Abstract

The distribution of a mosaic of biological soil crusts (BSCs) and shrubs is a common landscape surface feature in temperate deserts. With the continued climatic change, the desert shrub experiences varying rates of mortality which has serious negative impacts on soil structure and functions. However, it is not clear whether BSCs, which develop extensively in areas under shrub canopies, can mitigate the effects of shrub mortality on soil nutrient multifunctionality. Therefore, in this study, the Gurbantungut Desert, a typical temperate desert in northern China, was selected as the study area, and the dominant shrubs, *Ephedra przewalskii* shrub, and the moss crust were used as the study objects. Soil samples were collected from the bare sand and moss crusts under the living shrub and the dead shrub and analyzed to determine their carbon, nitrogen, phosphorus, and potassium contents. The results showed that the shrub mortality reduced the soil moisture content, pH, electric conductivity, and carbon, nitrogen, phosphorus, and potassium contents in the bare sand compared with the bare sand under the living shrub. The presence of the moss crust greatly mitigated the negative impacts of shrub mortality on soil carbon, nitrogen, phosphorus, and potassium contents, and the nutrient multifunctionality of the moss crust was only reduced by 4.01% compared with the reduction by bare sand (67.42%) after shrub mortality. The results of SEM analysis showed that with the coexistence of shrubs and crust, the effect of shrubs on soil multifunctionality was much stronger than that of the moss crust; compared with available nutrients, the total nutrient content was the most important factor driving changes in soil nutrient multifunctionality. In conclusion, in desert ecosystems with degraded shrubs, moss crusts can mitigate the reduction in soil nutrient contents caused by shrub degradation and, therefore, maintain the soil stability and nutrient multifunctionality as a ”substitute”.

Keywords: biological soil crusts, biogeochemical cycles, soil nutrients, climate change, temperate deserts, *syntrichia caninervis*

1 Introduction

The sensitivity of arid and semi-arid regions to climate change and land degradation is becoming more and more serious. Biological soil crusts, as engineers of desert ecosystems, play important roles in desertification control and ecological sustainability (Weber et al., 2022). Biological soil crusts (BSCs) are a complex amalgamation formed by algae, lichens, mosses, and soil microorganisms adhered to soil particles, occupying 30% of dryland areas and covering up to 70% of the surface area in some desert areas, and thus, are known as the ”living skin” of the earth (Bowker et al., 2018; Rodriguez -Caballero et al., 2018). Moss crusts are the most important contributor to the advanced stages of biological soil crust succession and also biomass production (Cornelissen et al., 2007) and also play important roles in soil resistance to both wind and water erosion (Fang et al., 2007), enhancing soil stability (Belnap and Büdel, 2016; Kidron et al., 2009), regulating the temperature of the desert surface (Eldridge et al., 2020b; Li et al., 2018), and promoting seed germination and vascular plant colonization (Belnap and Eldridge, 2001; Harper and Belnap, 2001); besides, they have important ecological functions. Due to the lack of water, desert ecosystems are unable to support a broad continuous distribution of vascular plants, resulting in the formation of a mosaic of small shrubs and arbors with BSCs (Pointing and Belnap, 2012), which profoundly affects the spatial heterogeneity of surface soil moisture content and nutrient contents (Dougill and Thomas, 2004; Li et al., 2019). However, previous studies have mostly focused on the effects of individual biological taxa of vascular plants or BSCs on soil nutrients alone, and there is a lack of research on the effects of vascular plants and BSCs on soil multifunctionality with the coexistence of shrubs and crust and the magnitude of the effects of both.

Soil multifunctionality can reflect the ability of soils to provide and maintain multiple ecosystem functions simultaneously (Manning et al., 2018; Wagg et al., 2014). An increasing number of studies has concluded that a single function cannot integrate the interactions and trade-offs among multiple functions that reflect the effects of environmental changes on ecosystem functions (Creamer et al., 2022), while soil multifunctionality is more sensitive and representative in response to ecosystem changes (Hu et al., 2021). Studies have shown that the contribution of BSCs to soil multifunctionality is influenced by environmental factors such as temperature, rainfall, drought, nitrogen deposition, and changes in land use (Dias et al., 2020; Guo et al., 2021; Wen et al., 2020; Yang et al., 2021; Zelikova et al., 2012). Moreover, BSCs can mitigate the negative effects of drought and environmental degradation and are of the greatest importance in dry regions (Delgado-Baquerizo et al., 2016; Moreno-Jiménez et al., 2020; Su et al., 2021). In addition, microenvironmental changes caused by different microhabitats also make differences in the soil multifunctionality of BSCs (Li et al., 2019). In desert ecosystems with a mosaic of shrubs and BSCs, the effects of these two on ecosystem multifunctionality are specific, i.e., plant patches increase the infiltration rate of water into soil and soil stability, thus, dominating soil multifunctionality, while patches of BSCs have multifunctional roles in soil stabilization and regulation of water and nitrogen pools (Garibotti et al., 2018). However, there are a few reports on how the changes in microhabitats after shrub mortality have affected the soil multifunctionality of BSCs.

In temperate deserts, perennial drought-tolerant shrubs are the dominant vascular plants, and the microhabitats created by shrubs provide good conditions for mosses within BSCs (Pintado et al., 2005; Zhang et al., 2007). However, in recent years, the negative impacts of global change, such as continuous warming and extreme droughts, have been enhanced, which have greatly reduced the productivity and species diversity of desert ecosystems and caused shrub mortality (Cardinale et al., 2012; Chamizo et al., 2012; Huang et al., 2016). As an important factor for wind and sand control and maintenance of desert ecosystems, shrub mortality would inevitably affect BSCs within the sub-canopy and soil environment (Sher et al., 2012; Stavi et al., 2021). Studies on the effects of the physiological ecology of moss crusts have shown that shrub mortality significantly decreased their physiological indicators such as chlorophyll fluorescence intensity and soluble protein content and mosses maintain normal physiological activities by increasing antioxidant enzyme activities and osmoregulatory substance contents under resource-limited conditions (Yin and Zhang, 2016; Yin et al., 2017). However, it is not yet clear how shrub mortality would affect soil multifunctionality in desert ecosystems and what role moss crusts play in causing changes in soil multifunctionality. Therefore, it is important to clarify whether the effects of moss crusts on the functions of the soil environment would be regulated by shrub growth and death to assess the maintenance mechanism of soil multifunctionality in degraded desert ecosystems under global change.

In summary, the following scientific hypotheses were proposed: 1) the loss of shrubs' functions after their death would change the natural environment that has a low temperature, high relative humidity, poor light, and high microbial activity and reduce nutrient aggregation, thus, negatively affecting the multifunctionality of desert soils; 2) the moss crust cover can alleviate the negative effects of shrub mortality and promote the multifunctionality of soils. To test the above-mentioned hypotheses, this study selected the dominant shrubs of the Gulbantungut Desert in northern China, the *Ephedra przewalskii* shrub, and the moss crust as the research objects. Soil samples were collected from bare sand areas and moss crusts under the living shrub and the dead shrub in their natural state. Soil carbon, nitrogen, phosphorus, and potassium contents and multifunctional characteristics were analyzed and compared in different microhabitats. The key drivers of the differences were investigated to provide data and important references in support of the conservation and maintenance of degraded desert ecosystems under global change.

2 Materials and methods

2.1 Overview of the study area

The Gurbantunggut Desert is located in the hinterland of Junggar Basin in northern Xinjiang, China (44.18°-46.33° N, 84.52°-90.00° E) and is the largest fixed and semi-fixed desert in China. This desert has an average annual precipitation of no more than 150 mm, average annual evaporation of more than 2000 mm, an average annual temperature of 6–10 °C, with extremes of 40 °C or more, annual cumulative temperatures of 3000–5000 °C with the variation of 10 °C, and average relative humidity of 50%-60%, usually below 45% for the months May-August (Zhang et al., 2007). Unlike other desert ecosystems, the Gurbantunggut Desert has a stable snowpack of 15–30 cm in winter, which accounts for 25% of the annual rainfall. The linear and dendritic longitudinal dunes create the basic landscape features of the desert, and the vegetation is mainly composed of *Haloxylon persicum*, *Haloxylon ammodendron*, *Ephedra przewalskii*, *Calligonum mongolicum*, etc. Other sandy soil plants constitute shrub and small tree communities (Zhang and Zhang, 2020). In addition, three types of BSCs (algal crusts, lichen crusts, and moss crusts) were widely distributed under the shrub vegetation and at the interstices of patches of lowland plants between the longitudinal dunes, and moss crusts were especially well developed under the *Ephedra przewalskii* and *Calligonum mongolicum* shrubs.

2.2 Experimental design and sample collection

The experiment was conducted in April 2015 in the hinterland of the Gurbantunggut Desert (45.24 N°, 87.60° E). To study the effects of shrub mortality and moss crust cover on soil multifunctionality, we selected a 50 m × 50 m large sample plot in the study area between the longitudinal dune lowlands where the climate and soil environmental conditions were relatively consistent, and the moss crust was well developed. We selected live and dead shrubs with the same habitat and size, and on this basis, we set up four BSCs treatments, including bare sand under the living shrub, moss crust under the living shrub, bare sand under the dead shrub, and moss crust under the dead shrub to compare moss crust with bare sand. To prevent edge effects and damage to the intact crust, soil samples were carefully collected from the 0–6 cm layer concentrically under the canopy of each different type of shrub patch using a homemade soil auger, with five replicates for each treatment. The soil samples were placed in sealed bags and quickly transferred to the laboratory for preliminary sample processing. They were first passed through a 2-mm sieve to remove large apoplastic material and moss residues from the crust layer and then divided into two parts; one was stored at –20 °C for the determination of the contents of available nitrogen, available phosphorus, and available potassium in the soil, and the other part was naturally dried and used for the determination of the contents of total carbon, total nitrogen, total phosphorus, and total potassium, pH, electrical conductivity, etc.

2.3 Analysis of soil physical and chemical properties

Soil samples were analyzed for water content, pH, electrical conductivity, total carbon, total nitrogen, total phosphorus, total potassium, available nitrogen, available phosphorus, and available potassium. Soil water content (SWC) was determined using the weighing method by placing fresh soil samples in an oven at 105 °C for 48 h until reaching the constant weight. pH was determined by the potentiometric method in a soil-to-water ratio of 1: 2.5. Electrical conductivity (EC) was determined by the AC conductivity method in a soil-to-water ratio of 1:5 (Bhattacharyya et al., 2021). Soil organic carbon (SOC) was determined by the carbon and nitrogen analyzer (Multi 3100C/N, Analytik Jena AG, Germany) using the HCL titration-combustion method. Soil total nitrogen (TN) and total phosphorus (TP) contents after digestion with concentrated sulfuric acid, perchloric acid, and hydrofluoric acid, and soil available phosphorus (AP) content after extraction with the 0.5 mol/L $NaHCO_3$ solution were determined by the fully automated flow analyzer (Bran Luebbe, AA3, Germany) using the Kjeldahl method, molybdenum antimony, and ascorbic acid colorimetric method for TN, TP, and AP, respectively. Soil available nitrogen (AN) content was determined by the alkaline diffusion method; soil total potassium (TK) content was determined by the NaOH melt-flame spectrophotometry, and available potassium (AK) content was determined by flame photometry after extraction with 1 mol/L NH_4OAc.

2.4 Soil nutrient multifunctionality

Soil multifunctionality is an important indicator used to assess the ability of soils to maintain multiple ecosystem functions simultaneously (Byrnes et al., 2014; Maestre et al., 2012a). Today, the most popular methods for the assessment of soil multifunctionality include the average approach, multi-threshold method, single-function method, and single-threshold method; but each method has its advantages and disadvantages, among which, the average approach is widely used in the evaluation of multifunctionality and provides intuitive and easily interpretable assessments of the ability of soils to maintain multiple functions (Byrnes et al., 2014). In this paper, we used an average approach to calculate the indices of soil nutrient multifunctionality for seven soil functional indicators, including soil organic carbon, total nitrogen, total phosphorus, total potassium, available nitrogen, available phosphorus, and available potassium contents. We standardized the measured values of these seven indicators using the maximum-minimum method as follows: f (x) = [x - min (x)]/[max (x) - min (x)], which unifies multiple functional indicators of different dimensions into the same dimension, ranging from 0 to 1, and subsequently, calculates the quantitative soil nutrient multifunctionality index. Soil nutrient multifunctionality was calculated by the following equation.

$$SMF = \frac{1}{F}\sum_{I=\ 1}^{F} f_i$$

where *SMF* is the soil nutrient multifunctionality index, *F* is the number of measurement functions, and *fi* is the measured value of each measurement function.

2.5 Data analysis

Data were initially processed using Microsoft Excel and tested for normality and homogeneity of variance using SPSS 25.0 software. A two-way ANOVA was conducted to compare the effects of shrub mortality, moss crust cover, and the interaction between these two on soil environmental factors (SWC, pH, and EC) and nutrient multifunctionality. One-way ANOVA and Tukey's multiple comparison test were performed for the analysis and comparison of soil environmental factors and nutrient multifunctionality of bare sand and moss crust cover after shrub mortality.

Principal component analysis of environmental factors and soil nutrient multifunctionality in both natural and dead shrubs was performed using the "FactoMineR" package, and Pearson's correlation was conducted using the "psych" package to investigate the vector changes and linear relationships between environmental factors and soil nutrient multifunctionality after shrub mortality. To quantify the relative contribution of each variable to the variation in soil nutrient multifunctionality, the "tidyverse" package was used to decompose the variance of shrub mortality, moss crust, and environmental factors (SWC, pH, and EC) and their interaction effects, and the "varclus" function from the "Hmisc" package was used to avoid redundancy and multicollinearity in the analysis of variance. Finally, the partial least squares path modeling (PLS-PM) was applied by using the "innerplot" function from the "plspm" package, and the soil main nutrients (SOC, TN, TP, and TK) and fast-acting nutrients (AN, AP, and AK) and their stoichiometric ratios (C: P, C: K, N: P, and N: K) in the set of models were used as the composite variables after removing redundancy and multicollinearity. Estimating the effect sizes of the direct or indirect pathways for each factor aims to further identify the key factors causing changes in soil nutrient multifunctionality and their possible impact pathways.

3 Results

3.1 Changes in soil environmental factors

Table 1 Two-way ANOVA results for the effects of moss crusts and shrub mortality on soil physicochemical properties and multifunctionality

Index	Moss	Shrub	Shrub × Moss
SWC	10731**	8.628*	2.079
pH	62.637**	70.567**	1.617
EC	2.296	8.949**	0.545
SOC	15.801**	39.638**	8.178*
TN	1.295	9.522**	4.934*
TP	0.02	4.774*	11.619**
TK	3.413	5.660*	2.45
AN	29.537**	0.04	0.785
AP	1.794	16.294**	1.122
AK	6.864*	49.480**	1.941
SMF	7.497*	21.120**	6.871*

Note: Soil water content (SWC), Electrical conductivity (EC), Soil organic carbon (SOC), Total nitrogen (TN), Total phosphorus (TP), Total potassium (TK), Alkaline nitrogen (AN), Available phosphorus (AP), Available potassium (AK), Soil nutrient versatility (SMF); * indicate $p < 0.05$, ** indicate $p < 0.01$.

The results of two-way ANOVA showed that moss crust and shrub mortality had significant effects on SWC and pH, and only shrub mortality had a significant effect on soil EC ($p < 0.01$, Table 1), while the interaction between these two had no significant effects on SWC, pH, and EC. Overall, moss crust significantly reduced soil pH in both the living and dead shrubs and increased SWC ($p < 0.01$ for the living shrub, $p = 0.16$ for the dead shrub) and EC under the dead shrub ($p < 0.05$) compared to bare sand. Shrub mortality reduced SWC, pH, and EC, especially pH that decreased at significant levels in both habitats ($p < 0.05$; Fig. 1).

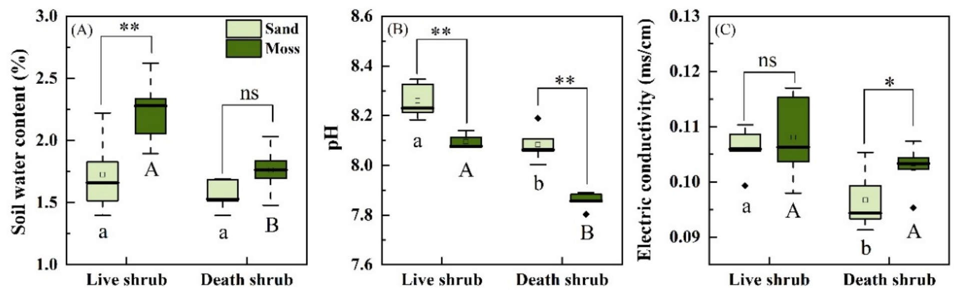

Fig. 1 Effects of moss crust and shrub mortality on soil environmental factors; results are means ±SE of five independent replicates. Different lowercase letters (for bare sand) and uppercase letters (for moss crust) indicate significant differences between different shrub thickets ($p < 0.05$). * and ** indicate significant ($p < 0.05$) and highly significant ($p < 0.01$) differences, respectively, between the same thicket with and without moss crust cover.

3.2 Changes in soil nutrient contents

In terms of the contents of total nutrients, moss crust had a significant effect only on SOC ($p < 0.01$), while shrub mortality and the interaction between shrub mortality and moss crust had significant effects on SOC, TN, TP, and TK ($p < 0.05$, Table 1). Compared to bare sand, moss crust significantly increased SOC and TN, TP, and TK contents under the dead shrub but significantly decreased TP content under the living shrub ($p < 0.05$). Shrub mortality significantly reduced SOC and TN, TP, and TK contents of bare sand soils ($p < 0.05$), with no significant effect on the parameters of the moss soil crust (Fig. 2).

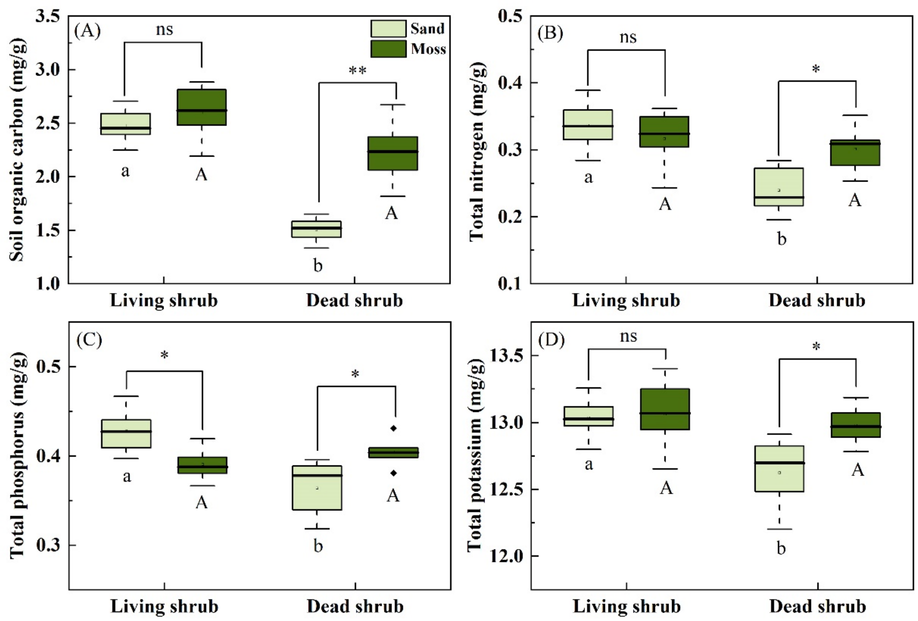

Fig. 2 Effects of moss crust and shrub mortality on total soil nutrient contents; results are means ±SE of five independent replicates. Different lowercase letters (for bare sand) and uppercase letters (for moss crust) indicate significant differences between different shrub thickets ($p < 0.05$). * and ** indicate significant ($p < 0.05$) and highly significant ($p < 0.01$) differences, respectively, between the same thicket with and without the moss crust cover.

As shown in Table 1 and Fig. 3, moss crust significantly increased soil AN and AK contents compared to bare sand (for both the living and dead shrubs, $p < 0.05$), whereas shrub mortality significantly decreased soil AP and AK contents in both bare sand and moss crust ($p < 0.05$). The interaction between moss crust and shrub mortality had no significant effect on AN, AP, and AK contents.

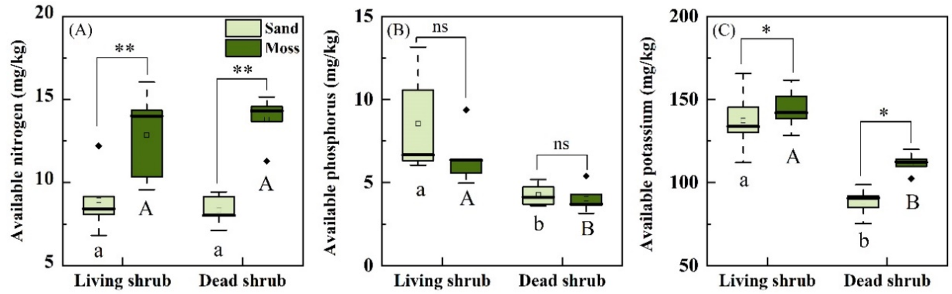

Fig. 3 Effects of moss crust and shrub mortality on soil available nutrient contents; results are means ±SE of five independent replicates. Different lowercase letters (for bare sand) and uppercase letters (for moss crust) indicate significant differences between different shrub thickets ($p < 0.05$). * and ** indicate significant ($p < 0.05$) and highly significant ($p < 0.01$) differences, respectively, between the same thicket with and without the moss crust cover.

3.3 Changes in soil nutrient multifunctionality

Moss crust, shrub mortality, and the interaction between them all had significant effects on soil nutrient multifunctionality ($p < 0.05$, Table 1). Compared to bare sand, moss crust cover increased soil nutrient multifunctionality, which reached significant levels under the dead shrub ($p < 0.01$); shrub mortality, however, reduced soil nutrient multifunctionality in bare sand (significantly, 67.42%) and in moss crust soil (not significantly, 4.01%, Fig. 4).

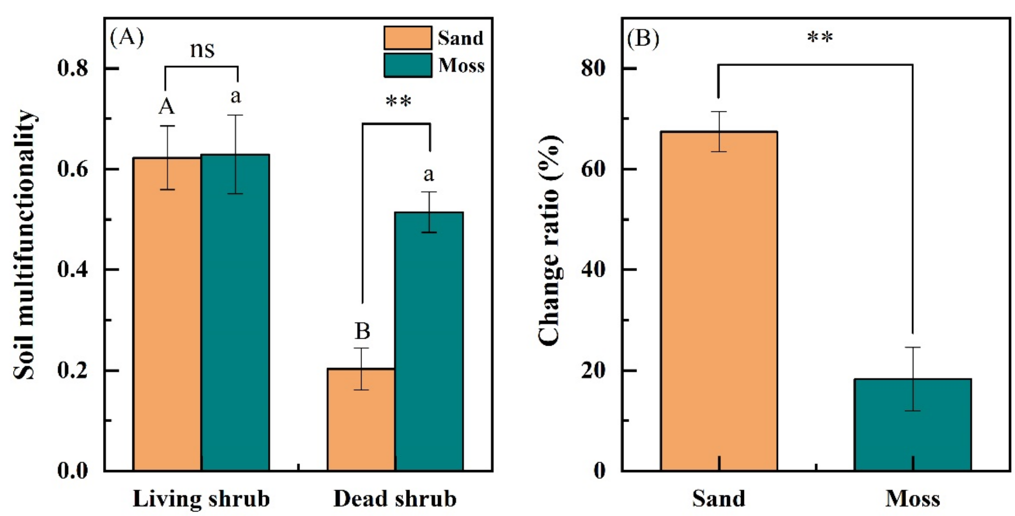

Fig. 4 Effects of moss crust and shrub mortality on soil nutrient multifunctionality; results are means ±SE of five independent replicates. Different lowercase letters (for bare sand) and uppercase letters (for moss crust) indicate significant differences between different shrub thickets ($p < 0.05$). * and ** indicate significant ($p < 0.05$) and highly significant differences ($p < 0.01$), respectively, between the same thicket with and without the moss crust cover.

3.4 Relationships between soil nutrient multifunctionality and environmental factors

The results of both the principal component analysis (PCA) and correlation analysis showed the same trends (Fig. 5). Under the living shrub, soil nutrient multifunctionality showed a significant positive correlation with EC but no significant correlation with other environmental indicators, while under the dead shrub, soil nutrient multifunctionality showed a significant negative correlation with pH but a highly significant positive correlation with the moss crust cover. The indicators were explained by 80% of the total variation under the living shrub by principal components; PC1 (Dim1) explained 48.1%, whereas PC2 (Dim2) explained 31.9% of the total variation; however, principal components explained 87.5% of the total variation under the dead shrub (Dim1, 66.3% + Dim2, 21.2%).

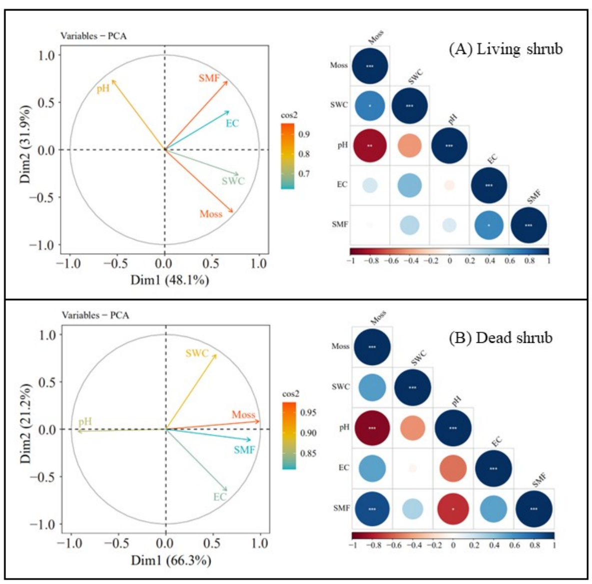

Fig. 5 PCA and correlation analysis of soil nutrient multifunctionality and environmental factors under the living shrub (A) and dead shrub (B); Soil water content (SWC), Electrical conductivity (EC), Soil organic carbon (SOC), Total nitrogen (TN), Total phosphorus (TP), Total potassium (TK), Alkaline nitrogen

(AN), Available phosphorus (AP), Available potassium (AK), and Soil nutrient multifunctionality (SMF); indicators with arrows pointing in the same direction indicate a large positive correlation, and longer arrows indicate a stronger correlation.

The results of variance decomposition of shrub mortality, moss crust, and soil environmental factors (SWC, pH, and EC) revealed that the interaction between shrub mortality and soil environmental factors had the greatest effect on nutrient multifunctionality (43%). Moss crust (3%), soil environment (7%), shrub mortality-moss crust interaction (8%), and moss crust-soil environment interaction (9%) had varying degrees of influence on soil nutrient multifunctionality (Fig. 6C). To avoid the confounding of interactions among the causal factors, we used the PLS-PM model to determine the direct and indirect effects of shrub mortality, moss crust cover, soil water content, pH, soil electrical conductivity, total nutrient contents, available nutrient contents, and nutrient stoichiometric ratios on soil nutrient multifunctionality. The results showed that the goodness of fit of the model was 76.24% (Figure 4A). The overall effects of shrub mortality (total effect = –0.35) and soil water content (total effect = –0.03) on soil nutrient multifunctionality were negative; the moss crust cover (total effect = 0.21), soil pH (total effect = 0.15), soil electrical conductivity (total effect = 0.25), total nutrient contents (total effect = 0.40), available nutrient contents (total effect = 0.24) and nutrient stoichiometric ratios (total effect = 0.02) had overall positive effects on soil nutrient multifunctionality. In addition, soil total nutrient contents had the strongest direct positive effect (direct effect = 0.26), while soil water content had the strongest direct negative effect (direct effect = –0.04), and soil electrical conductivity had the strongest indirect positive effect (indirect effect = 0.18), whereas shrub mortality had the strongest indirect negative effect (indirect effect = –0.45) on soil nutrient multifunctionality.

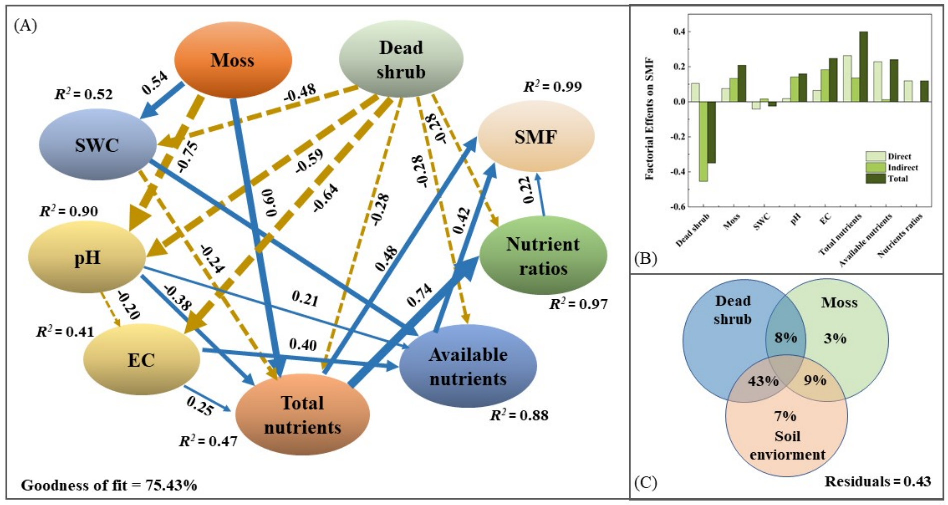

Fig. 6 Partial least squares path modeling (PLS-PM) showing the effects of environmental factors on soil nutrient multifunctionality(figures A and B) and variance decomposition showing the effects of shrub mortality, moss crust, and soil environmental factors (SWC, pH, and EC) on soil nutrient multifunctionality (figure C). The effects and effect pathways of shrub mortality, moss crust cover (Moss), soil water content (SWC), pH, electrical conductivity (EC), total nutrient contents (SOC, TN, TP, and TK), available nutrient contents (AN, AP, and AK), and nutrient stoichiometric ratios (C: P, C: K, N: P, and N: K) on soil nutrient multifunctionality were evaluated. Blue and brown arrows indicate the direct positive and negative effects of causal factors, respectively ($p < 0.05$).

4 Discussion

4.1 Effects of moss crust on soil nutrient multifunctionality

Consistent with the proposed initial hypothesis, the moss crust cover significantly contributed to the enhancement of soil carbon, nitrogen, phosphorus, and potassium contents and efficiency under the dead shrub in the Gurbantungut Desert (Figs. 2, 3). This is in agreement with previous results on the positive effects of BSCs on soil nutrients (Bowker et al., 2011; Delgado-Baquerizo et al., 2016; Maestre et al., 2012b). BSCs are important contributors of organic carbon to soil in desert ecosystems, regulating the rates of decomposition and mineralization of soil nutrients, which in turn affect the primary productivity and nutrient efficiency of soils (Chamizo et al., 2012). At the same time, in the soil covered moss crusts are rich in nitrogen-fixing microorganisms that can fix atmospheric N_2 by its conversion to plant-available inorganic N and increase soil

N content (Elbert et al., 2012; Rogers and Burns, 1994). In addition, BSC cover can significantly increase the diversity and abundance of soil microbial communities, promote the soil carbon, nitrogen, phosphorus, and potassium cycling, and therefore increase the content and efficiency of soil nitrogen, phosphorus, and potassium (Baumann et al., 2019; Cheng et al., 2020; Zhao et al., 2021).

In arid and semi-arid zones, the cover of moss crusts in the interstices of sparse vegetation patches profoundly affects the structure and functions of surface soils (Belnap and Büdel, 2016). The results showed that moss crusts did not have a significant direct effect on soil nutrient multifunctionality but indirectly regulated the changes in soil nutrient contents by affecting the soil environment (Figure 6A). For example, moss crusts can form a hard protective layer on the surface of deserts and create a stable soil environment by the movement of soil surface particles by wind through rhizoids, thus, improving soil structure and water and nutrient use efficiencies (Elbert et al., 2012; Nevins et al., 2020). A favorable soil environment can, in turn, serve as a refuge for desert microorganisms, thus, improving microbial activities and nutrient cycling efficiency (Liu et al., 2021; Xiao and Veste, 2017). In addition, mosses and their symbiotic nitrogen-fixing algae can fix atmospheric CO_2 and N_2 through photosynthesis and biological nitrogen fixation, respectively (Pointing and Belnap, 2012). At the same time, moss crusts can contribute to nutrient cycling by adsorbing atmospheric water and airborne particles floating in the atmosphere and using their high cation exchange capacity to secrete acidic metabolites (Sosa-Quintero et al., 2022).

Soil pH and electrical conductivity were also significantly increased by the moss crust cover, which was attributed to the higher wind-induced salt accumulation capacity and anion and cation exchange capacity of moss crust soils compared to bare sand (Chen and Duan, 2015). The results of this study showed that both soil pH (indirect effect = 0.14) and EC (indirect effect = 0.18) were the two factors exerting the strongest indirect positive effects on the soil nutrient multifunctionality (Fig. 6B). Consistent with the results of the present study, the importance of soil pH in driving overall soil nutrient multifunctionality has been demonstrated in several studies conducted worldwide (Eldridge et al., 2020), and the increase in soil pH can directly or indirectly affect soil quality and ecosystem functions (Han et al., 2022) and also serve as an environmental predictor affecting the resistance and resilience of soil nutrient multifunctionality in the face of disturbances (Zhang et al., 2019). In desert ecosystems, soil pH drives the positive response of soil nutrient multifunctionality to disturbances by controlling specific microbial taxa (Delgado-Baquerizo et al., 2017). Thus, the ameliorating effect of moss crust cover on the pH of alkaline soil provides a favorable environment for soil microbial communities to promote the accumulation of soil carbon, nitrogen, phosphorus, and potassium, which are essential for the improvement of soil nutrient multifunctionality. In addition, a decrease in soil pH can significantly increase cation exchange capacity (Ishiguro, 2019; Ishiguro et al., 2007), affecting indicators of soil structure and permeability, and nutrient transport (Ishiguro, 2019). These findings verified our results, revealing that moss crust cover significantly increased soil electrical conductivity (Fig. 2A), and the changes in electrical conductivity had a significant positive effect on the contents of both the soil total nutrients (direct effect = 0.25) and available nutrients (direct effect = 0.40).

It is noteworthy that there was an increase in soil nutrient multifunctionality caused by moss crust under dead shrub and not significant in living shrub (Fig. 4). This is consistent with the trends of SOC, TN, TP and TK nutrients (Fig. 2) and the results of correlation analysis (Fig. 5A). Although moss crusts also have a role in promoting soil nutrient cycling and multifunctionality (Su et al., 2021), their enhancing effect on soil nutrient contents was diminished under the "fertilizer island" effect of the shrub, mainly because the nutrient content increase did not have a simple linear relationship with moss crusts; when the nutrient content reaches a certain threshold, the cooperation among microorganisms gradually changes to the competition which results in the inhibition of the nutrient cycling due to spatial limitations (Jansson and Hofmockel, 2020). In addition, high nutrient levels increase the risk of nutrient leaching and dissipation (Thomas et al., 1999).

4.2 Effects of shrub mortality on soil nutrient multifunctionality

Desert ecosystems are sparsely vegetated and ecologically fragile, and their functions are highly sensitive in the face of global changes (Ferrenberg et al., 2015; Rutherford et al., 2017). Climate change and anthropogenic activities, mainly oil and gas exploration, grazing, etc., have resulted in shrub mortality in the Gurbantunggut Desert, causing degradation of desert ecosystems and changes in ecosystem structure and function (Carnicer et al., 2011; Miriti et al., 2007; Qu et al., 2017). In desert ecosystems, the unique microhabitat created by shrubs following their growth provides a shady, moist, and fertile shelter for the protection of BSCs as the low groundcover community, allowing moss crusts to develop extensively under shrub (McClaran et al., 2008; O'Donnell et al., 2020; Pérez et al., 2016; Yu et al., 2016). Studies on vegetation dynamics have found that factors such as vegetation cover and biodiversity are both important predictors of soil multifunctionality (Berdugo et al., 2017; Eldridge et al., 2020). Moreover, vegetation cover can relieve the stress caused to ecosystem functioning under the influence of drought (de Almeida et al., 2019), which emphasizes the critical role of desert vegetation cover in ecosystem structure and function. Consistent with the initial hypothesis that shrub mortality reduces soil nutrient multifunctionality and this effect is highly significant in areas without moss crust cover (Fig. 2A), similar results have been obtained in several studies; for example, in the Tibetan Plateau, the above- and below-ground biodiversity loss in degraded grasslands significantly reduced soil multifunctionality in meadows (Cui et al., 2022) and activities causing vegetation destruction such as grazing disturbance or land-use change could negatively affect soil multifunctionality (Manhães et al., 2022; Wang et al., 2022; Wen et al., 2020; Zhu et al., 2021). These findings demonstrate the importance of vegetation cover and diversity indicators for soil structure and function in degraded ecosystems and also the urgent need for vegetation management and conservation (Cardinale et al., 2012; Huang et al., 2016).

Changes in microhabitats are one of the important drivers of changes in soil multifunctionality, especially for desert ecosystems with harsher environments (Hu et al., 2021; Xu et al., 2022). In arid and semi-arid regions, shrub communities increase soil temperature, moisture content, and pH and improve soil structure through plant-soil feedback mechanisms, enhance soil nutrient accumulation and nitrogen mineralization rates, and exert a positive impact on the survival of soil organisms (protozoa, microorganisms, etc.) and cryptogamic plants (lichens, mosses, etc.) (Ding et al., 2019; Li et al., 2018; Schlesinger et al., 1996; Ward et al., 2018). Shrub mortality diminishes or even offsets its microenvironmental effects, profoundly affecting surface biological activities and biogeochemical cycles. Previous studies have found that the legacy effects of shrub mortality promoted the growth and development of herbaceous plants but reduced the photosynthetic activity of desert moss crusts (El-Keblawy et al., 2016; Stavi et al., 2021) and also affected soil nutrient cycling and microbial community (Sher et al., 2012). The results of the PLS-PM model showed that the overall effect of shrub mortality on soil nutrient multifunctionality was not negative, and it also had some direct positive effects (direct effect = 0.16), which may result from the formation of shrub mounds by wind and sand blockage through their residual root parts; thus, providing nutrients for the growth of herbaceous plants and increasing soil microbial activities (Nejidat et al., 2016; Stavi et al., 2021) and also due to the fact that plant residues (withered to some extent) block the direct sunlight reaching earth's surface and change soil physicochemical properties (Jia et al., 2018).

The negative effect of shrub mortality on soil nutrient multifunctionality mainly results from its indirect effect on soil environmental factors (SWC, pH, and EC) and soil nutrients and their stoichiometric characteristics (Fig. 6B). This is corroborated by the results of variance decomposition, in which the interaction between shrub mortality and soil environmental factors explained 43% of the total variance in soil nutrient multifunctionality (Fig. 6C). In terms of soil environmental factors, shrub mortality significantly reduced SWC in moss crust cover, while it had no significant effect on it in bare sand (Fig. 1A), mainly due to the loss of shading in its canopy after shrub mortality; the increase in radiation doses and temperature accelerated evaporation of soil water trapped in the surface layer by moss crust, while bare sand has poor water holding capacity and low inherent moisture content (Hao et al., 2016; Kidron and Benenson, 2014). In addition, shrub mortality significantly reduced soil pH values under both bare sand and moss crusts (Fig. 1B), mainly because the decomposition of litter and plant root residues after plant mortality altered soil nutrient cycling and promoted soil respiration and soil acidification in the short term (Jia et al., 2018; Liu et al., 2021). Changes in soil EC were consistent with the trends observed in SOC and TN, TP, and TK contents, which were attributed to the reduced cation sorption by reduced levels of organic residues, thereby limiting soil nutrient transformation and efficiency (Bronick and Lal, 2005).

The weakening and disappearance of the "fertilizer island" effect after shrub mortality are the main reasons for the decrease in soil nutrient multifunctionality (Aguirre et al., 2021; Manhães et al., 2022; Mueller et al., 2008). The analysis of soil nutrients in this study also showed that the soil carbon, nitrogen, phosphorus, and potassium contents, except for AN, were significantly reduced after shrub mortality. This was also confirmed by the results of a study conducted in arid grasslands in the southwestern United States, where typical shrubs lost 67–106% of their average organic carbon and total nitrogen contents at the 0–5 cm soil depth after 40 years of mortality (McClaran et al., 2008). However, the effect of shrub mortality on ecosystem functions is the result of not only a net loss of shrub but also a reduction in its ability to interact with BSCs. Studies carried out in the Negev Desert, Israel, have shown that successional processes, microbial community structure, soil moisture dynamics, and nutrient cycling of BSCs were disturbed to varying degrees after shrub mortality (Sher et al., 2012; Stavi et al., 2021). Therefore, it is crucial for moss crusts to maintain the stability of desert soil functions with their great ability to survive in the face of adversity by taking over from the shrubs (Zhang et al., 2011; Zheng et al., 2011) when there is a loss of the shelter of the shrub.

4.3 Roles played by moss crusts after shrub mortality

Consistent with our initial scientific hypothesis, the presence of moss crusts mitigated the negative effects of shrub mortality on soil nutrient multifunctionality, with the effect being much stronger than we had predicted. The shrub mortality reduced soil nutrient multifunctionality by 67.42% under bare sand compared to that under the living shrub, which was not significantly different from the reduction found in the presence of moss crusts (4.01%) (Fig. 2B). Therefore, BSCs represented by moss crusts have an important role in maintaining soil nutrient multifunctionality in degraded desert ecosystems. In addition, moss crusts with multiple roles are more advantageous than herbaceous plants that can play similar roles. In desert and grassland ecosystems, the colonization and invasion of shrubs show a mechanism of positive feedback between nutrients and the soil. However, fertile patches created by shrubs were not conducive to herbaceous plant growth, and the increase in contents of soil nutrients was not positive feedback contributing to the overall vegetation composition (Ward et al., 2018). On the contrary, shrub mortality had a facilitative effect on herbaceous plant colonization (El-Keblawy et al., 2016; Nejidat et al., 2016). Moss crusts are better able to survive in water- and nutrient-poor environments compared to herbaceous plants that have high water and nutrient requirements (Zheng et al., 2011). When the ecosystem is stable and healthy, mossy crusts can act as participants and facilitators under the living shrub; thus, filling spaces like the pore space between the shrub and the middle and lower parts of the shaded slopes of dunes, where resources are relatively scarce (Li et al., 2010; Sun and

Li, 2021). When the capacity of the ecosystem to generate services and functions is reduced after ecosystem degradation and shrub mortality (Cardinale et al., 2012), moss crusts are better able to mitigate the adverse effects of vegetation degradation and maintain the stability of soil nutrient multifunctionality compared to herbaceous plants in desert ecosystems (Fick et al., 2020).

5 Conclusion

Shrub mortality events in desert ecosystems caused by global change resulted in significant changes in soil nutrient cycling and multifunctionality under shrubs and moss crusts. Shrub mortality significantly reduced SWC, pH, EC, SOC, and TN, TP, TK, AP, and AK contents in bare sand, which ultimately greatly negatively impacted nutrient multifunctionality. Meanwhile, the exposed moss crust inhibited the loss of nutrients, except AP, by controlling the relevant soil environment and also maintained the stability of nutrient multifunctionality. The results of this study provide new evidence showing that moss-dominated BSCs have an important role in maintaining soil nutrient multifunctionality in shrub-degraded desert ecosystems and, therefore, require effective maintenance and protection to cope with the negative impacts of climate change on desert ecosystems.

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