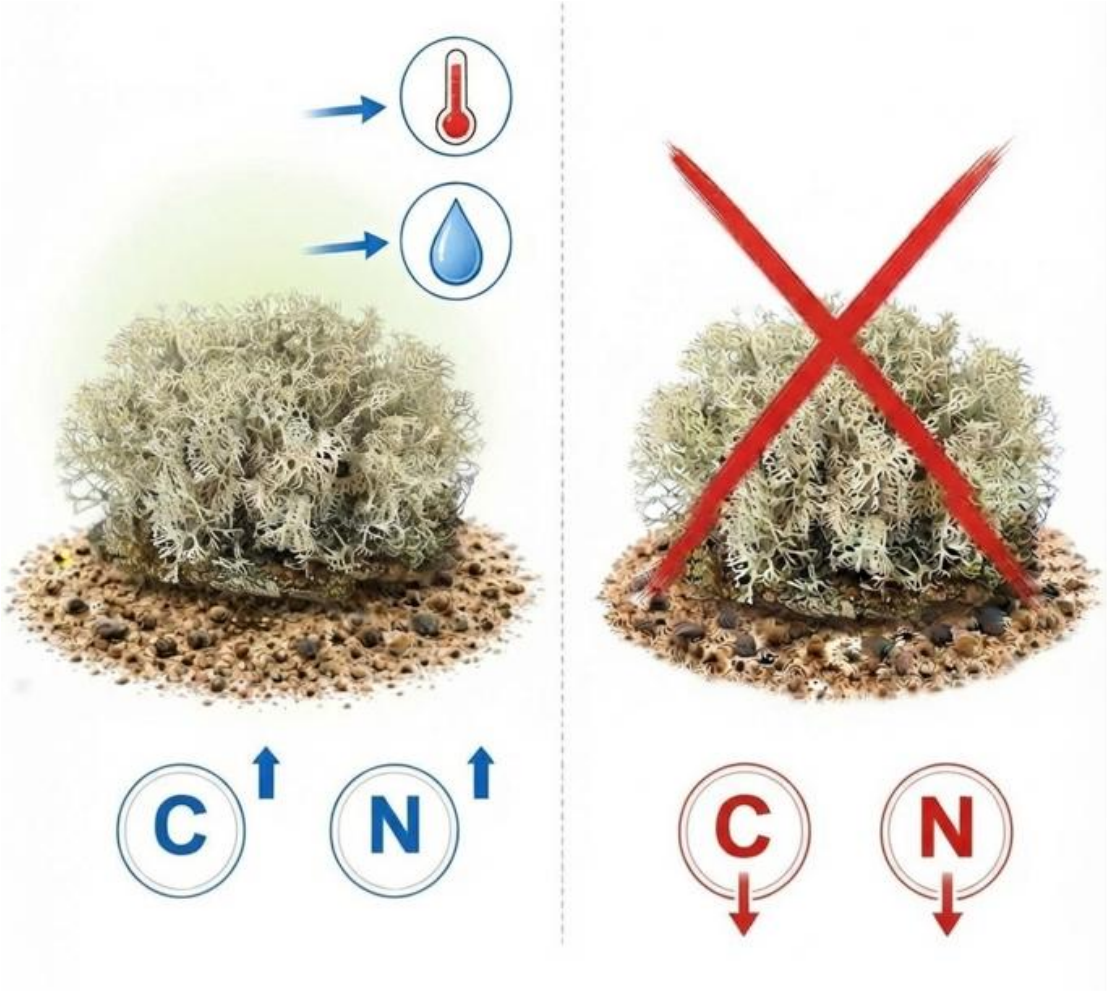
Sims, G. K., Ellsworth, T. R., & Mulvaney, R. L. (1995). Microscale determination of inorganic nitrogen in water and soil extracts. *Communications in Soil Science and Plant Analysis*, *26*(1–2), 303–316. https://doi.org/10.1080/00103629509369298

Vance, E. D., Brookes, P. C., & Jenkinson, D. S. (1987). An extraction method for measuring soil microbial biomass C. *Soil Biology and Biochemistry*, *19*(6), 703–707. https://doi.org/10.1016/0038-0717(87)90052-6

Zunzunegui, M., Esquivias, M. P., & Gallego-Fernández, J. B. (2022). Spatial and seasonal patterns of water use in Mediterranean coastal dune vegetation. *Plant and Soil 2022 477:1*, *477*(1), 807–828. https://doi.org/10.1007/s11104-022-05443-z

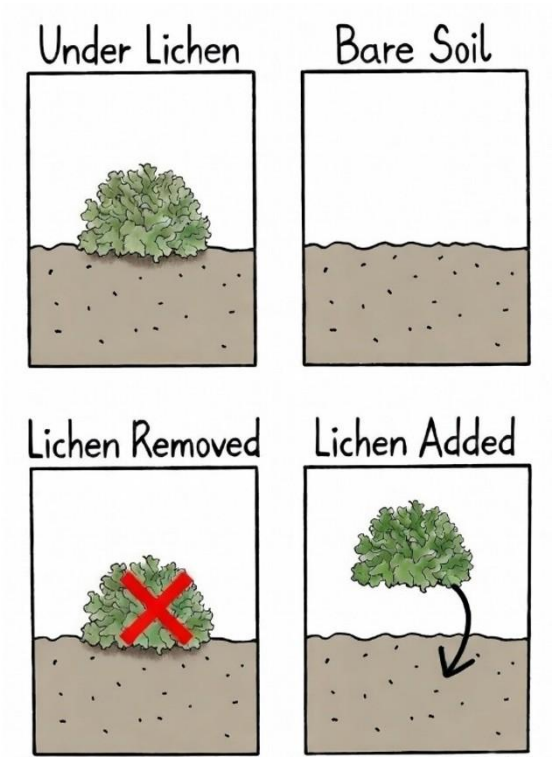
Downloaded from https://www.cambridge.org/core. UNIVERSIDAD AUTONOMA METROPOLITANA, on 17 Nov 2026 at 22:47:38, subject to the Cambridge Core terms of use, available at https://www.cambridge.org/core/terms. https://doi.org/10.1017/dry.2026.10058

Graphical Abstract



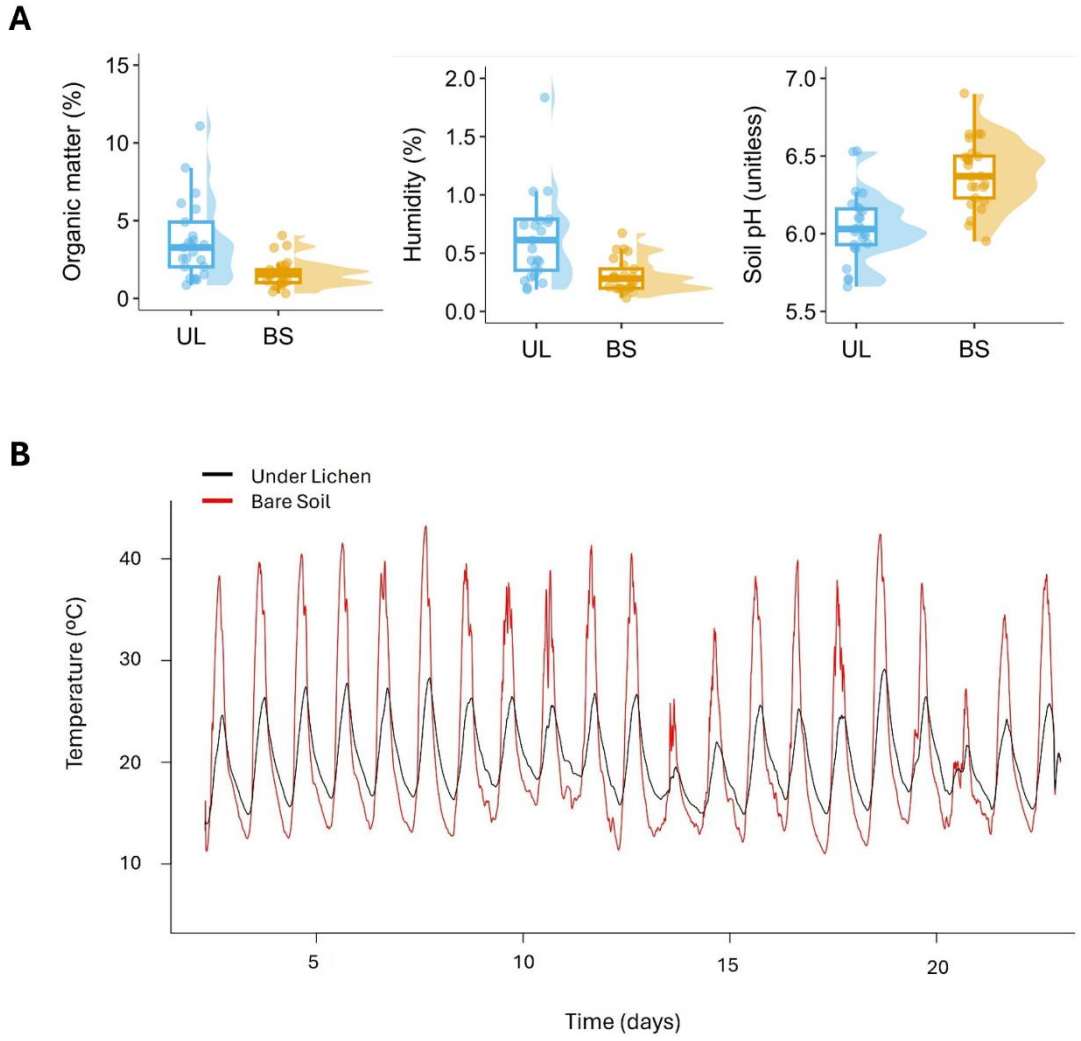
Downloaded from https://www.cambridge.org/core. UNIVERSIDAD AUTONOMA METROPOLITANA, on 17 Nov 2026 at 22:47:38, subject to the Cambridge Core terms of use, available at https://www.cambridge.org/core/terms. https://doi.org/10.1017/dry.2026.10058

Figure 1. Design of the in-situ transplant experiment. Four microsites were established: soils under intact lichen cover, adjacent bare soils without lichens, bare soils where lichens were experimentally added, and soils where lichens were removed. Here, “microsite” refers to a distinct spatial unit defined by the presence, addition or removal of lichen cover.



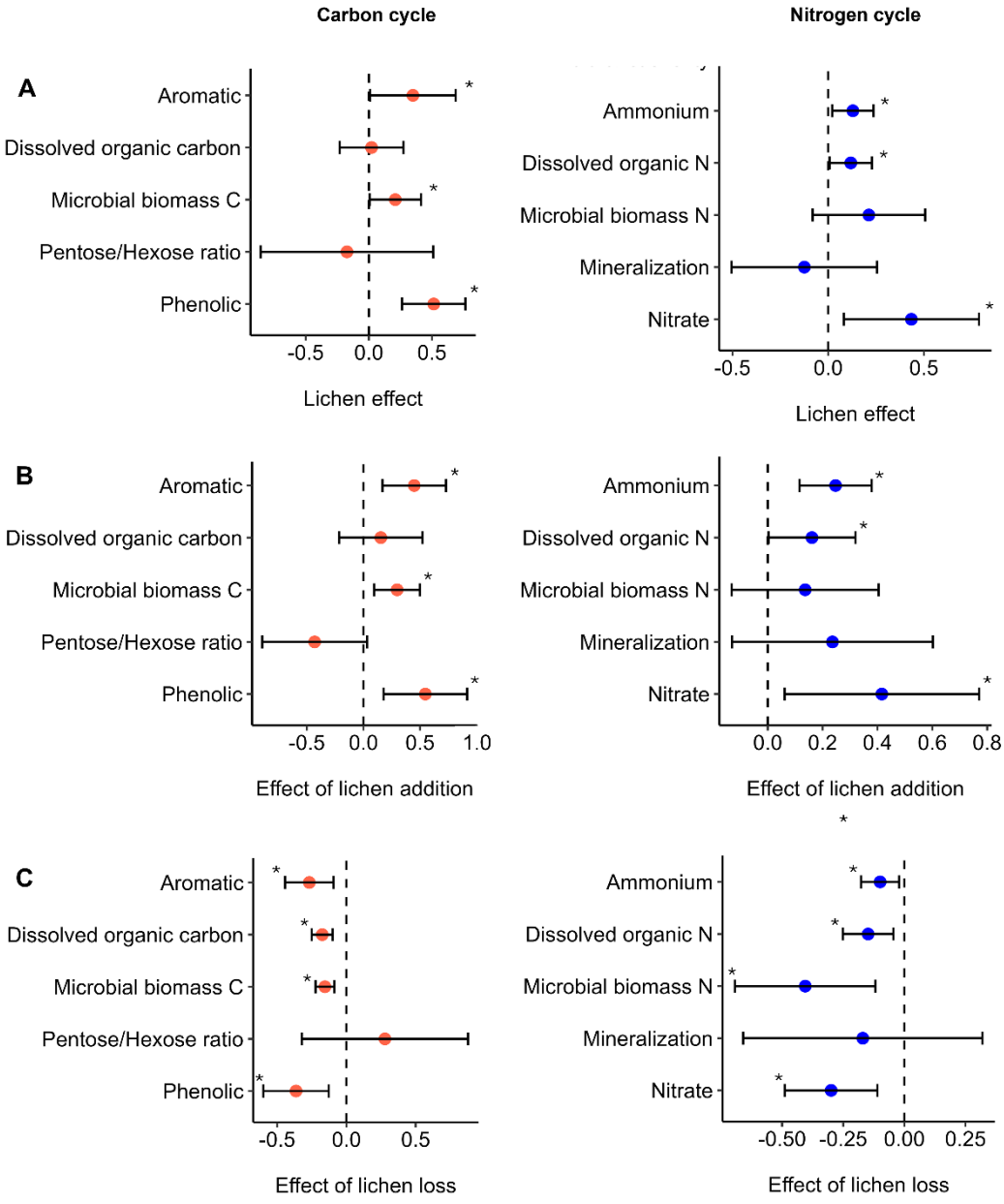
Downloaded from https://www.cambridge.org/core. UNIVERSIDAD AUTONOMA METROPOLITANA, on 17 Nov 2026 at 22:47:38, subject to the Cambridge Core terms of use, available at https://www.cambridge.org/core/terms. https://doi.org/10.1017/dry.2026.10058

Figure 2. Main differences between UL and BS microsites. Panel A shows variations in soil physical and chemical properties, while Panel B illustrates soil temperature dynamics over time. Boxplots show the median (central line) and interquartile range (box), while individual points represent replicate measurements for each block. Half-violin plots (shaded areas) represent the density distribution, with wider regions indicating more frequent values.



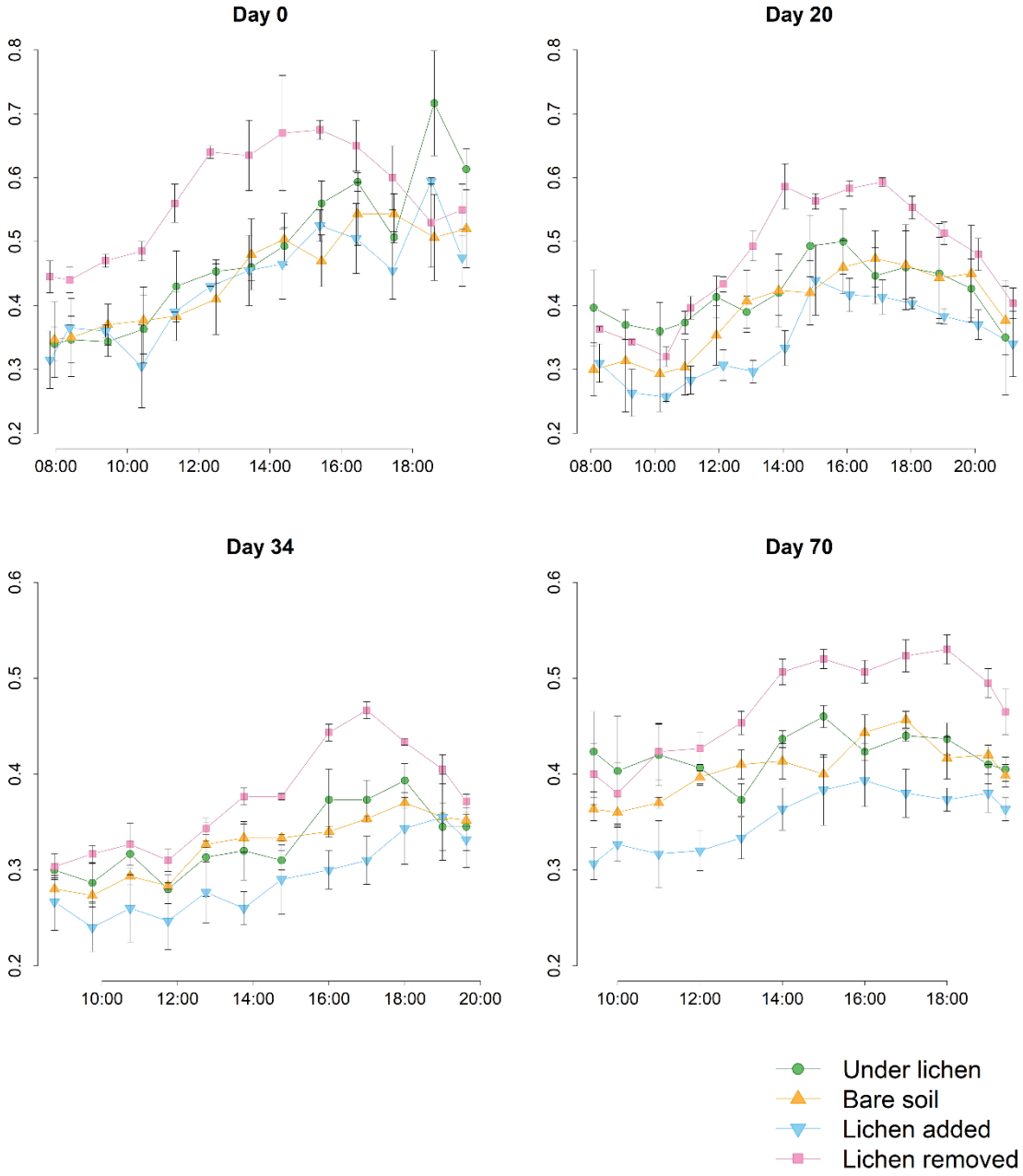
Downloaded from https://www.cambridge.org/core. UNIVERSIDAD AUTONOMA METROPOLITANA, on 17 Nov 2026 at 22:47:38, subject to the Cambridge Core terms of use, available at https://www.cambridge.org/core/terms. https://doi.org/10.1017/dry.2026.10058

Figure 3. **Effects of lichens on soil functions**. Panel A shows the effect of existing lichen cover, Panel B shows the effect of lichen addition, and Panel C shows the effect of lichen removal. Points represent mean RII across blocks, with horizontal lines indicating 95% confidence intervals. Variables are considered significant when the confidence interval does not cross zero.



Downloaded from https://www.cambridge.org/core. UNIVERSIDAD AUTONOMA METROPOLITANA, on 17 Nov 2026 at 22:47:38, subject to the Cambridge Core terms of use, available at https://www.cambridge.org/core/terms. https://doi.org/10.1017/dry.2026.10058

Figure 4. Effects of lichens on soil respiration. Panels show predicted mean respiration rates (±95% CI) for each microsite and day (0, 20, 34 and 70 days), accounting for hourly variation (hour as fixed covariate) and block as a random effect.



Downloaded from https://www.cambridge.org/core. UNIVERSIDAD AUTONOMA METROPOLITANA, on 17 Nov 2026 at 22:47:38, subject to the Cambridge Core terms of use, available at https://www.cambridge.org/core/terms. https://doi.org/10.1017/dry.2026.10058