

Kakeh Jalil (Orcid ID: 0000-0001-5010-3268)

Original Research Article, for submission to: *Land Degradation & Development*

Biocrust diversity enhances dryland saline soil multifunctionality

Running title: Biocrusts and dryland soil multifunctionality

Jalil Kakeh^{1*#}, Anvar Sanaei^{2#}, Emma J Sayer^{3,4}, Shadi Hazhir⁵, Manouchehr Gorji¹, Mohammad Hossein Mohammadi¹

¹ Soil Sciences Department, University of Tehran, Karaj, Iran.

² Systematic Botany and Functional Biodiversity, Institute of Biology, Leipzig University, Leipzig, Germany

³ Lancaster Environment Centre, Lancaster University, Lancaster, UK

⁴ Smithsonian Tropical Research Institute, Panama City, Panama

⁵ Rangeland Management Department, Faculty of Natural Resources, Tarbiat Modares University, Tehran, Iran

* Address for correspondence. Email: jalil.kaka@ut.ac.ir

These authors contributed equally to this work

The authors declare that they have no conflict of interest.

This article has been accepted for publication and undergone full peer review but has not been through the copyediting, typesetting, pagination and proofreading process which may lead to differences between this version and the [Version of Record](#). Please cite this article as doi: [10.1002/ldr.4476](https://doi.org/10.1002/ldr.4476)

This article is protected by copyright. All rights reserved.

Abstract

Biocrusts are multifaceted communities including mosses, lichens, and cyanobacteria that are crucial for sustaining soil functions in drylands. Most studies on biocrust functions to date have focused on biocrust cover and development, largely in non-saline soils, and we know very little about the importance of biocrust diversity for maintaining multifunctionality in saline dryland soils. We assessed the direct and indirect linkages between biocrust richness, soil texture and salinity and soil multifunctionality by measuring 13 variables characterizing soil biological, nutrient and hydrological functions across 32 plots in a salinized dryland in northeastern Iran. We assessed the species richness of biocrust patches and characterized soil functions in bare soils. Overall, biocrust species richness declined with soil clay content and soil salinity, whereas soil salinity increased with soil clay content. Structural equation modelling showed a strong positive association between biocrust species richness and all measured dryland soil functions (soil biological, nutrient and hydrological functions), but soil hydrological function declined with soil salinity. Overall, dryland soil multifunctionality was positively associated with biocrust species richness but negatively associated with soil clay content. Biocrust species richness likely enhances soil multifunctionality via the distinct roles of species and biocrust functional groups in providing carbon and nutrient inputs, creating favorable microsites, enhancing infiltration, and facilitating soil microbial colonization in saline dryland soils. Overall, our findings highlight a key role for biocrust diversity in facilitating and maintaining soil multifunctionality in drylands affected by soil salinity.

Keywords: Biocrust diversity, Biological soil function, Hydrological soil function, Nutrient soil function, Soil salinity, Multifunctionality, Saline dryland soils

1. Introduction

Drylands cover approximately 40% of Earth's terrestrial surface (Schimel, 2010; Právělie, 2016) and dryland soils contribute to numerous important ecosystem functions and services, including climate and water regulation (Greiner et al., 2018; Ye et al., 2019), nutrient cycling and carbon sequestration (Delgado-Baquerizo et al., 2017), and biodiversity (Kooch et al., 2021). Unfortunately, dryland soils are particularly susceptible to degradation (Eldridge et al., 2020a), which is concerning because drylands are being increasingly affected by multiple pressures. Anthropogenic pressures such as overgrazing (Middleton, 2018) and climate changes (Právělie et al., 2019; Ye et al., 2019) reduce soil water availability, degrade biotic communities and exacerbate soil erosion and salinity, resulting in declining productivity (Delgado-Baquerizo et al., 2013; Delgado-Baquerizo et al., 2016; Vandendorj et al., 2017). Given the capacity of dryland soils to supply multiple ecosystem services, conserving soil functions in these areas is necessary for sustaining life on Earth (Mahmoudi et al., 2021). Soil multifunctionality is a powerful indicator for assessing the impacts of disturbance and the success of restoration efforts in drylands and other ecosystems globally (Read et al., 2016; Eldridge et al., 2020a). In drylands, soil surface attributes, including biotic communities, could be particularly effective proxies of soil multifunctionality because they respond rapidly to changes in climate and land-use, and influence numerous important soil processes (Maestre et al., 2012; Eldridge et al., 2020a; Kooch et al., 2021).

Biological soil crusts, or biocrusts, on the soil surface are ecosystem engineers that have a major influence on soil multifunctionality by mediating biogeochemical cycles, and yet they are often overlooked in dryland ecosystems (Maestre et al., 2021). Biocrusts are multifaceted communities of mosses, lichens, cyanobacteria and algae living in association with the first centimeters of the topsoil (Belnap, 2006). In drylands, they are found in plant interspaces within

Accepted Article

the spatial mosaic of vegetation patches and bare soil (Rodriguez-Caballero et al., 2018; Kakeh et al., 2020). By forming a living skin on the soil surface, biocrusts modify the inputs, outputs and transfer of material and energy between above- and belowground subsystems (Belnap et al., 2016; Mallen-Cooper et al., 2020). Importantly, biocrusts regulate soil water content by controlling infiltration, runoff, and evaporation, which in turn affects plant establishment and growth, soil biological activity, and nutrient cycling (Rodriguez-Caballero et al., 2018). Consequently, biocrusts are a major organizing component of drylands that alter many processes and support critical soil functions such as nutrient availability and hydrology (Belnap et al., 2016). In recent years, an increasing number of studies have demonstrated that biocrusts perform multiple important functions in dryland ecosystems (Maestre et al., 2012; Delgado-Baquerizo et al., 2016; Eldridge et al., 2020b; Raggio et al., 2021), which can be assessed with measurable functional indicators (Eldridge et al., 2020a; Mallen-Cooper et al., 2020). Biocrusts contribute to erosion resistance by influencing soil aggregate stability and soil shear strength (Belnap & Büdel, 2016), regulate hydrology by influencing hydrophobicity and infiltration (Eldridge et al., 2020b; Kakeh et al., 2021b), and contribute to nutrient availability by carbon and nitrogen fixation and soil nutrient pools (Barger et al., 2016; Sancho et al., 2016). Biocrusts also contribute to overall dryland productivity (Rossi et al., 2018) and soil microbial diversity and activity. Most of the soil functions and processes supported by biocrusts are related to attributes such as cover and species richness or composition (Liu et al., 2017; Chen et al., 2020; Eldridge et al., 2020a), and influenced by soil surface properties such as salinity (Kakeh et al., 2021b).

Biocrust diversity has been recognized as the main driver of soil multifunctionality because numerous soil processes and functions are strongly linked to biocrust diversity and cover (Bowker et al., 2013). Biocrust species richness could be a better indicator of soil multifunctionality than

cover (Soliveres & Eldridge, 2020) because biocrust-forming mosses and lichens differ in their influence on soil functions and some processes, such as nitrogen fixation, are highly species-specific (Maestre et al., 2012; Delgado-Baquerizo et al., 2015; Liu et al., 2017). Biocrust diversity is maintained by interactions among biocrust species and between biocrust organisms and soil surface attributes (Sun & Li, 2021). Collectively, biocrust and soil surface attributes can therefore be used to determine soil multifunctionality and one of the most important soil surface attributes interacting with biocrusts in drylands is soil salinity. Salinity affects many of the soil functions and processes that are facilitated by biocrusts, including erosion resistance (Daliakopoulos et al., 2016), soil hydrology (Kakeh et al., 2021b), nutrient cycling (Wang et al., 2021), growth and survival of vegetation (Jiang et al., 2018), and soil microbial diversity (Zhang et al., 2019). Given that biocrusts regulate many of these important soil properties and processes, biocrusts could mitigate the effects of salinity and maintain or improve soil functioning (Kakeh et al., 2021b). Many drylands with saline soils are characterized by a mosaic comprising patches of biocrusts, annual vascular plants, and bare highly saline soils (Chen et al., 2020). Patches with stable biocrust cover could play an important role in maintaining soil multifunctionality and thus in mitigating the overall impacts of soil salinity. Understanding the impact of biocrust diversity on the functioning of saline soils has regional and global importance because salinization is a major issue in many drylands worldwide (Hassani et al., 2021; Stavi et al., 2021). Soil salinization results from increased evaporation and salt accumulation due to physical and chemical degradation (e.g. caused by overgrazing; Bolo et al., 2019; Goldberg et al., 2021). Salinization reduces soil stability and water infiltration, limits water availability and therefore creates strong stress conditions for dryland organisms (Daliakopoulos et al., 2016). However, most studies of biocrust functioning have

Accepted Article

focused on non-saline soils, and the relative influence of biocrust diversity and soil salinity on soil multifunctionality represent a major knowledge gap in our understanding of dryland ecosystems.

Here, we assessed the role of biocrust richness for maintaining multifunctionality in saline dryland soils by measuring soil surface properties and microbial activity in the arid Qara Qir rangeland in Iran. We hypothesized that biocrust species richness would enhance dryland soil multifunctionality by regulating crucial processes such as soil nutrient availability, biological activity and hydrological cycles (Figure 1; Table 1). Thus, the main objectives of our study were to: 1) to assess the direct and indirect pathways by which soil attributes (soil texture and salinity) influence different soil functions and overall dryland soil multifunctionality; and 2) determine the predictive power of biocrust species richness for explaining variation in different soil functions and overall dryland soil multifunctionality.

2. Material and methods

2.1. Study area

The study was performed in the Qara Qir rangeland around the Alagol Lake, Golestan province, Northern Iran (37°15' - 37°23' N and 54°33' - 54°39' E; Figure S1). The landscape is characterized by a parabolic sand dune of Holocene age with a 3-5% slope, and an altitude of 15 to 47 m a.s.l. The soils are derived from an overlying layer of loess deposits and are classified as Sodic Haplogypsis (Baillie, 2001); they are deep (*c.* 3 m) and naturally saline (Moser, 2009), with a loamy topsoil texture (Kakeh et al., 2020). The climate of the study area is arid, with a mean annual precipitation of 273 mm, most of which falls in winter (January and February). The mean annual

temperature is 19.1°C and annual potential evaporation is 1700 mm (Iranian Meteorological Organization, IRIMO).

The study area is a mosaic of bare saline soils and patches covered with biocrusts and vascular vegetation, which is sparse as a result of historic and current overgrazing (Figure S1d). Thus, vegetated patches consisting of biocrusts and some vascular plants are interspersed with bare soil patches with high salinity. The vegetated patches are dominated by mosses (mean cover 67.3%), followed by lichens (20.1%) and vascular plants (12.6%, Table S1). The predominant moss species at our study site were *Tortula revolvens* (Schimp.) G. Roth and *Barbula trifaria* (Hedw.) Mitt., and the most abundant lichens was *Diploschistes diacapsis* (Ach.) Lumbsch. A detailed list of vascular plant and biocrust species (lichens and mosses) is given in Table S1.

2.2. Soil sampling and measurement of soil functional indicators

To ensure representative sampling, we selected four random sites along a 5 Km-transect across the study area (Figure S1c), with at least 500-m between sampling sites. The study therefore covered a total area of *c.* 9800 ha that was broadly representative of regional climatic and soil conditions, as well as vegetation and biocrust composition. Within each site, we established eight plots on summit sand dune positions: four dominated by biocrusts and four bare soils (Table S1; Figure S1d). Each plot measured 0.5 m² (0.62 m × 0.82 m), with min. 1 m between adjacent pairs of plots to ensure spatial independence. Thus, we quantified soil functions in a total of 32 plots, 16 of which were dominated by biocrusts and 16 were bare soil. Although biocrusts can influence some soil functions (e.g. hydrological functions) throughout the surface horizons (Kakeh et al., 2021b) their effect on other functions (e.g. nutrient and biological functions) occurs close to the soil

Accepted Article

surface (Setia et al., 2013; Nevins et al., 2020). To evaluate the effect of biocrusts on soil multifunctionality, all samples and measurements were made at 0-5-cm depth.

Soil hydrological attributes and soil properties to 0-5-cm depth were measured immediately adjacent to the sampling plots in previous experiments in 2017-2018 (Kakeh et al., 2020; Kakeh et al., 2021b). In brief, we used a pressurized rainfall simulator mounted 2 m above the soil surface to apply 40 mm rainfall h^{-1} during 90 min, after which we measured total runoff and calculated runoff time, runoff volume, sediment yield and infiltration rates following Holden and Burt (2002). Hydrological measurements were made seasonally and all three seasonal values were considered for this study regardless of the measured time. Soil surface samples were collected from each plot after hydrological measurements. To calculate biocrust species richness, we identified all mosses and lichens in each plot to species level; biocrust richness was considered the total number of moss and lichen species per plot. Although biocrust communities also include cyanobacteria, they are usually associated with mosses and lichens, and were not assessed separately here. A list of the dominant biocrust species and their diversity within plot is given in Table S1.

Soil properties at 0-5-cm depth were determined using standard methods. Soil physical attributes were: soil clay content measured using the hydrometer method (Gee & Bauder, 1986), bulk density determined by the clod method (Blake & Hartge, 1986), and soil porosity based on bulk and particle density data (Pires et al., 2014). Soil nutrient contents were used as a proxy for nutrient availability; we measured calcium carbonate content using the vacuum-gasometric method (Jones & Kaiteris, 1983), electrical conductivity and pH based on a 1:5 soil:water solution (Rhoades, 1982), water-soluble potassium and sodium using flame photometry (Rhoades, 1982), calcium and magnesium using the EDTA volumetric method (Lanyon & Heald, 1982), chloride and bicarbonate using silver nitrate titration and neutralization titration (Ryan, 2017), and we

Accepted Article

calculated the sodium adsorption ratio based on water-soluble potassium, calcium and magnesium (McGeorge, 1954). We further measured soil organic carbon using the Walkley-Black method (Nelson & Sommers, 1996), total soil nitrogen using the Kjeldahl method (Bremner & Mulvaney, 1982), Olsen-extractable phosphorus (P_{extr}; Olsen & Sommers, 1982), and ammonium-acetate extractable potassium (K⁺ extr; Knudsen et al., 1982). Soil hydrological measurements were: gravimetric soil water content (θ_g ; Topp, 1993), available water content (Dane & Hopmans, 1986), and total infiltration and runoff measured using rainfall simulation (Holden & Burt, 2002). Finally, we determined the following soil biological properties: microbial biomass carbon and microbial biomass nitrogen using chloroform fumigation extraction (Vance et al., 1987), soil basal respiration using static incubation (Anderson, 1983), the soil metabolic quotient (calculated according to (Anderson & Domsch, 1990), and estimated microbial population size using the most probable number method in nutrient broth medium (Alexander, 1965). We calculated soil stocks of carbon, nitrogen, phosphorus and potassium at 0-5 cm depth using the measurements of soil bulk density and clay content (Schrumpf et al., 2011). To calculate soil salinity, we averaged the values for electrical conductivity, sodium, potassium, calcium + magnesium, chloride, and the sodium adsorption ratio after standardizing each variable by Z-transformation (Kakeh et al., 2021b).

2.3. Data analyses

Soil multifunctionality calculation

We measured dryland soil multifunctionality using 13 functional attributes, grouped into three sets of four or five attributes representing soil biological function (microbial biomass carbon and

nitrogen, soil basal respiration, microbial population size and soil metabolic quotient), soil hydrological function (gravimetric soil water content, available water content, infiltration and runoff), and soil nutrient function (soil organic carbon stock, soil nitrogen stock, extractable phosphorus stock and extractable potassium stock). We chose these functions because they are widely used as indicators of overall ecosystem functioning in drylands (Vandandorj et al., 2017; Chen et al., 2020; Li et al., 2020) and they are closely related to previously reported functional roles of biocrusts (Dias et al., 2020; Eldridge et al., 2020a; Thomas et al., 2022). We standardized each attribute individually using the Z-score transformation (Eq. 1) and then used each set of attributes to calculate indices representing soil hydrological function (using four attributes), nutrient function (using four attributes) and biological function (using five attributes), respectively; we then calculated an index of overall soil multifunctionality using all 13 attributes:

$$Z - score_{ij} = \frac{F_{ij} - MeanF_i}{SDF_i} \quad (\text{Equation 1})$$

Where F_{ij} is the value of a function i in the community j , and $MeanF_i$ and SDF_i are the mean and standard deviation of function F_i (Le Bagousse-Pinguet et al., 2019).

Statistical analyses

We used independent samples t-tests to compare soil properties and functions between biocrust plots and bare soils (Figure 2). We investigated the direct, indirect, and total contributions of soil texture (clay content), salinity and biocrust species richness to variation in dryland soil functioning using structural equation models (SEMs). We constructed separate models for soil multifunctionality, and for soil hydrological (four attributes), biological (five attributes), and nutrient (four attributes) functions (Figure 1; Table 1). The goodness of fit of each model was assessed using a χ^2 test and the associated p -value, the standardized root mean square residual

(SRMR), Bentler's comparative fit index (CFI), and the goodness of fit index (GFI; Malaeb et al., 2000). Prior to SEM analysis, all continuous explanatory variables were Z-score transformed to make effect sizes comparable among the variables. To assess biocrust species richness, soil texture and salinity as predictors of multifunctionality, we performed bivariate regression relationships according to hypothesized paths (Figure 3). We also tested the Pearson's correlation coefficients to check pairwise relationships between variables (Figure S2).

All data were analysed in R 3.6.1 (R Development Core Team, 2019), using the *multifunc* package (Byrnes, 2014) to calculate multifunctionality indices and the *lavaan* package (Rosseel, 2012) to construct and test SEMs.

3. Results

Most measured soil surface properties differed substantially between bare soil and soils with biocrust cover. Overall, bare soils had 74.6% higher clay content and 2× greater salinity than soils with biocrusts (Figure 2a,d). Runoff was also 1.3× higher in bare soils compared to soils with biocrusts (Figure 2m). By contrast, soils covered with biocrusts had more favorable hydrological properties (Figure 2 j-m), with 48.9% greater infiltration rates and 40.6% higher soil water content than bare soils (Figure 2i,k). Biocrust soils also had higher values of most measured soil biological properties, with 34.9% and 34.8% greater microbial biomass carbon and nitrogen, respectively, and 40% higher basal respiration rates compared to bare soils (Figure 2e-g). Finally, soil nutrient contents were also generally much higher under soils with biocrusts compared to bare soils (Figure 2n-q). Soil carbon and nitrogen stocks were 44.7% and 67.9 % higher, respectively (Figure 2n,o)

in biocrusted soils compared to bare soils, while soil phosphorus and potassium contents were 25.31% and 12.3% higher (Figure 2b,c) in bare soils compared to soils under biocrusts .

Linear regressions revealed that dryland soil multifunctionality declined with salinity but increased significantly with biocrust richness (Figure 3a,b). Biocrust species richness explained 71% of the variation in biological functions (Figure 3c), 34% of the variation in hydrological functions (Figure 3d) and 15% of the variation in nutrient functions (Figure 3e). Soil salinity increased with clay content (Figure 3f) and consequently, biocrust species richness was lowest in soils with high clay content (Figure 3g) and high soil salinity (Figure 3h). Biological and hydrological soil functions declined moderately with increasing salinity but there was no relationship between nutrient functions and soil salinity (Figure 3i,j,k).

Consistent with the results of the linear regressions, our SEMs demonstrated that dryland soil multifunctionality was strongly associated with biocrust richness (Figure 4a). The relationships between different sets of soil functions and biocrust species richness were strongest for soil biological functions, followed by hydrological and nutrient functions (Figure 4b). Soil salinity was strongly related to clay content (Figure 4a) but the SEMs revealed no direct relationship between soil salinity and biocrust species richness, and only hydrological soil functions declined significantly with soil salinity (Figure 4b). Instead, biocrust species richness declined substantially with increasing soil clay content (Figure 4a,b) and thus soil multifunctionality was indirectly related to clay content via biocrust species richness (Table S2). Our SEMs therefore indicate that soil clay content is a strong predictor of both salinity and biocrust species richness, but that biocrust species richness is the most important predictor of soil multifunctionality.

4. Discussion

Our study contributes to our understanding of dryland soil functioning by demonstrating that biocrust species richness supports soil multifunctionality in saline soil. Whereas most previous work has focused on biocrust cover or development, we show that key soil functions are strongly associated with the species richness of biocrust communities. Importantly, biocrusts play a central role in key processes in drylands that are otherwise facilitated by vascular plant cover, i.e., nutrient inputs, the creation of favorable microsites, enhanced infiltration rates, retention of soil moisture, and resources for soil microbial colonization, all of which can contribute to reduced dryland soil salinity (Jiang et al., 2018; Kakeh et al., 2020; Sommer et al., 2020). Here, we discuss the potential mechanisms by which biocrust species richness could influence soil biological, hydrological, and nutrient functions.

4.1 Influence of biocrust richness on soil biological functions

The strong association between biocrust species richness and soil biological functions (Figure 4b) demonstrates that biocrusts promote soil microbial communities and microbial biomass (Su et al., 2021). Biocrust species richness can promote soil biological functions by facilitating soil microbial colonization in salinized drylands in two ways: First, biocrusts facilitate nutrient cycling and soil organic matter inputs (Barger et al., 2016; Duran et al., 2021) and consequently enhance soil nutrient functions (Figure 4b). Second, biocrusts provide more favorable microsites by enhancing infiltration, soil water content (soil hydrological functions), and reducing soil salinity compared to adjacent saline bare soils (Kakeh et al., 2020; Sommer et al., 2021). Therefore, biocrusts indirectly relieve water and nutrient limitations and salinity stress for soil microbes and their activities (Delgado-Baquerizo et al., 2016). Previous work indicated that soil bacterial diversity and

Accepted Article

microbial biomass were highest under well-developed biocrusts (Su et al., 2021). Our results add to our understanding of biocrust functions in drylands by demonstrating the importance of biocrust species richness for most of the biological variables we measured (Figure S3). The richness of biocrust species likely plays a key role in enhancing biological functions because the quality and quantity of resource inputs to the soil are species-specific. For example, the carbon inputs by mosses and cyanobacteria to dryland soils differ depending on water availability (Zhang et al., 2018), and cyanobacteria likely contribute most to soil nitrogen stocks. However, some of the lichen species found at our study site (e.g. *Collema tenax*, *Caloplaca tominii* and *Psora decipiens*; Kakeh et al., 2018) can also contribute to carbon inputs and nitrogen fixation (Delgado-Baquerizo et al., 2015), which supplies energy and nutrients for heterotrophic microbes in the topsoil (Su et al., 2021). Furthermore, soil respiration, enzyme activities and concentrations of nitrogen and phosphorus were found to be higher in soils under late-successional lichen species such as *Diploschistes diacapsis* (Miralles et al., 2012; Concostrina-Zubiri et al., 2013). By contrast, other species (e.g. *Fulgensia subbracteatacan*, which also occurred at our study area) can have a negative impact on the abundance of soil bacteria (Delgado-Baquerizo et al., 2015). Therefore, the different metabolites produced by biocrust species could contribute to the formation of ecological niches favorable to distinct soil microbial communities (Miralles et al., 2020).

Soil biological variables and functions declined with salinity (Figures 3i and S2) but our SEMs demonstrated that this was largely because salinity was highest in soils with high clay content (Figure 3f), and biocrust richness declined with increasing soil clay content (Figure 3g). Hence, the apparent negative association between salinity and soil biological functions was largely a result of declining biocrust richness on high-clay soils. Global models show lower soil carbon stocks in saline soils due to the adverse effects of salinity on plant growth and microbial activity (Setia et

Accepted Article

al., 2013), which is consistent with our findings that soil organic carbon and microbial biomass were lower on bare saline soils than under biocrusts. Inconsistent results on the effects of soil salinity on soil microbial function, biomass and activity among studies (Yuan et al., 2007; Rath et al., 2017; Zhang et al., 2019) can be explained by the substantial impacts of water limitation and low soil pH, which often accompany salinity in dryland soils, making it hard to determine the main factor driving changes in microbial community composition, biomass and activity (Zhang et al., 2019). Nonetheless, the effects of these multiple stressors on soil microbial communities can produce negative feedbacks, in which soil organic matter decreases as microbial biomass and activity declines, reducing aggregate stability and promoting further carbon loss through erosion (Daliakopoulos et al., 2016; Zhang et al., 2019; Zhang et al., 2021). Therefore, biocrusts, especially in later successional stages, enhance soil biological functions by maintaining resources and environmental conditions to support soil microbial activity, which is particularly important in drylands like our study area, where vascular plant cover is low (Delgado-Baquerizo et al., 2016; Miralles et al., 2020).

4.2. Influence of biocrust richness on hydrological functions

The positive association between biocrust species richness and soil hydrological functions (Figures 4a, b and S4) reflects the role of mosses and lichens in reducing surface run-off and promoting water infiltration in dryland soils (Figure S3; Kakeh et al., 2021b). Biocrusts dominated by mosses enhance hydrological functions by increasing soil aggregation and porosity and providing infiltration islands; redistribution of water through soil profile then results in greater overall available soil water content (Figure S3; Chamizo et al., 2016; Eldridge et al., 2020b; Kakeh et al., 2021a). In our study area, diverse biocrust communities included species of mosses (e.g. *Tortula*

revolvens and *Barbula trifaria*) and crustose or squamulose lichens (e.g. *Diplochistes diacapsis*, *Diploschistes muscorum*, *Squamarina lentigera* and *Buellia zoharyi*) with rootlike structures (rhizoids in mosses and rhizines in lichens) that create channels and micropores at the soil surface, which provide entry points for water into the upper soil layers (Garibotti et al., 2018; Kakeh et al., 2021b). In addition, well-developed, species-rich biocrust communities that include mosses and lichens can modify soil particle size distribution by creating a protective cover at the soil surface, which reduces erosion and traps or retains fine sediment (Gao et al., 2017; Gao et al., 2020), and cyanobacteria produce extracellular polymeric substances (EPS), which help bind soil particles (Belnap & Gardner, 1993; Sepehr et al., 2019). In our study area, many biocrust patches were dominated by mosses (mean cover 67.3%), which provide a high level of protection for the soil surface and likely influence soil particle size distribution (Gao et al., 2020). Therefore, biocrust patches with higher coarser soil particle create considerable infiltration than bare soils (Table 1; Gonzales et al., 2018).

The overall decline in hydrological soil functions with increasing soil salinity (Figure. 3j) is likely due to reduced soil aggregate stability, increased surface sealing and runoff, and consequently lower water holding capacity (Kakeh et al., 2018; Kakeh et al., 2021b). We have previously demonstrated that salinity reduces infiltration rates and evaporation leads to salt accumulation, especially in bare clay soils, due to the strong capillary force of micropores between clay particles (Kakeh et al., 2021a). Reduced infiltration rates can further enhance salt accumulation on the soil surface. Biocrusts can play an important role in limiting salinization by promoting infiltration and therefore greater water movement through the soil profile, which should leach soluble salts into deeper soil layers and reduce salinity in the topsoil (Kakeh et al., 2021b). Reduced surface salinity and greater water availability under biocrusts could thus result in positive

Accepted Article

feedbacks that would enhance biocrust development, promote greater biocrust diversity and therefore support multiple soil functions (Jiang et al., 2018). By contrast, high levels of soil salinity create substantial stress for biocrust and soil organisms, reducing nutrient absorption and plant available water, which prevents the development of biocrusts and the establishment of vascular plants (Jiang et al., 2018; Kakeh et al., 2020).

Strong relationships between clay content, soil salinity and hydrological functions, such as those we observed in our study (Figures 3f and 4), can arise when swelling of clay minerals under saline conditions destroys soil aggregates and promotes surface sealing, thereby increasing run-off and reducing infiltration (Kakeh et al., 2021b; Ying et al., 2021). Thus, high clay content and high soil salinity interact to reduce soil hydrological functions (Su et al., 2021). By contrast, the effects of salinity on soil hydrological functions are negligible in soils with low clay content (Kakeh et al., 2020; Ying et al., 2021). It is notable that, although biocrusts occurred across a wide gradient of soil salinity, there were no biocrusts on soils with >15% clay content in our study (Figure 2). Thus, in dryland soils with high clay content, the absence of well-developed biocrusts might contribute to salinization and reduced hydrological functions. However, as soil salinity increased with increasing clay content, and biocrusts did not occur on soils with high clay content (Figure 3g), we cannot discern whether soils with clay content are more saline due to the absence of biocrusts, or whether biocrusts do not occur on soils with high clay content because they are more saline. However, as biocrust establishment is more rapid on clay soils in cool drylands (Chock et al., 2019), we hypothesize that greater evaporative losses (Wythers et al., 1999) in soils with high clay content at our study site simultaneously promote salinization and reduce the establishment success of biocrust communities. Thus, experimental approaches would be needed to disentangle the effects of clay content vs. salinity on hydrological functions and biocrust development.

Nevertheless, biocrusts clearly have the capacity to improve hydrological functions in drylands (Chamizo et al., 2016; Fick et al., 2019).

4.3. Influence of biocrust richness on nutrient functions

The strong relationship between biocrust species richness and soil nutrient functions in our study (Figure 3e) demonstrates that patches covered by biocrusts form fertile islands surrounded by bare highly saline soils (Kakeh et al., 2018). By contrast, the lack of relationship between soil nutrient functions and salinity (Figures 3k, 4b and S5) might be because phosphorus stocks were very low across all sites (Figure 2p) and soil salinity was strongly correlated with soil clay content. Soils with high clay content (Figure 3f, Figure 2) contain large amounts of cation nutrients that can bind to negatively charged clay surfaces, and can be released into soil solution via exchange reactions (Mukhopadhyay et al., 2019). Thus, clay content can maintain or enhance availability of some nutrients (e.g. potassium in our study) in bare soils (Bohn et al., 2015). Thus, higher potassium stocks in bare soils, combined with very low overall phosphorus stocks, likely explain why salinity had little influence on nutrient functions, despite lower carbon and nitrogen stocks in bare soils (Figure 2).

Whereas the sparse cover of vascular plants in drylands provides few plant residues and has little impact on soil nutrient function, well-developed biocrust communities contribute substantially to nutrients in surface soils through carbon inputs, nitrogen fixation, and increased availability of potassium and phosphorus (Liu et al., 2017; Kakeh et al., 2018; Xu et al., 2022). We propose that the species richness of biocrust communities plays a key role in soil nutrient functions due to the distinct quality and quantity of inputs from individual species. For example, biocrust-mosses (e.g. *Tortula revolvens*, *Barbula calycina*) enhance cycling and stocks of carbon,

nitrogen and phosphorus in drylands by providing organic matter inputs as resources for soil microbial communities (Delgado-Baquerizo et al., 2016). Cyanobacteria and some photobiont cyanolichens (e.g. *Collema tenax*) fix nitrogen and release it into the soil (Garibotti et al., 2018). Mosses, lichens and lichen-associated fungi and bacteria also secrete phosphatase enzymes, which increase the availability of phosphorus in the soil by releasing phosphorus bound to soil minerals or organic matter (Delgado-Baquerizo et al., 2015; Delgado-Baquerizo et al., 2016; Garibotti et al., 2018; Kakeh et al., 2018). Finally, some biocrust species secrete metabolites such as chelates that help retain cations (e.g. potassium) and make them available for vascular plants and soil biota (Concostrina-Zubiri et al., 2013). Thus, varied resource inputs from a species-rich biocrust community can improve nutrient availability and promote nutrient cycling in dryland soils, which in turn enhances soil biological functions.

Conclusions

Taken together, our results demonstrate that biocrust species richness maintains soil multifunctionality and buffers the deleterious effects of salinity and aridity by promoting soil biological, hydrological, and nutrient functionality. Determining the precise mechanisms by which biocrust diversity promotes various soil functions requires studies at a finer scale to investigate the effects of functional groups or individual species of mosses, lichens, and cyanobacteria. We propose that the positive influence of biocrust species richness on soil multifunctionality is particularly important in the drylands, where the cover and diversity of vascular plants is reduced by soil salinity and water limitation. As many biocrust species have low nutrient and water requirements and high resistance to salinity stress, they can survive under the harsh conditions of drylands and support many of the crucial soil functions supported by vascular plants in other

ecosystems. Biocrusts can also self-reinforce their survival and functional roles in the ecosystem via positive feedback loops that promote soil biological, hydrological and nutrient functions, thereby reducing soil salinity and other adverse abiotic soil surface attributes. Our findings thus demonstrate that understanding the role of biocrust species in maintaining soil multifunctionality has the potential to contribute to better management of saline dryland soils at a regional scale. Therefore, conservation of biocrusts is crucial for preventing soil degradation through salinization, and also soil conservation and rehabilitation in drylands.

Acknowledgements

We acknowledge funding from the Iran National Science Foundation (INSF), Science Deputy of Presidency, under grant number 96004551.

References

- Alexander, M. (1965). Most - probable - number method for microbial populations. *Methods of Soil Analysis: Part 2 Chemical and Microbiological Properties*, 9, 1467-1472.
- Anderson, J.P. (1983). Soil respiration. *Methods of soil analysis: part 2 chemical and microbiological properties*, 9, 831-871.
- Anderson, T.-H., Domsch, K.H. (1990). Application of eco-physiological quotients (qCO₂ and qD) on microbial biomasses from soils of different cropping histories. *Soil biology and Biochemistry*, 22(2), 251-255.
- Baillie, I.C. (2001). Soil Survey Staff 1999, Soil Taxonomy. *Soil Use and Management*, 17(1), 57-60. doi:<https://doi.org/10.1111/j.1475-2743.2001.tb00008.x>
- Barger, N.N., Weber, B., Garcia-Pichel, F., Zaady, E., Belnap, J. (2016). Patterns and controls on nitrogen cycling of biological soil crusts Trans.). In (Ed.),^(Eds.), Biological soil crusts: an organizing principle in drylands (ed., Vol. pp. 257-285). Springer. (Reprinted from.
- Belnap, J. (2006). The potential roles of biological soil crusts in dryland hydrologic cycles. *Hydrological Processes*, 20(15), 3159-3178. doi:10.1002/hyp.6325
- Belnap, J., Büdel, B. (2016). Biological soil crusts as soil stabilizers Trans.). In (Ed.),^(Eds.), Biological Soil Crusts: An Organizing Principle in Drylands (ed., Vol. pp. 305-320). Springer. (Reprinted from.

- Accepted Article
- Belnap, J., Gardner, J.S. (1993). Soil microstructure in soils of the Colorado Plateau: the role of the cyanobacterium *Microcoleus vaginatus*. *The Great Basin Naturalist*, 40-47.
- Belnap, J., Weber, B., Büdel, B. (2016). Biological soil crusts as an organizing principle in drylands Trans.). In (Ed.),^(Eds.), *Biological Soil Crusts: An Organizing Principle in Drylands* (ed., Vol. pp. 3-13). Springer. (Reprinted from.
- Blake, G.R., Hartge, K. (1986). Bulk density. *Methods of soil analysis: Part 1 Physical and mineralogical methods*, 5, 363-375.
- Bohn, H.L., Strawn, D.G., O'Connor, G.A. (2015). Soil chemistry (Trans. Ed.^Eds. ed. Vol.). John Wiley & Sons.
- Bolo, P.O., Sommer, R., Kihara, J., Kinyua, M., Nyawira, S., Notenbaert, A.M.O. (2019). Rangeland degradation: Causes, consequences, monitoring techniques and remedies. *CIAT Publication*.
- Bowker, M.A., Maestre, F.T., Mau, R.L. (2013). Diversity and patch-size distributions of biological soil crusts regulate dryland ecosystem multifunctionality. *Ecosystems*, 16(6), 923-933.
- Bremner, J., Mulvaney, C. (1982). Nitrogen-total Trans.). In (Ed.),^(Eds.), *Methods of soil analysis. Part 2. Chemical and microbiological properties* (ed., Vol. pp. 595-624). American Society of Agronomy-Soil Science Society of America. (Reprinted from.
- Byrnes, J. (2014). multifunc: Analysis of Ecological Drivers on Ecosystem Multifunctionality R Package Version 0.6.2 *R Foundation for Statistical Computing, Vienna*.
- Chamizo, S., Belnap, J., Eldridge, D.J., Cantón, Y., Issa, O.M. (2016). The Role of Biocrusts in Arid Land Hydrology Trans.). In (Ed.),^(Eds.), *Biological Soil Crusts: An Organizing Principle in Drylands* (ed., Vol. pp. 321-346). Springer. (Reprinted from.
- Chen, N., Yu, K., Jia, R., Teng, J., Zhao, C. (2020). Biocrust as one of multiple stable states in global drylands. *Science advances*, 6(39), eaay3763.
- Chock, T., Antoninka, A.J., Faist, A.M., Bowker, M.A., Belnap, J., Barger, N.N. (2019). Responses of biological soil crusts to rehabilitation strategies. *J Arid Environ*, 163, 77-85.
- Concostrina-Zubiri, L., Huber-Sannwald, E., Martínez, I., Flores Flores, J.L., Escudero, A. (2013). Biological soil crusts greatly contribute to small-scale soil heterogeneity along a grazing gradient. *Soil Biology and Biochemistry*, 64, 28-36. doi:10.1016/j.soilbio.2013.03.029
- Daliakopoulos, I., Tsanis, I., Koutroulis, A., Kourgialas, N., Varouchakis, A., Karatzas, G., Ritsema, C. (2016). The threat of soil salinity: A European scale review. *Science of the Total Environment*, 573, 727-739.
- Dane, J.H., Hopmans, J.W. (1986). Water retention and storage: Pressure plate extractor Trans.). In (Ed.),^(Eds.), *Methods of soil analysis. Part 1. Physical and mineralogical properties, including statistics of measurement and sampling*. (ed., Vol. pp.). American Society of Agronomy-Soil Science Society of America. (Reprinted from.
- Delgado-Baquerizo, M., Eldridge, D.J., Maestre, F.T., Karunaratne, S.B., Trivedi, P., Reich, P.B., Singh, B.K. (2017). Climate legacies drive global soil carbon stocks in terrestrial ecosystems. *Science Advances*, 3(4), e1602008. doi:doi:10.1126/sciadv.1602008
- Delgado-Baquerizo, M., Gallardo, A., Covelo, F., Prado-Comesaña, A., Ochoa, V., Maestre, F.T. (2015). Differences in thallus chemistry are related to species-specific effects of biocrust-forming lichens on soil nutrients and microbial communities. *Functional Ecology*, 29(8), 1087-1098. doi:<https://doi.org/10.1111/1365-2435.12403>

- Delgado-Baquerizo, M., Maestre, F.T., Eldridge, D.J., Bowker, M.A., Ochoa, V., Gozalo, B., Berdugo, M., Val, J., Singh, B.K. (2016). Biocrust-forming mosses mitigate the negative impacts of increasing aridity on ecosystem multifunctionality in drylands. *The New phytologist*, 209(4), 1540-1552. doi:10.1111/nph.13688
- Delgado-Baquerizo, M., Maestre, F.T., Gallardo, A., Bowker, M.A., Wallenstein, M.D., Quero, J.L., Ochoa, V., Gozalo, B., García-Gómez, M., Soliveres, S. (2013). Decoupling of soil nutrient cycles as a function of aridity in global drylands. *Nature*, 502(7473), 672-676.
- Dias, T., Crous, C.J., Ochoa-Hueso, R., Manrique, E., Martins-Loução, M.A., Cruz, C. (2020). Nitrogen inputs may improve soil biocrusts multifunctionality in dryland ecosystems. *Soil Biology and Biochemistry*, 149, 107947. doi:<https://doi.org/10.1016/j.soilbio.2020.107947>
- Duran, P., Mora, M.d.I.L., Matus, F., Barra, P.J., Jofré, I., Kuzyakov, Y., Merino, C. (2021). Biological crusts to increase soil carbon sequestration: new challenges in a new environment. *Biology*, 10(11), 1190.
- Eldridge, D.J., Delgado-Baquerizo, M., Quero, J.L., Ochoa, V., Gozalo, B., García-Palacios, P., Escolar, C., García-Gómez, M., Prina, A., Bowker, M.A., Bran, D.E., Castro, I., Cea, A., Derak, M., Espinosa, C.I., Florentino, A., Gaitán, J.J., Gatica, G., Gómez-González, S., Ghiloufi, W., Gutierrez, J.R., Gusmán-Montalván, E., Hernández, R.M., Hughes, F.M., Muiño, W., Monerris, J., Ospina, A., Ramírez, D.A., Ribas-Fernández, Y.A., Romão, R.L., Torres-Díaz, C., Koen, T.B., Maestre, F.T. (2020a). Surface indicators are correlated with soil multifunctionality in global drylands. *Journal of Applied Ecology*, 57(2), 424-435. doi:<https://doi.org/10.1111/1365-2664.13540>
- Eldridge, D.J., Reed, S., Travers, S.K., Bowker, M.A., Maestre, F.T., Ding, J., Havrilla, C., Rodriguez-Caballero, E., Barger, N., Weber, B., Antoninka, A., Belnap, J., Chaudhary, B., Faist, A., Ferrenberg, S., Huber-Sannwald, E., Malam Issa, O., Zhao, Y. (2020b). The pervasive and multifaceted influence of biocrusts on water in the world's drylands. *Global Change Biol*, 26(10), 6003-6014. doi:<https://doi.org/10.1111/gcb.15232>
- Fick, S.E., Barger, N.N., Duniway, M.C. (2019). Hydrological function of rapidly induced biocrusts. *Ecohydrology*, 12(4), e2089.
- Gao, L., Bowker, M.A., Sun, H., Zhao, J., Zhao, Y. (2020). Linkages between biocrust development and water erosion and implications for erosion model implementation. *Geoderma*, 357, 113973.
- Gao, L., Bowker, M.A., Xu, M., Sun, H., Tuo, D., Zhao, Y. (2017). Biological soil crusts decrease erodibility by modifying inherent soil properties on the Loess Plateau, China. *Soil Biology and Biochemistry*, 105, 49-58. doi:<https://doi.org/10.1016/j.soilbio.2016.11.009>
- Garibotti, I.A., Gonzalez Polo, M., Tabeni, S. (2018). Linking biological soil crust attributes to the multifunctionality of vegetated patches and interspaces in a semiarid shrubland. *Functional Ecology*, 32(4), 1065-1078.
- Gee, G.W., Bauder, J.W. (1986). Particle-size Analysis Trans.). In (Ed.), (Eds.), *Methods of Soil Analysis* (ed., Vol. pp. 383-411). (Reprinted from.
- Goldberg, N., Assouline, S., Mau, Y., Nachshon, U. (2021). Compaction effects on evaporation and salt precipitation in drying porous media. *Hydrology and Earth System Sciences Discussions*, 1-40.
- Gonzales, H.B., Ravi, S., Li, J., Sankey, J.B. (2018). Ecohydrological implications of aeolian sediment trapping by sparse vegetation in drylands. *Ecohydrology*, 11(7), e1986.

- Greiner, L., Nussbaum, M., Papritz, A., Fraefel, M., Zimmermann, S., Schwab, P., Grêt-Regamey, A., Keller, A. (2018). Assessment of soil multi-functionality to support the sustainable use of soil resources on the Swiss Plateau. *Geoderma Regional*, 14, e00181. doi:<https://doi.org/10.1016/j.geodrs.2018.e00181>
- Hassani, A., Azapagic, A., Shokri, N. (2021). Global predictions of primary soil salinization under changing climate in the 21st century. *Nature communications*, 12(1), 1-17.
- Holden, J., Burt, T. (2002). Infiltration, runoff and sediment production in blanket peat catchments: implications of field rainfall simulation experiments. *Hydrological Processes*, 16(13), 2537-2557.
- Jiang, Z.-Y., Li, X.-Y., Wei, J.-Q., Chen, H.-Y., Li, Z.-C., Liu, L., Hu, X. (2018). Contrasting surface soil hydrology regulated by biological and physical soil crusts for patchy grass in the high-altitude alpine steppe ecosystem. *Geoderma*, 326, 201-209. doi:<https://doi.org/10.1016/j.geoderma.2018.04.009>
- Jones, G.A., Kaiteris, P. (1983). A vacuum-gasometric technique for rapid and precise analysis of calcium carbonate in sediments and soils: Research-method paper. *Journal of Sedimentary Research*, 53(2).
- Kakeh, J., Gorji, M., Mohammadi, M.H., Asadi, H., Khormali, F., Sohrabi, M. (2021a). Effect of biocrusts on profile distribution of soil water content and salinity at different stages of evaporation. *Journal of Arid Environments*, 191, 104514. doi:<https://doi.org/10.1016/j.jaridenv.2021.104514>
- Kakeh, J., Gorji, M., Mohammadi, M.H., Asadi, H., Khormali, F., Sohrabi, M., Cerda, A. (2020). Biological soil crusts determine soil properties and salt dynamics under arid climatic condition in Qara Qir, Iran. *The Science of the total environment*, 732, 139168. doi:10.1016/j.scitotenv.2020.139168
- Kakeh, J., Gorji, M., Mohammadi, M.H., Asadi, H., Khormali, F., Sohrabi, M., Eldridge, D.J. (2021b). Biocrust islands enhance infiltration, and reduce runoff and sediment yield on a heavily salinized dryland soil. *Geoderma*, 404, 115329. doi:<https://doi.org/10.1016/j.geoderma.2021.115329>
- Kakeh, J., Gorji, M., Sohrabi, M., Tavili, A., Pourbabaee, A.A. (2018). Effects of biological soil crusts on some physicochemical characteristics of rangeland soils of Alagol, Turkmen Sahra, NE Iran. *Soil and Tillage Research*, 181, 152-159. doi:<https://doi.org/10.1016/j.still.2018.04.007>
- Knudsen, D., Peterson, G., Pratt, P. (1982). Lithium, sodium, and potassium Trans.). In (Ed.), (Eds.), *Methods of soil analysis. Part 2. Chemical and microbiological properties* (ed., Vol. pp. 225-246). American Society of Agronomy-Soil Science Society of America. (Reprinted from.
- Kooch, Y., Ghorbanzadeh, N., Wirth, S., Novara, A., Shah Piri, A. (2021). Soil functional indicators in a mountain forest-rangeland mosaic of northern Iran. *Ecological Indicators*, 126, 107672. doi:<https://doi.org/10.1016/j.ecolind.2021.107672>
- Lanyon, L.E., Heald, W.R. (1982). Magnesium, calcium, strontium, and barium. Periodical Magnesium, calcium, strontium, and barium, (Issue), 247-262. Retrieved from Website Magnesium, calcium, strontium, and barium website:
- Le Bagousse-Pinguet, Y., Soliveres, S., Gross, N., Torices, R., Berdugo, M., Maestre, F.T. (2019). Phylogenetic, functional, and taxonomic richness have both positive and negative effects on ecosystem multifunctionality. *Proceedings of the National Academy of Sciences*, 116(17), 8419. doi:10.1073/pnas.1815727116

- Li, H., Huo, D., Wang, W., Chen, Y., Cheng, X., Yu, G., Li, R. (2020). Multifunctionality of biocrusts is positively predicted by network topologies consistent with interspecies facilitation. *Molecular Ecology*, 29(8), 1560-1573. doi:<https://doi.org/10.1111/mec.15424>
- Liu, Y.-R., Delgado-Baquerizo, M., Trivedi, P., He, J.-Z., Wang, J.-T., Singh, B.K. (2017). Identity of biocrust species and microbial communities drive the response of soil multifunctionality to simulated global change. *Soil Biology and Biochemistry*, 107, 208-217.
- Maestre, F.T., Benito, B.M., Berdugo, M., Concostrina-Zubiri, L., Delgado-Baquerizo, M., Eldridge, D.J., Guirado, E., Gross, N., Kéfi, S., Le Bagousse-Pinguet, Y., Ochoa-Hueso, R., Soliveres, S. (2021). Biogeography of global drylands. *New Phytologist*, 231(2), 540-558. doi:<https://doi.org/10.1111/nph.17395>
- Maestre, F.T., Castillo-Monroy, A.P., Bowker, M.A., Ochoa-Hueso, R. (2012). Species richness effects on ecosystem multifunctionality depend on evenness, composition and spatial pattern. *Journal of Ecology*, 100(2), 317-330. doi:<https://doi.org/10.1111/j.1365-2745.2011.01918.x>
- Mahmoudi, N., Caeiro, M.F., Mahdhi, M., Tenreiro, R., Ulm, F., Mars, M., Cruz, C., Dias, T. (2021). Arbuscular mycorrhizal traits are good indicators of soil multifunctionality in drylands. *Geoderma*, 397, 115099. doi:<https://doi.org/10.1016/j.geoderma.2021.115099>
- Malaeb, Z.A., Summers, J.k., Pugsek, B.H. (2000). Using structural equation modeling to investigate relationships among ecological variables. *Environmental and Ecological Statistics*, 7(1), 93-111. doi:10.1023/a:1009662930292
- Mallen-Cooper, M., Bowker, M.A., Antoninka, A.J., Eldridge, D.J. (2020). A practical guide to measuring functional indicators and traits in biocrusts. *Restoration Ecology*, 28(S2), S56-S66. doi:<https://doi.org/10.1111/rec.12974>
- McGeorge, W.T. (1954). Diagnosis and Improvement of Saline and Alkaline Soils. *Soil Science Society of America Journal*, 18(3), 348-348. doi:<https://doi.org/10.2136/sssaj1954.03615995001800030032x>
- Middleton, N. (2018). Rangeland management and climate hazards in drylands: dust storms, desertification and the overgrazing debate. *Natural Hazards*, 92(1), 57-70. doi:10.1007/s11069-016-2592-6
- 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(0), 113-121. doi:10.1016/j.soilbio.2012.06.017
- Miralles, I., Lázaro, R., Sánchez-Marañón, M., Soriano, M., Ortega, R. (2020). Biocrust cover and successional stages influence soil bacterial composition and diversity in semiarid ecosystems. *Science of the Total Environment*, 709, 134654.
- Moser, M. (2009). Report on Ramsar Advisory Mission No. 60, Alagol, Ulmagol Ajigol, Ramsar site 49, Islamic Republic of Iran, 14 - 16 May 2009. .
- Mukhopadhyay, S., Masto, R.E., Tripathi, R.C., Srivastava, N.K. (2019). Chapter 14 - Application of Soil Quality Indicators for the Phytorestoration of Mine Spoil Dumps Trans.). In Pandey, V.C., Baudh, K. (Ed.),^(Eds.), Phytomanagement of Polluted Sites (ed., Vol. pp. 361-388). Elsevier. (Reprinted from.
- Nelson, D.W., Sommers, L.E. (1996). Total carbon, organic carbon, and organic matter Trans.). In (Ed.),^(Eds.), Methods of Soil Analysis. Part 2. Chemical and Microbiological

Properties (ed., Vol. pp. 961-1010). American Society of Agronomy-Soil Science Society of America. (Reprinted from.

- Nevins, C.J., Strauss, S.L., Inglett, P.W. (2020). Biological soil crusts enhance moisture and nutrients in the upper rooting zone of sandy soil agroecosystems. *Journal of Plant Nutrition and Soil Science*, 183(5), 615-626. doi:<https://doi.org/10.1002/jpln.202000218>
- Olsen, S., Sommers, L. (1982). Phosphorus. p 403-430. *Methods of soil analysis, part, 2(2)*.
- Pires, L.F., Brinatti, A.M., Saab, S.C., Cássaro, F.A. (2014). Porosity distribution by computed tomography and its importance to characterize soil clod samples. *Applied radiation and isotopes : including data, instrumentation and methods for use in agriculture, industry and medicine*, 92, 37-45. doi:10.1016/j.apradiso.2014.06.010
- Prävālie, R. (2016). Drylands extent and environmental issues. A global approach. *Earth-Science Reviews*, 161, 259-278.
- Prävālie, R., Bandoc, G., Patriche, C., Sternberg, T. (2019). Recent changes in global drylands: Evidences from two major aridity databases. *Catena*, 178, 209-231. doi:<https://doi.org/10.1016/j.catena.2019.03.016>
- R Development Core Team. (2019). R version 3.6.1 R foundation for statistical computing, Vienna, Austria.
- Raggio, J., Green, A., Pintado, A., Sancho, L.G., Büdel, B. (2021). Functional performance of biocrusts across Europe and its implications for drylands. *J Arid Environ*, 186, 104402. doi:<https://doi.org/10.1016/j.jaridenv.2020.104402>
- Rath, K.M., Maheshwari, A., Rousk, J. (2017). The impact of salinity on the microbial response to drying and rewetting in soil. *Soil Biology and Biochemistry*, 108, 17-26.
- Read, Z.J., King, H.P., Tongway, D.J., Ogilvy, S., Greene, R.S.B., Hand, G. (2016). Landscape function analysis to assess soil processes on farms following ecological restoration and changes in grazing management. *European Journal of Soil Science*, 67(4), 409-420. doi:<https://doi.org/10.1111/ejss.12352>
- Rhoades, J. (1982). Soluble salts. Periodical Soluble salts, (Issue), 167-179. Retrieved from Website Soluble salts website:
- Rodriguez-Caballero, E., Belnap, J., Büdel, B., Crutzen, P.J., Andreae, M.O., Pöschl, U., Weber, B. (2018). Dryland photoautotrophic soil surface communities endangered by global change. *Nature Geoscience*, 11(3), 185-189.
- Rosseel, Y. (2012). lavaan: An R package for structural equation modeling. *Journal of Statistical Software*, 48(2), 1-36. doi:10.18637/jss.v048.i02
- Rossi, F., Mugnai, G., De Philippis, R. (2018). Complex role of the polymeric matrix in biological soil crusts. *Plant and Soil*, 429(1), 19-34. doi:10.1007/s11104-017-3441-4
- Ryan, J. (2017). Methods of Soil, Plant, and Water Analysis: A manual for the West Asia and North Africa region. Periodical Methods of Soil, Plant, and Water Analysis: A manual for the West Asia and North Africa region, (Issue). Retrieved from Website Methods of Soil, Plant, and Water Analysis: A manual for the West Asia and North Africa region website:
- Sancho, L.G., Belnap, J., Colesie, C., Raggio, J., Weber, B. (2016). Carbon budgets of biological soil crusts at micro-, meso-, and global scales Trans.). In (Ed.),^(Eds.), Biological soil crusts: an organizing principle in drylands (ed., Vol. pp. 287-304). Springer. (Reprinted from.
- Schimel, D.S. (2010). Drylands in the earth system. *Science*, 327(5964), 418-419.

- Schrumpf, M., Schulze, E., Kaiser, K., Schumacher, J. (2011). How accurately can soil organic carbon stocks and stock changes be quantified by soil inventories? *Biogeosciences*, 8(5), 1193-1212.
- Sepehr, A., Hassanzadeh, M., Rodriguez-Caballero, E. (2019). The protective role of cyanobacteria on soil stability in two Aridisols in northeastern Iran. *Geoderma Regional*, 16, e00201. doi:<https://doi.org/10.1016/j.geodrs.2018.e00201>
- Setia, R., Gottschalk, P., Smith, P., Marschner, P., Baldock, J., Setia, D., Smith, J. (2013). Soil salinity decreases global soil organic carbon stocks. *Science of The Total Environment*, 465, 267-272. doi:<https://doi.org/10.1016/j.scitotenv.2012.08.028>
- Singh, K. (2016). Microbial and enzyme activities of saline and sodic soils. *Land Degradation & Development*, 27(3), 706-718. doi:<https://doi.org/10.1002/ldr.2385>
- Soliveres, S., Eldridge, D.J. (2020). Dual community assembly processes in dryland biocrust communities. *Functional Ecology*, 34(4), 877-887.
- Sommer, V., Karsten, U., Glaser, K. (2020). Halophilic algal communities in biological soil crusts isolated from potash tailings pile areas. *Frontiers in Ecology and Evolution*, 8, 46.
- Sommer, V., Palm, A., Schink, A., Leinweber, P., Gose, N., Karsten, U., Glaser, K. (2021). Artificial biocrust establishment on materials of potash tailings piles along a salinity gradient. *Journal of Applied Phycology*. doi:10.1007/s10811-021-02609-7
- Stavi, I., Thevs, N., Priori, S. (2021). Soil salinity and sodicity in drylands: A review of causes, effects, monitoring, and restoration measures. *Frontiers in Environmental Science*, 330.
- Su, Y.g., Liu, J., Zhang, Y.m., Huang, G. (2021). More drought leads to a greater significance of biocrusts to soil multifunctionality. *Functional Ecology*, 35(4), 989-1000.
- Sun, J., Li, X. (2021). Role of shrubs in the community assembly of biocrusts: the biotic and abiotic influences along a biocrust succession gradient. *Plant and Soil*, 460(1), 163-176.
- Thomas, A.D., Elliott, D.R., Hardcastle, D., Strong, C.L., Bullard, J., Webster, R., Lan, S. (2022). Soil biocrusts affect metabolic response to hydration on dunes in west Queensland, Australia. *Geoderma*, 405, 115464.
- Topp, G.c. (1993). Soil water content. In M.R. Carter (ed.). *Soil sampling and methods of analysis*. Lewis Publishers, London. .
- Vance, E., Brookes, P., Jenkinson, D. (1987). Microbial biomass measurements in forest soils: the use of the chloroform fumigation-incubation method in strongly acid soils. *Soil Biology and Biochemistry*, 19(6), 697-702.
- Vandandorj, S., Eldridge, D.J., Travers, S.K., Delgado-Baquerizo, M. (2017). Contrasting effects of aridity and grazing intensity on multiple ecosystem functions and services in Australian woodlands. *Land Degradation & Development*, 28(7), 2098-2108. doi:<https://doi.org/10.1002/ldr.2736>
- Wang, H., Lv, G., Cai, Y., Zhang, X., Jiang, L., Yang, X. (2021). Determining the effects of biotic and abiotic factors on the ecosystem multifunctionality in a desert-oasis ecotone. *Ecological Indicators*, 128, 107830. doi:<https://doi.org/10.1016/j.ecolind.2021.107830>
- Wythers, K., Lauenroth, W., Paruelo, J. (1999). Bare - soil evaporation under semiarid field conditions. *Soil Science Society of America Journal*, 63(5), 1341-1349.
- Xu, H., Zhang, Y., Shao, X., Liu, N. (2022). Soil nitrogen and climate drive the positive effect of biological soil crusts on soil organic carbon sequestration in drylands: A Meta-analysis. *Science of The Total Environment*, 803, 150030.
- Ye, J.S., Delgado - Baquerizo, M., Soliveres, S., Maestre, F.T. (2019). Multifunctionality debt in global drylands linked to past biome and climate. *Global Change Biol*, 25(6), 2152-2161.

- Ying, Z., Cui, Y.-J., Benahmed, N., Duc, M. (2021). Salinity effect on the compaction behaviour, matric suction, stiffness and microstructure of a silty soil. *Journal of Rock Mechanics and Geotechnical Engineering*, 13(4), 855-863.
doi:<https://doi.org/10.1016/j.jrmge.2021.01.002>
- Yuan, B.-C., Li, Z.-Z., Liu, H., Gao, M., Zhang, Y.-Y. (2007). Microbial biomass and activity in salt affected soils under arid conditions. *Applied Soil Ecology*, 35(2), 319-328.
- Zhang, C., Niu, D., Song, M., Elser, J.J., Okie, J.G., Fu, H. (2018). Effects of rainfall manipulations on carbon exchange of cyanobacteria and moss-dominated biological soil crusts. *Soil Biology and Biochemistry*, 124, 24-31.
- Zhang, G., Bai, J., Tebbe, C.C., Zhao, Q., Jia, J., Wang, W., Wang, X., Yu, L. (2021). Salinity controls soil microbial community structure and function in coastal estuarine wetlands. *Environmental Microbiology*, 23(2), 1020-1037. doi:<https://doi.org/10.1111/1462-2920.15281>
- Zhang, K., Shi, Y., Cui, X., Yue, P., Li, K., Liu, X., Tripathi, B.M., Chu, H. (2019). Salinity is a key determinant for soil microbial communities in a desert ecosystem. *MSystems*, 4(1), e00225-00218.

Table 1. Hypotheses and key mechanisms relating soil attributes (clay content and salinity), biocrust richness, and dryland soil multifunctionality, based on the results of previously published works (References).

Pathway	Hypotheses and mechanisms	References
Soil clay content → soil salinity	Higher soil clay content increases soil salinity by clogging soil pores, decreasing leaching potential and increasing accumulation of salts in the topsoil	Stavi et al. (2021)
Soil clay content → biocrust richness	Lower clay content leads to the development and diversity of biocrusts by facilitating infiltration and consequently decreasing salinity in the topsoil through leaching.	Gao et al. (2020); Kakeh et al. (2020)
Soil salinity → biocrust richness	High levels of soil salinity create physiological stress and limit water and nutrient availability, which prevents the establishment and development of biocrusts.	Jiang et al. (2018); Kakeh et al. (2020)
Soil salinity → biological functions	Soil salinity reduces biological functions because salt stress decreases soil biodiversity and the activity of microorganisms.	Daliakopoulos et al. (2016); Singh (2016)
Soil salinity → hydrological functions	Soil salinity decreases hydrological functions by reducing soil aggregate stability and increasing surface sealing and runoff.	Kakeh et al. (2021b)
Soil salinity → nutrient functions	Soil salinity reduces nutrient functions by reducing nutrient availability and uptake, and microbial and enzyme activities, which creates nutrient imbalances for biocrusts and vascular plants.	Daliakopoulos et al. (2016); Hassani et al. (2021)
Biocrust richness → biological functions	Biocrust species richness increases biological functions by providing organic matter inputs that promote soil microbial communities, and microbial biomass growth.	Su et al. (2021)
Biocrust richness → hydrological functions	Biocrust species richness improves hydrological functions by increasing soil aggregation and porosity and providing infiltration islands, which result in higher soil water content that is redistributed through the soil profile.	Chamizo et al. (2016); Eldridge et al. (2020b)
Biocrust richness → nutrient functions	Biocrust species richness increases nutrient functions by contributing to carbon and nitrogen fixation and promoting microbial activity, thereby forming fertility islands	Su et al. (2021)

Figure captions

Figure 1. A conceptual diagram of the potential links between dryland soil multifunctionality and biocrust richness, soil salinity, or soil texture (clay content).

Figure 2. Changes in soil physical and chemical properties (a:d), biological (e:i), hydrological (j:m) and nutrient (n:q) attribute functions for bare and biocrusted soils in a salinized dryland in northeastern Iran. Significance levels are shown as *** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$ and NS $P > 0.05$. Different asterisks above boxes represent significant differences between bare soil and biocrusted soil (t-test). The violin plots represent the kernel probability density of the values. The boxplots denote the interquartile range (box) and median (center line) of the values for $n = 16$ samples for bare and biocrusted soil.

Figure 3. Bivariate relationships based on the hypothesized causal paths from structural equation models (SEMs) based on the conceptual model in Figure 1. Solid lines indicate significant relationships at $P < 0.05$ and dashed lines are non-significant relationships at $P > 0.05$.

Figure 4. Final structural equation models (SEMs) linking (a) overall soil multifunctionality and (b) different sets of soil functions (i.e., soil biological; hydrological, and nutrient functions) to biocrust richness, soil salinity and soil texture in saline dryland soils. Solid blue and red arrows represent significant ($P \leq 0.05$) positive or negative relationships, respectively, and dashed blue and red arrows represent non-significant relationships.

Figure 1.

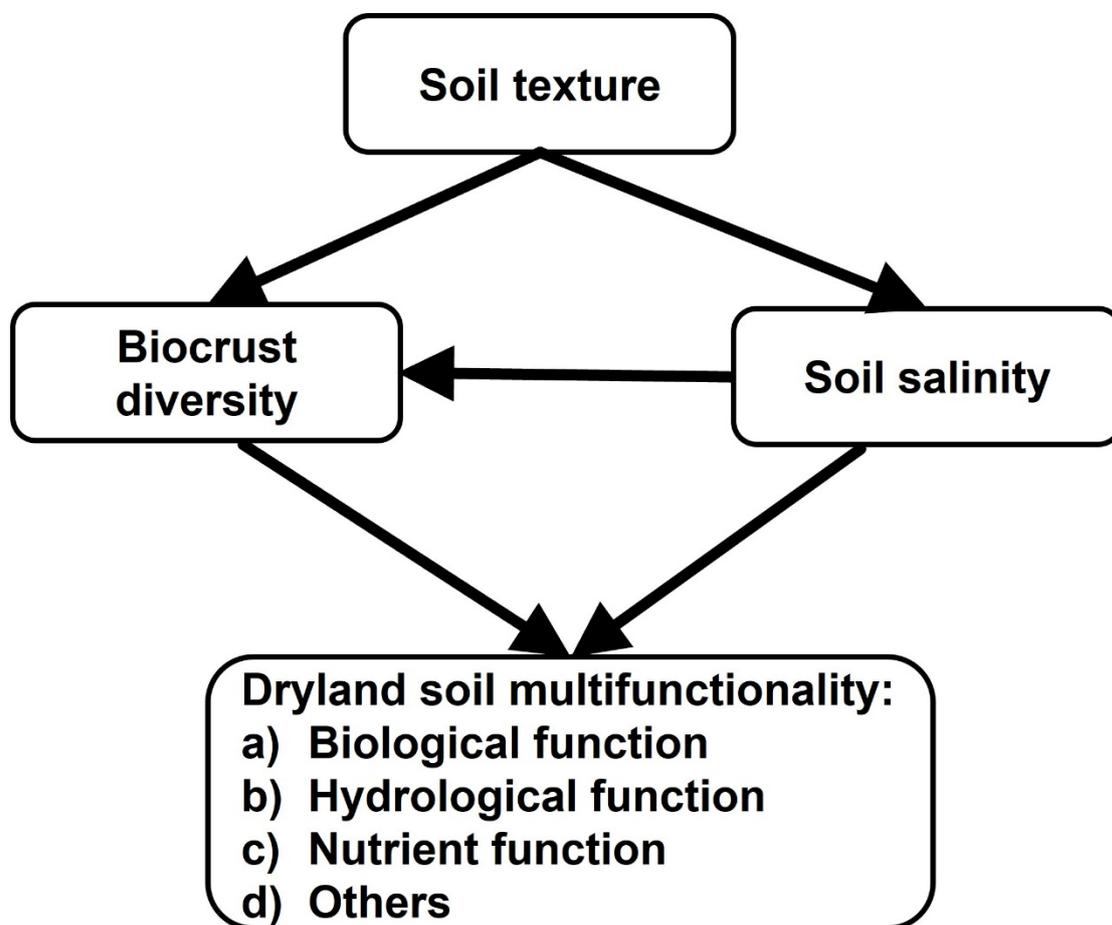


Figure 2.

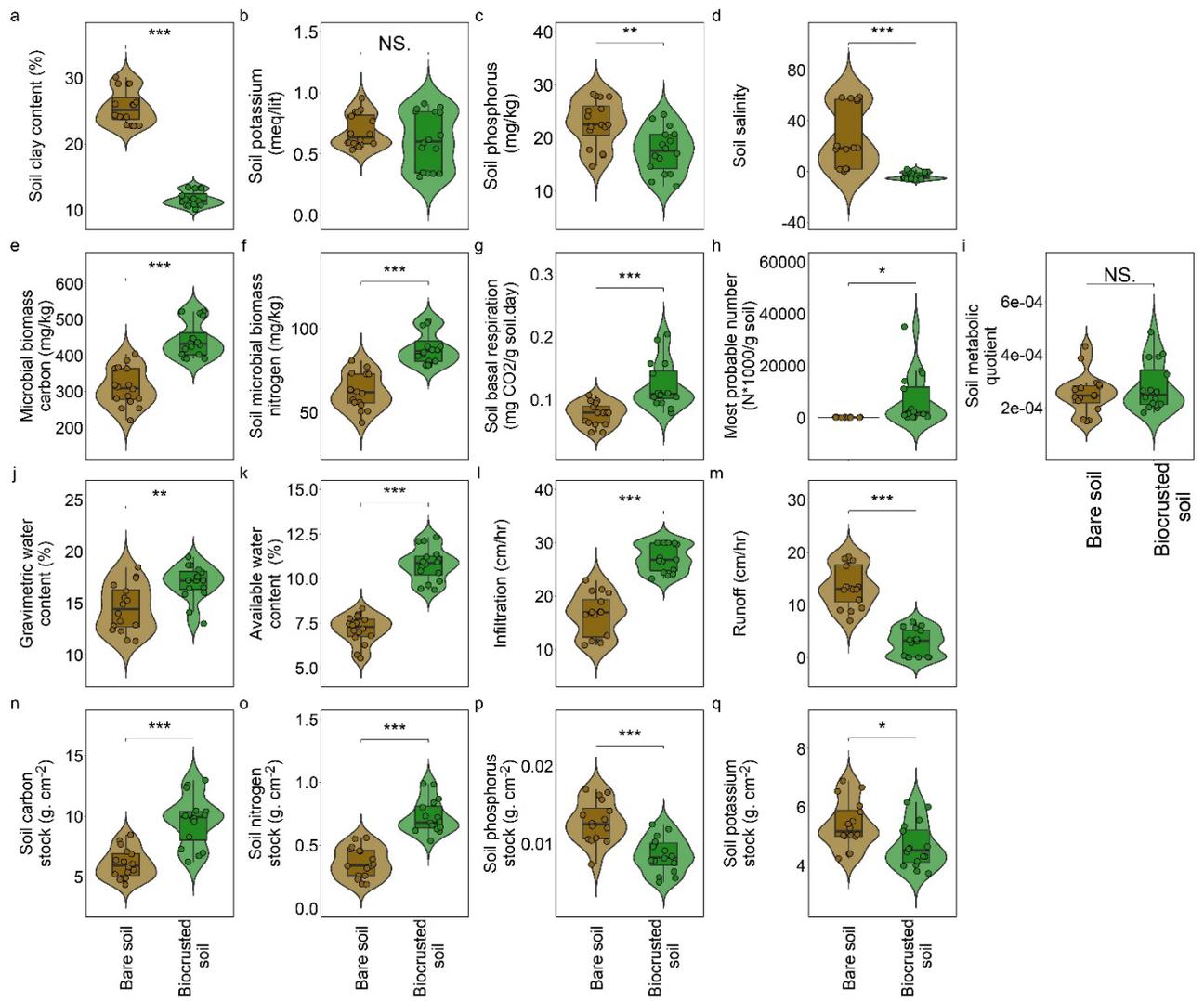


Figure 3.

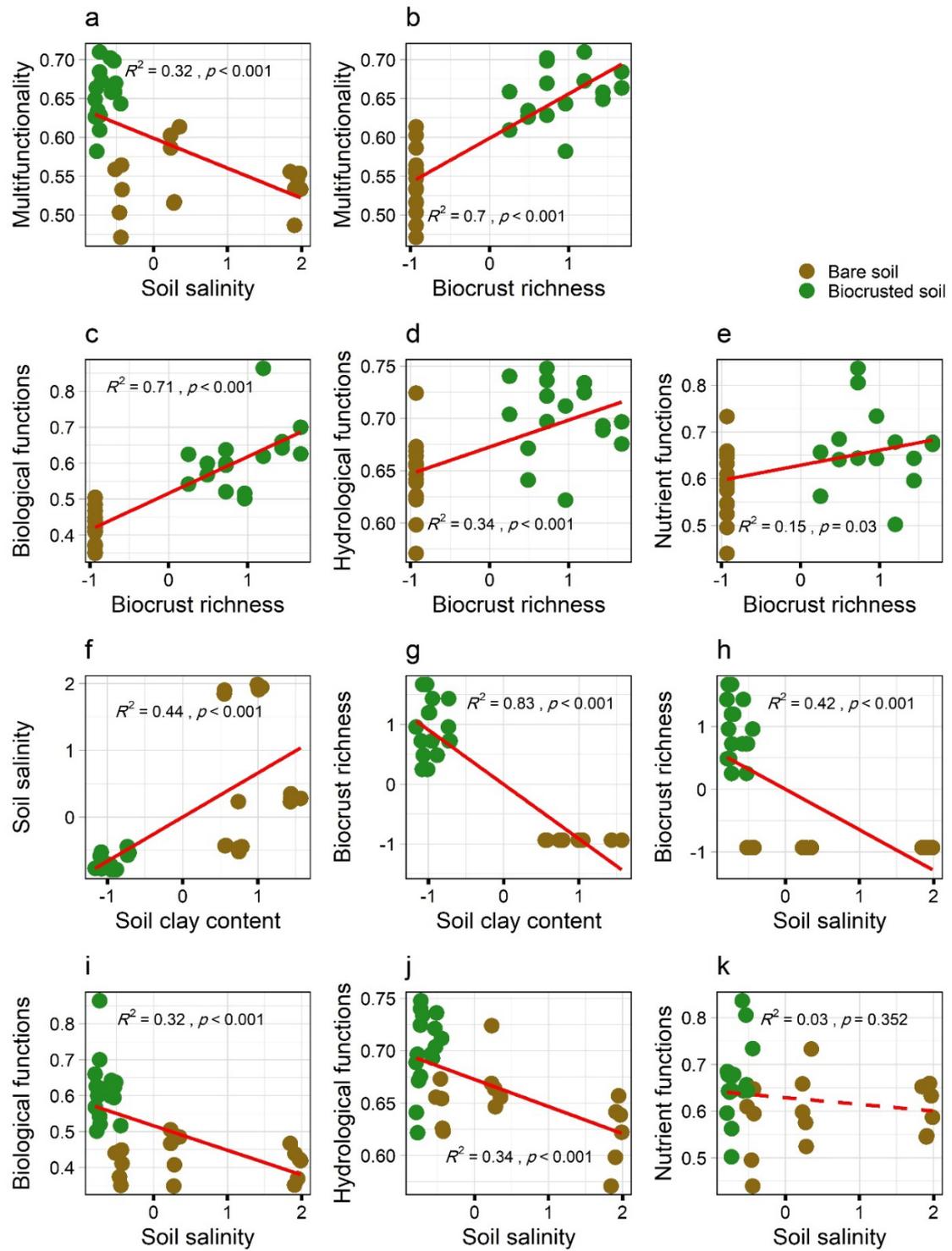
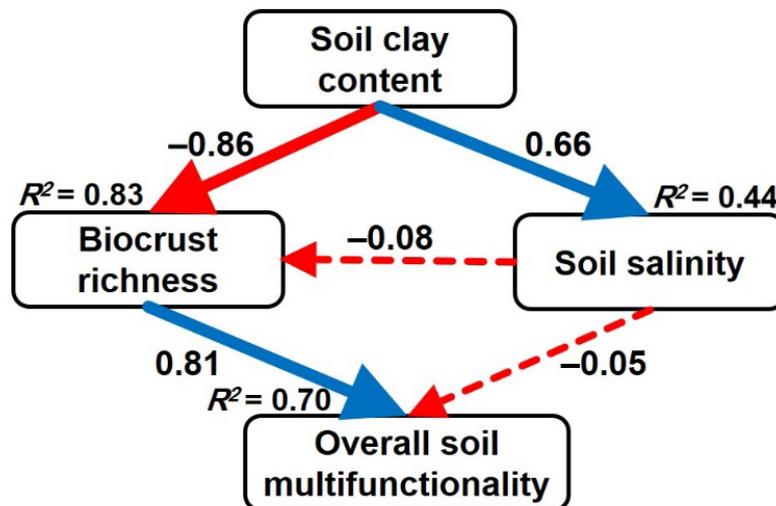


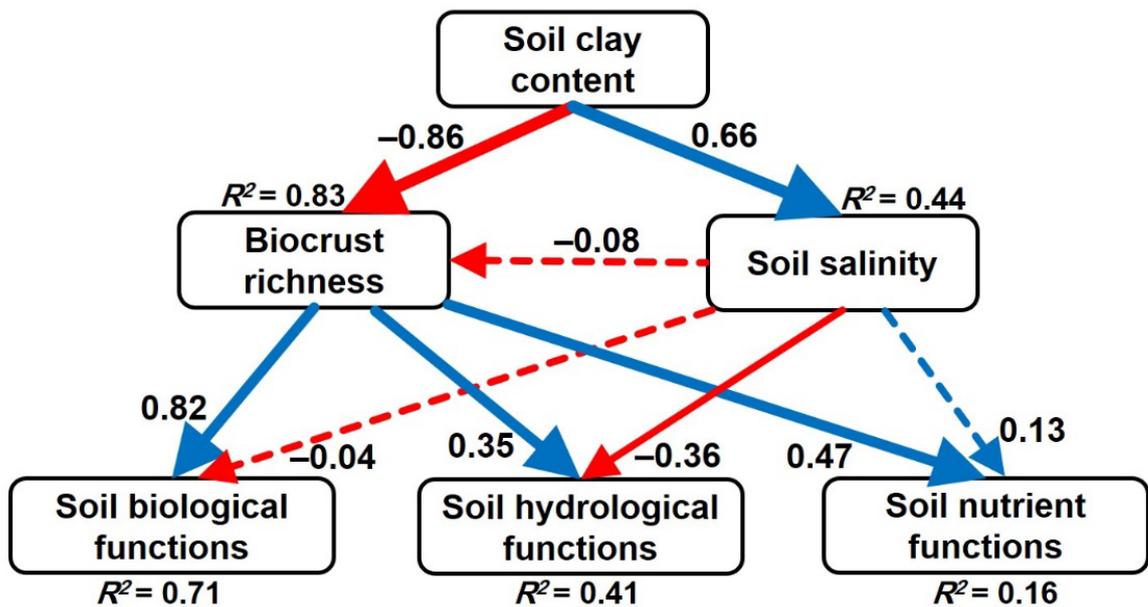
Figure 4.

a) Overall soil multifunctionality



Model fit statistics
 $\chi^2 = 0.156$ ($P = 0.693$); $df = 1.00$; GFI = 1.00; CFI = 1.00; SRMR = 0.005

b) Different soil functions



Model fit statistics
 $\chi^2 = 0.320$ ($P = 0.956$); $df = 3.00$; GFI = 0.999; CFI = 1.00; SRMR = 0.007