ORIGINAL ARTICLE

Multifunctionality of biocrusts is positively predicted by network topologies consistent with interspecies facilitation

Hua Li[1,2] (iD)　|　Da Huo[1,3]　|　Weibo Wang[4]　|　Youxin Chen[1]　|　Xiaoli Cheng[4]　|　Gongliang Yu[1]　|　Renhui Li[1]

[1]CAS Key Laboratory of Algal Biology, Institute of Hydrobiology, Chinese Academy of Sciences, Wuhan, China

[2]Academy of Plateau Science and Sustainability, Qinghai Normal University, Xining, China

[3]University of the Chinese Academy of Sciences, Beijing, China

[4]CAS Key Laboratory of Aquatic Botany and Watershed Ecology, Wuhan Botanical Garden, Chinese Academy of Sciences, Wuhan, China

Correspondence
Hua Li and Renhui Li, Institute of Hydrobiology, Chinese Academy of Sciences, Wuhan, China.
Emails: lih@ihb.ac.cn; reli@ihb.ac.cn

Funding information
National Natural Science Foundation of China, Grant/Award Number: 31400368 and 41877419

Abstract

The potential of biodiversity loss to impair the delivery of ecosystem services has motived ecologists to better understand the relationship between biodiversity and ecosystem functioning. Although increasing evidence underlines the collective contribution of different biodiversity components on the simultaneous performance of multiple functions (multifunctionality), we know little about the trade-offs between individual diversity effects and the extent to which they determine multifunctionality differentially. Here, at a subcontinental scale of 62 dryland sites, we show in phototrophic microbiota of biological soil crusts (biocrusts) that, whereas richness alone is unable to guarantee the maxima of multifunctional performance, interspecies facilitation and compositional identity are particularly stronger but often neglected predictors. The inconsistent effects of different biodiversity components imply that soil multifunctionality can be lost despite certain species remaining present. Moreover, we reveal a significant empirical association between species functional importance and its topological feature in co-occurrence networks, indicating a functional signal of species interaction. Nevertheless, abundant species tend to isolate and merely interact within small topological structures, but rare species were tightly connected in complicated network modules. Our findings suggest that abundant and rare species of soil phototrophs exhibit distinct functional relevance. These results give a comprehensive view of how soil constructive species drive multifunctionality in biocrusts and ultimately promote a deeper understanding of the consequences of biodiversity loss in real-world ecosystems.

KEYWORDS
biodiversity-functionality relationship, biological soil crusts, co-occurrence network, functional importance, multifaceted diversity, rare species, soil phototrophs

1　|　INTRODUCTION

Soils harbour a vast diversity of microorganisms that is of pivotal significance for soil functionality (Bardgett & van der Putten, 2014; Wagg, Bender, Widmer, & van der Heijden, 2014), whilst increasing evidence has demonstrated that provisioning of these crucial functions is threatened by an ongoing loss of biodiversity worldwide (Bender, Wagg, & van der Heijden, 2016; Carey, 2016; Delgado-Baquerizo et al., 2017; Maestre et al., 2016). This tendency is particularly obvious when multiple functions of soils (i.e., multifunctionality)

are considered because various species may affect different individual functions inconsistently (Bowker, Maestre, & Mau, 2013; Bradford et al., 2014; Meyer et al., 2018). Notably, emerging studies have shown that current biodiversity loss is nonrandom and probably causes species extinction for certain functional groups that contribute over-proportionally to multifunctionality (Bender et al., 2016; Selmants, Zavaleta, Pasari, & Hernandez, 2012). Functional subsets of the soil community that sustain key ecosystem functions thus should be identified and prioritized with respect to practical importance for ecological management actions (Krause et al., 2014; Mori, Furukawa, & Sasaki, 2013).

Biodiversity is comprised of multiple components, invoking compositional, phylogenetic, and interactional properties, in addition to the number of species present (i.e., richness) (Cadotte et al., 2010; Cernansky, 2017; Karimi et al., 2017; Kirwan et al., 2007). A major challenge is to predict the functional consequences of declined biodiversity across multifaceted components, as the functional impacts of different facets may complement or offset each other (Bender et al., 2016; Hooper et al., 2005). For instance, the probability of maintaining the multifunctionality of soils increases with lichen richness but declines with evenness, indicating intermodulation of them (Maestre, Castillo-Monroy, Bowker, & Ochoa-Hueso, 2012). Despite intensive concerns regarding on the biodiversity-functioning relation, we are still at the beginning of understanding how soil communities respond to environmental perturbations and the mechanisms by which microbial diversity determines ecosystem functionality (Baveye, Berthelin, & Munch, 2016; Jing et al., 2015; Mori, 2016). Concurrently, recent studies propose that, as an overlooked metric of biodiversity, microbial interaction is of particular importance from which the performance of soil multifunctionality depends (Karimi et al., 2017; Rottjers & Faust, 2018; Valiente-Banuet et al., 2015). Evidence is mounting that the architecture of interaction networks, which represents association patterns of co-occurring microorganisms, can reveal information on the response-ability and functioning of soil ecosystems (de Vries et al., 2018; Karimi et al., 2017). Historically, network approaches applied to macro-organisms have demonstrated that the resilience of ecosystems and the stability of their functions link to taxonomic diversity, as well as to interspecies interaction (Schmid et al., 2009). However, it remains unclear whether the relative effects of changes in different biodiversity components are similarly important to soil multifunctionality and how topological characteristics of microbial species in a co-occurrence network transfer to functional signal (Berry & Widder, 2014; Faust & Raes, 2012; Karimi et al., 2017; Rottjers & Faust, 2018).

In addition, microbial communities typically pose a skewed distribution of species abundance, dominated by a few species that account for most of the biomass (abundant species) alongside a large number of species represented by limited individuals (rare species) (Pedros-Alio, 2012). It has been argued that the diversity of abundant species and their functional traits drive ecosystem functioning, rather than the entire community (mass-ratio hypothesis) (Gonzalez & Loreau, 2009; Winfree, Fox, Williams, Reilly, & Cariveau, 2015). Yet, rare species are increasingly recognized to play key roles in

biogeochemical cycling and providing necessary properties under oscillating ambient conditions (e.g., insurance hypothesis) (Jousset et al., 2017; Yachi & Loreau, 1999). This debate may arise from the contrasting responses of abundant and rare species to different ecological processes (Peter et al., 2010), therefore resulting in a fluctuation of the sensitivity to the loss of species regarding rarity (Lyons & Schwartz, 2001; Smith & Knapp, 2003). Therefore, to facilitate the realistic assessment of biodiversity effects in soils, subcommunities of microbes (abundant versus rare species) need to be underlined for a comprehensive evaluation of their relative influence on individual soil functions and multifunctionality (Soliveres, Manning, et al., 2016).

We conducted a subcontinental survey of soil multifunctionality across 62 dryland sites dominated by biological soil crusts (biocrusts) (Figure 1). In these harsh habitats, where climatic and edaphic conditions constrain the germination of vascular vegetation, biocrusts constitute the uppermost millimeters of soil, forming a cohesive and resistive layer that covers 70% of the surface (Belnap & Lange, 2003; Pointing & Belnap, 2012). They can serve as a useful model system for biodiversity-functionality research because biocrusts play a central role in many arid ecosystems, and functional attributes of species persisted are relatively well-known (Belnap, 2003; Bowker et al., 2014; Büdel, 2002). As one of the most pivotal functional subsets, soil photoautotrophic organisms account for the majority of net primary productivity in biocrusts and strongly influence the overall physiological properties of the soil community (Colica et al., 2014; Maier et al., 2018). We uncovered relationships between multifaceted biodiversity within abundant and rare subcommunities of phototrophic microbiota and soil multifunctionality of biocrusts. To do so, we quantified the richness, evenness, and phylogenetic dissimilarity of species using high-throughput amplicon sequencing data. Network analysis was employed to measure topological features of species and calculated an integrated index, as a proxy for the interaction strength of a given community. Soil multifunctionality was evaluated using seven key individual functional variables: potential productivity, belowground biomass, soil nitrogen/phosphorus content, plant-available nutrients, soil carbon stock, and water-holding capacity. They represent a set of rational indicators for biocrusts, which prevent drylands from soil erosion and quick loss of soil functioning (Bowker, 2007; Mallen-Cooper, Bowker, Antoninka, & Eldridge, 2019).

Because phototrophic microbiota occupies a crucial but relative narrow niche of soil ecosystems, we expected that (a) the richness of soil phototrophs in biocrusts would not be a strong predictor for multifunctionality, due to high functional redundancy; nonetheless, (b) given that each facet has its characteristic impact on ecosystem functioning (Bender et al., 2016), multifaceted diversity may account for a greater proportion of variance in multifunctionality; (c) the topological feature of species interaction would associate with functional performances, and its effects would be comparable as that of taxonomic diversity; and (d) because of their distinct ecological relevance, abundant and rare subcommunities would impact soil functionalities through different ways. Our results could enable a deeper understanding of the consequences of biodiversity loss in real-world ecosystems, and promote our practices on dryland management by means of the diversity-function theory.
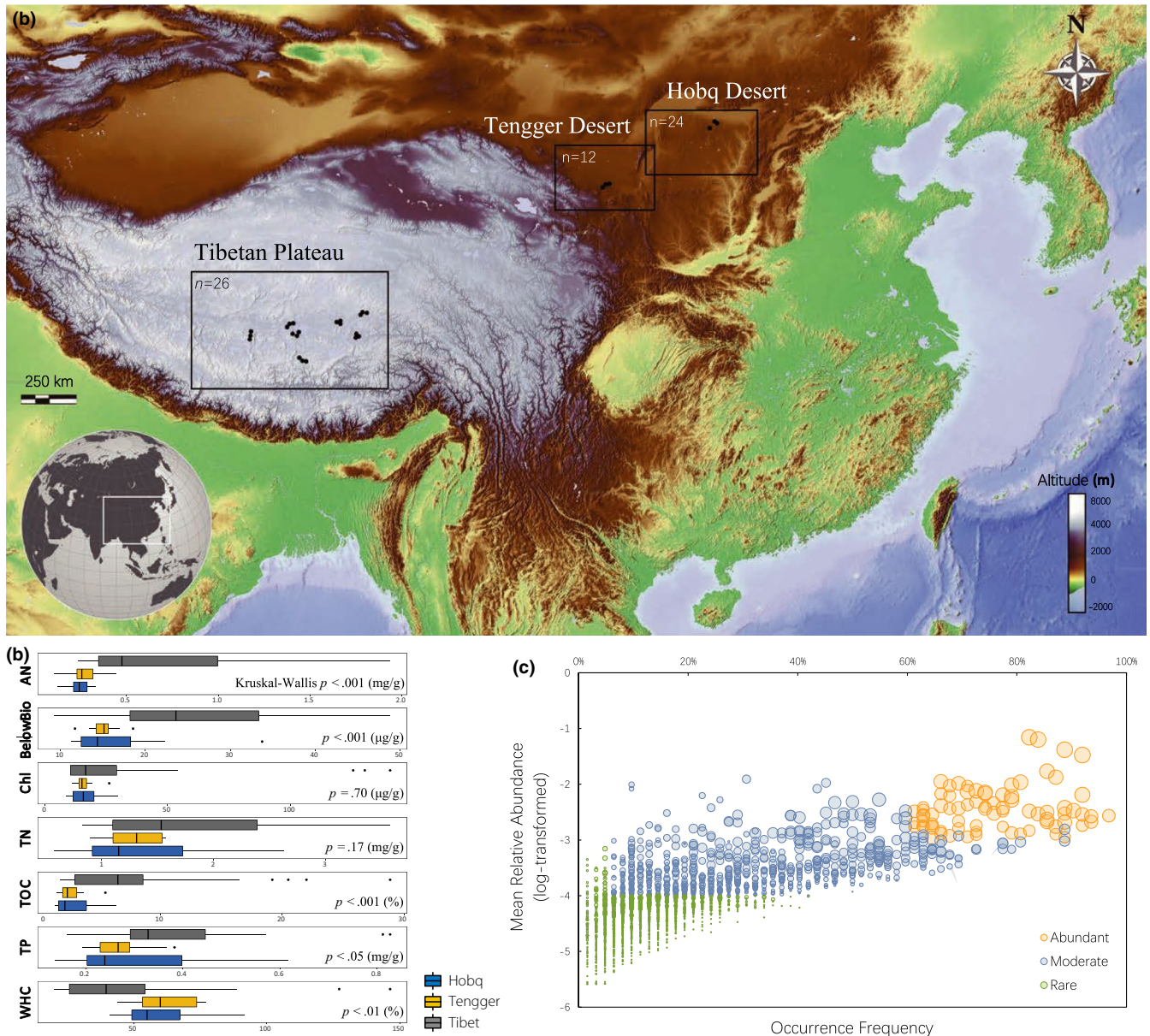
FIGURE 1 Geographic and functional properties of the studying areas across arid lands of subcontinental China. (a) Map of 62 sampled sites from three regions located in Tibetan Plateau, Tengger Desert, and Hobq Desert. (b) Seven key variables of soil functioning were identified and compared cross-regionally, including belowground biomass (BelowBio), total nitrogen (TN), available nutrients (AN), chlorophyll content (Chl), total phosphorus (TP), total organic carbon (TOC), and water-holding capacity (WHC). The significance of difference among regions was checked by the Kruskal-Wallis test at a significance criterion of 0.05. (c) The bubble diagram represents the distribution of phototrophic species in the abundance-occupancy space. Orange, blue and green circles indicate the mean relative abundance and occurrence frequency values of abundant, moderate, and rare species in biological soil crusts, respectively. The size of circles is proportional to the value of species dominance frequency (see details in Methods) [Colour figure can be viewed at wileyonlinelibrary.com]

2 | MATERIALS AND METHODS

2.1 | Characteristics of the study sites and sampling

We obtained the field data and took the samples from 62 sites (each of a 20 × 20 m square field) across the drylands of northern and western China, located in Hobq Desert, Tengger Desert, and Tibetan Plateau (Figure 1a). These sites cover a substantial biogeographic gradient and account for a wide regional range of environmental

conditions (elevation and latitude ranged from 1,016 to 4,716 m and from 31°N to 40°N, respectively; Table S1). Most of the sites are unvegetated or with sparse shrub, dominated by the representative cyanobacterial and moss crusts on the topsoil surface (Figure S1).

Within each site, five plots (50 × 50 cm) were selected randomly in the open field between perennial herbs and apart from shrubs (if present). Upper biocrust cores (0–2 cm) were collected in triplicate by a 7.0 cm Ø ring knife in each plot. Then, cores from the same site were bulked and homogenized (approximately 1,150 cm³ in total).

Samples were air-dried to constant weight in a short time, packed in paper bags, and stored in a portable refrigerator immediately. After the field survey, samples were transferred to the laboratory and further ground by using mortar and pestle and sieved through 2 mm mesh to remove gravel. Subsamples were stored at −20°C until laboratory measurements.

2.2 | Environmental and edaphic variables measurement

We summarized the climatic feature of the sampling sites by the local temperature and precipitation patterns (Table S2). To do so, we collected interpolated climate data from Worldclim (Hijmans, Cameron, Parra, Jones, & Jarvis, 2005), which was used to constitute four climate variables: (a) efficient temperature (annual mean temperature and mean temperature of the wettest quarter); (b) temperature variance (mean diurnal range, temperature seasonality, and temperature annual range); (c) efficient precipitation (annual precipitation and precipitation of warmest quarter); and (d) precipitation variance (precipitation seasonality and precipitation annual range). The principal component score (PC) was extracted to represent each matrix, conducted in principal component analysis and associated parallel analysis of the *R* package psych. Spatial data (elevation, longitude, and latitude) was measured by a handheld GPS device in the field. Local edaphic parameters at each site were summarized by using soil pH and salinity, which play key roles in the community assemblage of soil microorganisms (Janatkova et al., 2013; Rath, Fierer, Murphy, & Rousk, 2019). These variables were measured as described in Supporting Information 1 and constituted an abiotic matrix for subsequent analyses.

2.3 | Multifunctionality assessment in biocrusts

We estimated soil multifunctionality of biocrusts using seven crucial functional variables, including belowground biomass, soil nitrogen/phosphorus retention, plant-available nutrients, potential productivity (that is, the content of chlorophylls), soil carbon stock, and water-holding capacity (see Supporting Information 2 for measuring methods; Figure 1b). The selected functions are closely related to phototrophs in biocrusts and reflect the ecological performances on metabolic potential, soil fertility, primary productivity, carbon sequestration, and climate resistance (Mallen-Cooper et al., 2019; Pointing & Belnap, 2012). They are widely used as the indicators to evaluate the primary succession of the ecosystem in drylands, where soils are lost quickly but biocrusts stabilize the surface under harsh stresses (see Supporting Information 3 for detailed interpretation) (Belnap & Lange, 2003; Green, Porras-Alfaro, & Sinsabaugh, 2008; Lan, Wu, Zhang, & Hu, 2013; Reynolds, Belnap, Reheis, Lamothe, & Luiszer, 2001). In addition, the stabilizing effect of biocrusts on contemporary soils is considered to significantly depend on species composition (Pointing & Belnap, 2012). It demonstrates how these

quantified variables of soils, as a rational proxy for ecosystem functioning, link with the characteristics of microbial community. Soil variables were measured from crust samples collected at each site. Seven individual functions were standardized using the min-max transformation (range from 0 to 1). The minimum and maximum values of a soil function were calculated for the 62 studied sites. Then, these normalized ecological functions were used to obtain "averaged" multifunctionality index, which was a synthetic rotated score from principal component analysis (explained 73% of total variance), and all selected single functions of soils were positively correlated with it. The values of synthetic multifunctionality index were highly similar to the normally used index calculated by arithmetical average (pairwise χ^2 test, $p > .05$, linear slope: 1.05, $R^2 = .995$, Figure S2). Besides, we also applied multiple thresholds method to evaluate the level of multifunctionality for each site, which was measured as the number of individual functions that exceeded a given percentage threshold of the maximum observed value across all sites (Byrnes et al., 2014). Here, we calculated the maximum observed value of each function as the average of top five sites to concern the bias of outliers (Bradford et al., 2014).

2.4 | Identifying of abundant-rare species and analysis of diversity

The community composition of soil phototrophs was assessed using a high-throughput sequencing method on the Illumina MiSeq PE300 platform (Wen et al., 2017). Group-specific primer pair for phototroph with barcodes was used to amplify 16S ribosomal RNA gene sequences (see details in Supporting Information 4). Species were identified based on the similarity level of 100% threshold, therefore each distinct sequence defined a separate OTU (zero-radius OTU, ZOTU, hereafter referred to as species) (Edgar, 2018). Unclassified species, and those with less than three reads or assigned to moss and vascular plants, were declined from subsequent analyses. To standardize the sequencing effort, we then randomly resampled the subset of sequences with 18,463 reads from each sample, and gained a filtered data set, containing 1,144,706 reads within 2,771 taxa, which caught a substantial portion of α- and β-diversity (Figure S3). It indicated that the amount and the density of sampled crustal cores were reliable to recapitulate soil phototrophic compositions of biocrusts from our study field. To evaluate the abundance, quantitative PCR was employed to measure the absolute copy numbers of the identifying gene segment (Supporting Information 4). For the downstream analyses, relative abundance data of MiSeq sequencing was adjusted by the absolute phototrophic abundance of each sample. This can increase the specificity of co-occurrence network (see below) due to apparent correlations of relative abundance data (Berry & Widder, 2014). Sequencing data sets are available on the NCBI website under the accession numbers SRR9694426 through SRR9694487 of BioProject PRJNA554760.

In this study, the definition of abundant/rare species considered three criteria: (a) occurrence frequency; (b) mean relative abundance;

and (c) dominant frequency, which together reflect causalities of rarity, such as stochastic assemblage, fitness trade-offs, and habitat specificity (Jousset et al., 2017). Abundant species were defined as observed in more than 60% of sites (occurrence frequency) with the mean relative abundance of >0.1% across regions, and local relative abundance that >0.1% occurs in more than 30% of sites (dominant frequency). Rare species were defined as mean relative abundance <0.01% across all sites or observed only in less than 5% of sites. Then, the rest intermediate species were categorized as moderate ones (Figure 1c). These thresholds were set partly according to recent publications, and we also evaluated the rationality of the criteria by using multivariate cutoff level analysis (Gobet, Quince, & Ramette, 2010). It demonstrated that the classification of abundant and rare species is appropriate (Figure S4). The abundant species lies in the outlier area of the relative abundance distribution as expected in previous literature (Figure S5) (Liao et al., 2017; Liu, Yang, Yu, & Wilkinson, 2015; Logares et al., 2013).

We summarized the multifaceted diversity feature using three basic metrics, including richness, evenness and phylogenetic dissimilarity (Table S3). More specifically, abundance coverage-based estimator (ACE, as richness index) was measured by EstimateS, and Pielou's evenness (J_{sw}) was then calculated accordingly. To account for phylogenetic dissimilarity, we calculated the mean pairwise phylogenetic distance (MPD) between the pairs of phototrophic species using the R package Picante (Kembel et al., 2010). The PC1 score of three diversity components was extracted by principal component analysis, which explained 85%, 95%, 59%, and 89% of the total variance in overall and three subcommunities (abundant, moderate and rare species), respectively.

2.5 | Network analyses

Given that validation of real community-wide interactions in soils is currently difficult if not impossible, to quantify the topological features of species interaction, we alternatively established an integrated co-occurrence network with all samples across regions. The infrequent species that occur in a single site were removed from the data set to ensure the total Jaccard similarity index of community composition >20%, which could increase the sensitivity of the network (Figure S6) (Berry & Widder, 2014). The sparse graphical model with undirected edges was inferred using the concept of conditional independence by the R package SpiecEasi based on inverse covariance, which avoids the detection of indirectly correlated false associations between species (Kurtz et al., 2015; Rottjers & Faust, 2018). These indirect edges would be prominent if sample heterogeneity is high (Rottjers & Faust, 2018). However, because we only focused on the specific phototrophic communities in biocrusts, which are relatively less heterogenous regardless of sampling scale, it is reasonable to consider that the rate of spurious associations in the network could be further controlled. The sparseness of the network was evaluated by involving random subsampling of the data set to find a network with low variability in the selected set of edges (Kurtz

et al., 2015). To reduce the complexity and ensure the robustness, we retained the edges with high correlation (edge weight >0.30) for subsequent network analyses. The network was visualized with the interactive platform Cytoscape (Shannon et al., 2003).

Although establishing useful biological knowledge from co-occurrence network properties is still unsubstantial, their important roles in exploring and identifying putative microbial interaction have been demonstrated in real-ecosystems (Barberan, Bates, Casamayor, & Fierer, 2012; de Vries et al., 2018; Faust & Raes, 2012). We focused on three topological features of the network: (a) node degree, which is defined as the number of edges linked to a node; (b) betweenness centrality, which reflects the amount of influence that one node exerts over the interactions of other nodes (Yoon, Blumer, & Lee, 2006); and (c) closeness centrality, which is a measure of how fast information spreads from a given node to other reachable nodes (Berry & Widder, 2014). We then applied principal component analysis on three topological features to evaluate the extent of node keystoneness (explained 88% of total variance), which represents the synthetic performance of species in a co-occurrence network. In addition, species keystoneness index was measured for each different study site and obtained a distribution individually. We calculated the mean, variance, skewness, and kurtosis of the 62 keystoneness distributions (Supporting Information 5) (Gross et al., 2017). As just the mean value of keystoneness distribution had widely significant influence (Figure S7), the topological characteristics of local sites (interaction strength) were summarized by the averaged keystoneness index of all species co-occurring in a given community (Berry & Widder, 2014).

2.6 | Effects of diversity and interaction on soil multifunctionality

To separate confounding factors, all biotic predictors and functional variables were corrected for co-varying environmental variability of climate and soils, as described in ref. (Soliveres, van der Plas, et al., 2016). For that, the residuals were calculated by fitting multiple regression models. To avoid the problem of multicollinearity, we used three PC scores of the aforementioned abiotic matrix achieved by orthogonal rotation as explanatory variables. The environment-corrected residual data were retained for subsequent analyses. In addition, because both biotic predictors and functional variables were not established based on relatively temporary activity parameters (e.g., using DNA biomarker to track diversity traits, rather than RNA), it minimized the potential effects of seasonality to fluctuate the detection of diversity-function relationship in biocrusts.

We employed multiple threshold analysis to assess the effects of richness, multifaceted diversity, and interaction strength on soil multifunctionality in the R package Multifunc (Byrnes et al., 2014), which explicitly incorporates the trade-offs between different soil functions. The measure of multifunctionality was applied along with a continuous gradient of thresholds of individual functions from 1%

to 99% with intervals of 1%. The correlations of biotic predictors and multifunctionality were evaluated by fitting a series of general linear models with normalized ACE, integrated diversity traits, and averaged keystoneness index of the 62 studied communities, respectively. A set of particular metrics were highlighted to identify key parameters of the relationships: (a) the min and max independent multifunctionality levels (M_{min}/M_{max}), which indicate the boundary of effects that arise due to biotic predictors from those by chance; (b) the maximized multifunctionality level (M_{mde}); (c) the realized maximum effect (R_{mde}); and (d) their associated threshold values (T_{min}, T_{max} and T_{mde}) (Byrnes et al., 2014).

We also used the least absolute shrinkage and selection operator regression (LASSO) to evaluate the relationship of different diversity components and keystoneness distribution with synthetic multifunctionality index in the R package glmnet (Friedman, Hastie, & Tibshirani, 2010). This analysis fits a generalized linear model via penalized maximum likelihood, and performs the variable selection and model regularization simultaneously, which concern the problems of multicollinearity and overfitting in the model selection process (Hastie, Tibshirani, & Friedman, 2009). We built five models invoking predictors as (a) intact model, all selected biotic predictors in the submodels; (b) overall model, predictors of all species; (c) abundant model, predictors of abundant species; (d) moderate model, predictors of moderate species; and (e) rare model, predictors of rare species. Model averaging was performed based on adjusted R^2 values within paired models between intact model and four submodels, respectively (Table S4). Then, the incorporated slope was used to estimate the effect of each predictor on soil multifunctionality. We included the presence of moss (i.e., microhabitat shift) as a categorical predictor in all models to control for its potential influence. The relative contribution of normalized predictors on explaining total variance was evaluated as the percentage of the parameter estimate of each predictor compared with all estimates in the model.

2.7 | Species multifunctional importance

The extent to which different subcommunities of species maintain the high level of soil multifunctionality could be discrepant due to functional redundancy (Mori et al., 2016; Nielsen, Ayres, Wall, & Bardgett, 2011). We quantified the multifunctional importance of soil phototrophs at the species level, relying on randomization tests (Gotelli, Ulrich, & Maestre, 2011). The species-specific value of multifunctional importance was calculated as the correlation coefficient between the abundance of target species and the number of soil functions that equaled or exceeded a critical threshold across all sites (multiple threshold approach). We used 999 randomizations reassigning observed values in different sites and repeated the null modeling for all species. The standardized effect size (SES) of multifunctional importance value was measured, which quantified the extent to which an observed metric deviated from distribution of metrics generated by a stochastic simulation (Gotelli &

McCabe, 2002). If |SES_i| of species i is greater than 1.96, the value of functional importance approximately falls into the 5% tail of a normal distribution, which means that species i poses significantly effect on maintaining soil multifunctionality, otherwise inconsiderable than expected by chance (|SES_i| < 1.96). We calculated SES values in a series of thresholds of individual functions from 1% to 99% with an interval of 2%. In addition, we also performed null modeling with the synthetic multifunctionality index (averaging approach). The randomization tests were conducted in a Fortran 95 program Impact. The patterns of SES derived from abundance data and presence-absence matrix were compared, which exhibited high consistency (data not shown). Species that occurred only once or twice in the meta-community across regions were declined from analyses.

3 | RESULTS

3.1 | Community composition

In total, 2,771 ZOTUs occurred in the meta-community of soil phototrophs from three studied regions. In the samples, we found 637 ± 38 (mean ± *SEM*) ZOTUs from Tibetan Plateau, 436 ± 19 different ZOTUs from Hobq Desert, and 404 ± 34 ZOTUs from Tengger Desert. The detailed diversity indices of each region were presented in Table S3. In the data set, 79.7% of reads belonged to Cyanobacteria, 4.8% belonged to eukaryotic algae, and 10.1% were assigned to Chloroflexi (Figure 2a). The cyanobacterial species found across regions primarily belonged to three phylogenetic orders, namely, Nostocales/Oscillatoriales (88.6% of cyanobacterial reads in 714 ZOTUs), Phormidesmiales (3.0% in 63 ZOTUs), and Leptolyngbyales (1.5% in 46 ZOTUs). The Chloroflexi species were dominated by Thermomicrobiales (97.9% of Chloroflexi reads in 774 ZOTUs). At local and cross-regional levels, 78 ZOTUs (2.81%) were identified as abundant species representing 50.49% of all reads, whereas 1 862 ZOTUs (67.20%) with 8.32% of reads were categorized to rare species (Figure S4). Of these ZOTUs, 48 of abundant (62%), 204 of moderate (25%), and 235 of rare ZOTUs (13%) were shared between different regions (Figure S8). Furthermore, the analysis of phylogenetic structure using the MPD matrix revealed that 96.8% and 85.5% of studied sites were composed of abundant and moderate species with an over-dispersive or random tendency, whereas more than half of sites supported a phylogenetic clustering of rare species (Figure S9).

3.2 | Co-occurrence network

In the context of soil phototrophs, we supposed to consider that positive co-occurrence is a pattern that would be expected if there was facilitation, otherwise negative co-occurrence suggests competition (Harris, 2016). The integrated co-occurrence network consisted of 2,088 nodes connected by 1,835 robust edges with 1,807 positive and 28 negative links, in which 1,198 edges linked
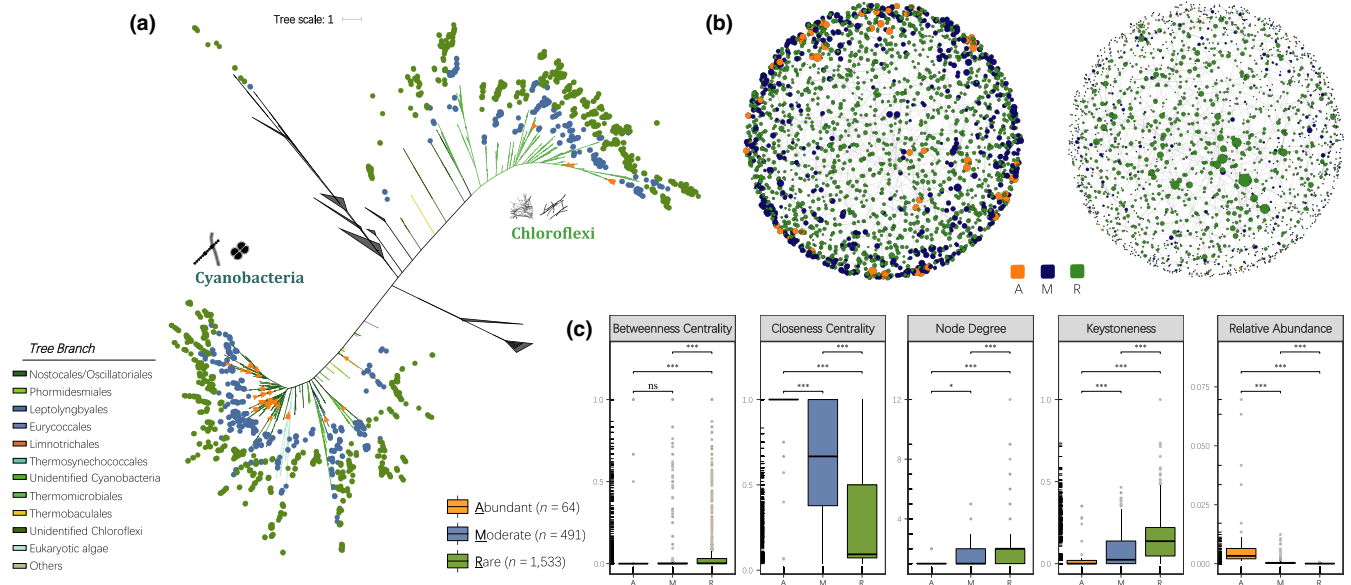
FIGURE 2 Phylogenetic composition and co-occurrence network of phototrophic species in biological soil crusts. (a) The unrooted tree of phototrophic 16S ribosomal RNA gene sequences, constituted by two main clades of Cyanobacteria and Chloroflexi, indicates the phylogenetic positions of abundant (orange triangles), moderate (blue circles), and rare species (green circles). (b) Tree branches are labelled by different colours, according to the taxonomic orders. Co-occurrence networks with undirected edges between species coloured by rarity (A, abundant; M, moderate; and R, rare species). The parameter setting for the sparsity of interaction is that λ.min.ratio = 1e^{-2} and nλ = 30 (SPIEC-EASI), and the stability coefficient of the network is 0.049, which gets close to the desired significant threshold of 0.05. The connections stand for strong correlations (edge weight > 0.30). The size of each node is proportional to the mean relative abundance (left panel) or to the number of connections (i.e., node degree, right panel). (c) Box-plot diagrams showing the comparison of the topological features of integrated network and relative abundances between species with different rarity. The pairwise verifying of significance was conducted by using the Wilcoxon test and indicated as ^{ns}, nonsignificant; *p < .05; ***p < .001 [Colour figure can be viewed at wileyonlinelibrary.com]

two nodes clearly assigned to different phylogenetic orders (see Figure 2b; Figure S10), reflecting a dominant of interspecies facilitation than competition. The node degree distribution obeyed a power-law form (ρ = 0.872, R^2 = .91), indicating a scale-free and nonrandom co-occurrence pattern (Barabasi & Oltvai, 2004). The integrated network composed of one major module and eleven minor modules, of which Module 1 contained 45.5% and 56.1% of total nodes and edges, respectively. The remaining minor modules accounted for less than 10% of nodes and 11% of edges in the entire network (Table S5). This result indicated that a considerable portion of soil phototrophs adapted to the same niche of biocrusts (Faust & Raes, 2012), implying a status of functional redundancy. There were only two out of 64 abundant species found in these complex modules (belonged to Chloroflexi), and most abundant species interacted with special phototrophs in a relatively simple manner, which exhibited low modularity of common species than rare species. Hub species in networks are supposed to pose a high level of topological properties (i.e., keystoneness) (Berry & Widder, 2014;Rottjers & Faust, 2018). We compared the topological features and relative abundance of species categorized according to rarity (Figure 2c). The results exhibited that abundant, moderate, and rare species were distinct with a significant gradient (Wilcoxon tests, p < .05). Rare species had the highest values of betweenness centrality, node degree, and keystoneness index, whereas the highest closeness centrality was found for abundant species.

3.3 | Factors associated with multifunctionality

The phototrophic richness in biocrusts presented a moderate negative relationship with soil multifunctionality (Figure 3a,b). The effect became significant ranging from 61% (T_{min}) to 81% (T_{max}) of the functional thresholds with an extreme value of subtracting by 3.22 functions along with the change of richness (R_{mde}) at the threshold of 74% (T_{mde}). In contrast, if multifaceted diversity traits were considered (i.e., richness, evenness, and phylogenetic dissimilarity), the integrated diversity associated with soil multifunctionality positively despite the narrow range of significant thresholds (approximately 60% to 71%). At its highest level, integrated diversity achieved 47.8% of the maximum potential of effect size on soil multifunctionality. We found that averaged keystoneness, as a proxy for interaction strength, posed obviously stronger positive effect on multifunctionality than richness and integrated diversity. The effect began to be significant from a very low threshold (9%, T_{min}) and reached its peak at a high threshold (96%, T_{mde}) with an effect size of 2.56 functions added. Moreover, we scrutinized the individual diversity components and four keystoneness distribution parameters by using LASSO regression. The result showed that diversity, interspecies facilitation, and moss accounted for 14%, 21% and 65% of explained variance (mean adjusted R^2 = .51), revealing the important impact of microhabitat shift on soil functioning (Li et al., 2013), albeit
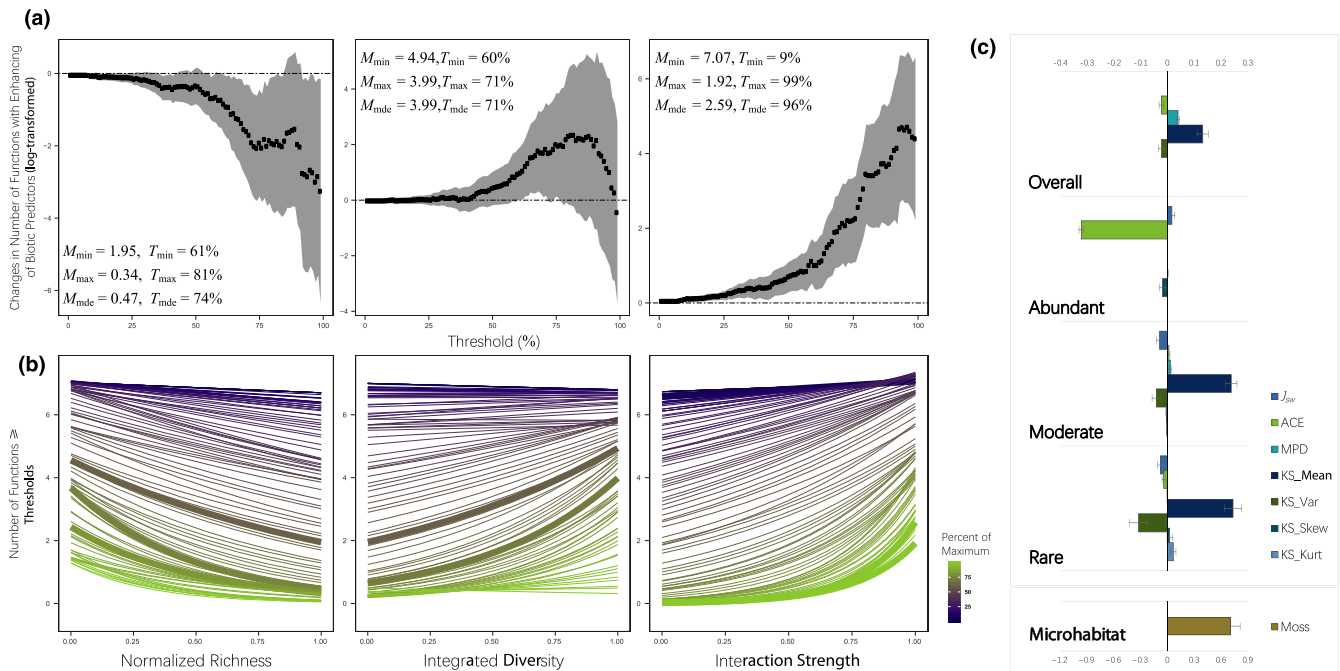
(a)

(b)

(c)

FIGURE 3 Environment-corrected effect of biotic predictors on soil multifunctionality. Relatedness patterns of normalized richness, integrated diversity index, and interaction strength along with a range of soil multifunctionality were evaluated by the multiple threshold approach, respectively (a,b). (a) Upper panels exhibit the changes in numbers of individual soil functions, reaching a range of percentage thresholds of the maximum observed value, following the enhancing of standardized biotic predictors. Circles represent the fitted values of regressions between biotic predictors and the number of soil variables above a certain threshold, and grey shading indicates the 95% confidence interval. The M_{min}, M_{max}, M_{mde} values and their corresponding thresholds T_{min}, T_{max}, and T_{mde} are indicated. (b) Lower panels show the regression lines, and the bold lines represent the boundaries and the maximum of significant effects ($p < .05$), respectively. (c) Colours of lines indicate the thresholds from 1% (purple) to 99% (green). Average slope estimates of model predictors (mean ± SEM), expressed as the individual standardized effects on soil multifunctionality, were evaluated by the least absolute shrinkage and selection operator regression (LASSO) analysis (see Table S4 for details of model averaging). KS mean, variance, skewness, and kurtosis are the distribution parameters of species keystoneness of a certain community. J_{sw}, Pielou's evenness; ACE, richness index; MPD, mean pairwise phylogenetic distance [Colour figure can be viewed at wileyonlinelibrary.com]

both phylogenetic dissimilarity (MPD) and interaction strength (averaged keystoneness) played significantly crucial roles in maintaining multifunctionality, as well as on single functionalities of biocrusts (Figure 3c; Table S6). Nonetheless, species with different rarity exhibited distinct influencing patterns. For instance, most of diversity and interaction topological features of abundant species were unrelated to multifunctionality, but the individual effects of richness and MPD offset each other and collectively led to a negative effect as an integral one. For moderate and rare species, although averaged keystoneness was the predominant factor to promote soil multifunctionality, their evenness and the variance of keystoneness consistently showed negative effects. In addition, most of the findings on individual factors reminded when using multiple threshold approach (Figure S7).

3.4 | Multifunctional importance and keystoneness

Across the range of thresholds, multifunctional importance index (SES) indicated that 6.83 ± 0.70% (mean ± SEM) of species were significantly more important on influencing soil multifunctionality

positively than the null expectation, whereas 16.85 ± 0.99% of species posed significantly negative effects (Figure 4a). Most of the phototrophs (76.32 ± 0.85%) were not functionally significant than expected by chance ($p > .05$). Despite that, the mean values of multifunctional importance across significantly positive species increased along with the thresholds of soil functionalities from low to high (OLS slope: 0.748, $R^2 = .75$, $F = 143.5$, and $p < .001$). Meanwhile, the number of species with significant negative effects was lower at higher levels of the threshold. Additionally, the standardized functional importance calculated by the averaging approach exhibited a similar tendency that most species fell in the nonsignificant interval, whereas abundant species usually showed significantly negative correlations with soil multifunctionality (Figure 4b). More importantly, we observed a bimodal distribution of soil phototrophs according to their importance on multifunctionality and on certain individual functionalities (e.g., TN, TOC, and Chl). The first main distribution covered the whole range of species functional importance (green curve), and the second one merely held a significantly positive interval (red curve). The latter distribution consisted of approximate 360 rare species and 134 moderate species, in which numbers of cyanobacterial genera presented dominantly, such as
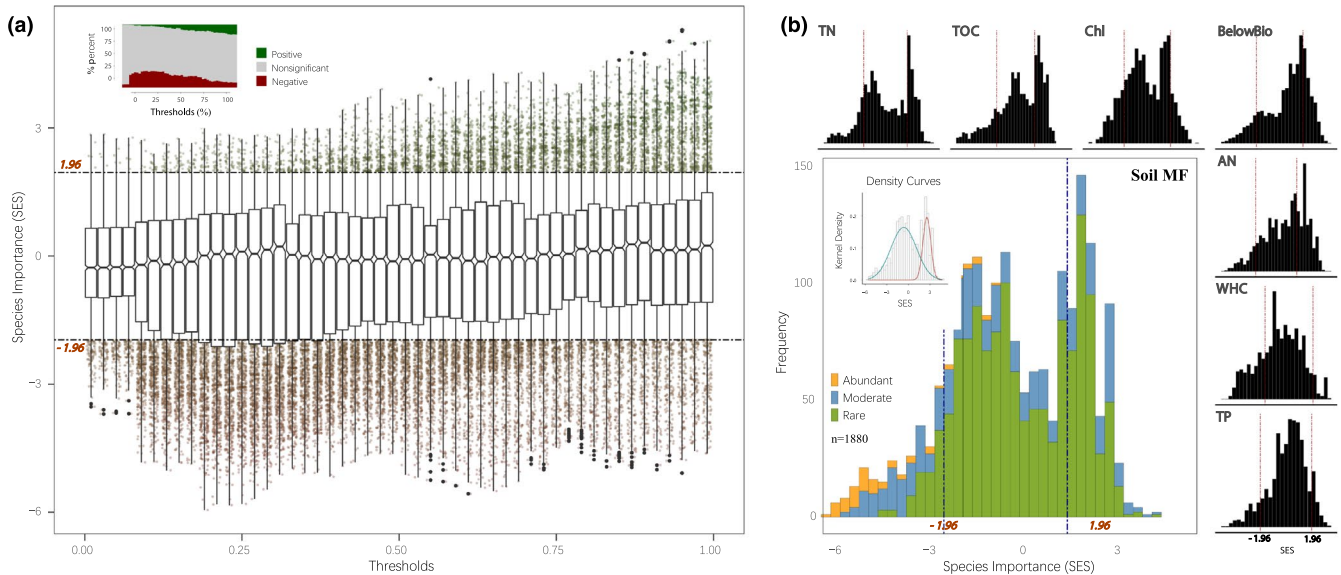
FIGURE 4 Functional importance of phototrophic species to maintain soil multifunctionality of biological soil crusts. (a) Boxplot diagram presents the distribution of standardized functional importance values (SES) at every 2% of the thresholds from 1% to 99%, using the multiple threshold approach. The top and bottom boundaries represent the upper/lower quartiles and medians of functional importance values. Black horizontal dashed lines indicate 95% confidence intervals. Green and red hollow points represent species with significant positive and negative effects on soil multifunctionality than expected by chance ($p < .05$), respectively. Their percentage ratio along the thresholds of maximum observed variables is presented in the inserted diagram. (b) Accumulative histograms show the frequency distribution of functional importance values of abundant, moderate, and rare phototrophic species on soil multifunctionality (MF, calculated by the averaging approach) and on individual soil functions. Dashed lines indicate 95% confidence intervals. The inserted histogram presents the feature of a bimodal distribution of species functional importance on soil multifunctionality with respective kernel density curves [Colour figure can be viewed at wileyonlinelibrary.com]

Lyngbya, *Tolypothrix*, *Nostoc*, *Nodosilinea*, *Leptolyngbya*, *Pleurocapsa*, *Coleofasciculus*, and *Rivularia*.

To test whether topological features of soil phototrophs in co-occurrence network couples with functional performance, we evaluated the relationship between keystoneness and multifunctionality importance at the species level. After separating environmental and spatial factors, there was a significantly positive correlation of species multifunctionality importance (SES) with the keystoneness index (Slope$_{common}$ = 3.21, $p < .001$) (Figure 5). It revealed that the potential loss of keystone phototrophic species in biocrusts could result in a substantial decline in soil functionality. However, the relationships were not consistent among abundant, moderate, and rare species. Although keystoneness of moderate and rare species showed significant association with their multifunctional importance (Slope$_{moderate}$ = 5.15; Slope$_{rare}$ = 0.96; both $p < .05$), ecological behaviour of abundant species lacked topological signals in the co-occurrence network ($p > .05$). The results remained when we just invoked sites composed of cyanobacterial crusts in the analysis ($n = 38$), to control for the potential bias induced by moss prevalence.

4 | DISCUSSION

By focusing on phototrophic communities in biocrusts, our findings provide a unique insight into the underlying links of biodiversity components with soil individual and multiple functionalities.
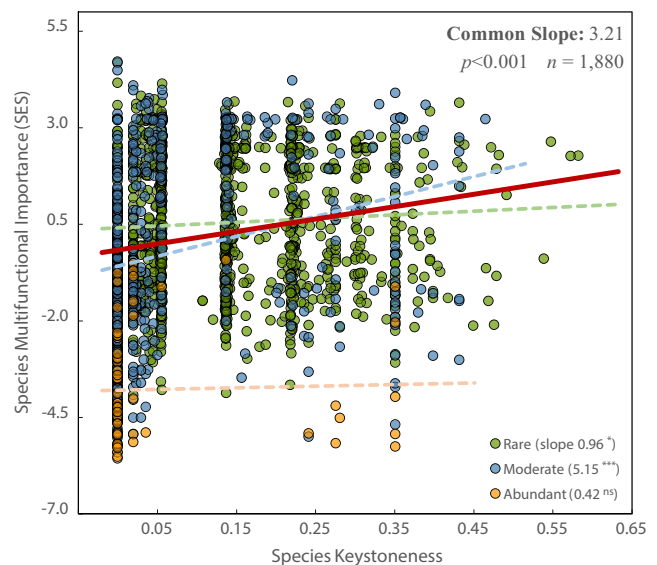

FIGURE 5 Relationships of species multifunctional importance with keystoneness. Species importance was calculated based on the values of soil multifunctionality obtained by the averaging approach. Red line represents the linear significant fit ($p < .001$) that accounts for all phototrophic species. Orange, blue, and green dashed lines represent the linear fits of abundant, moderate, and rare species, respectively. Slope values for the linear fits and associate significant levels are shown ([ns], nonsignificant; *$p < .05$; ***$p < .001$). The scatterplot indicates that species multifunctional performance is positively associated with their topological feature in a co-occurrence network significantly [Colour figure can be viewed at wileyonlinelibrary.com]

We show that higher taxonomic richness of soil phototrophs, inconsistent with aboveground producers (i.e., vascular plants) (Hector et al., 1999; Zavaleta, Pasari, Hulvey, & Tilman, 2010), is not positively correlated to individual functions and even impairs the delivery of multifunctionality (Figure 3a,b; Table S6). In contrast, when taxonomic and phylogenetic properties of the phototrophic community are jointly considered, multifaceted diversity appears to sustain larger numbers of soil functions at moderate levels of thresholds (60%–71%). This incongruence arises from the trade-off between richness and phylogenetic dissimilarity (MPD) with opposite effects and collectively leads to an overall slightly positive effect on soil multifunctionality. Moreover, we observed a shift of species functional role in supporting belowground multifunctionality along with thresholds (Figure 4a). While the majority of phototrophic microorganisms increase or decrease multiple functioning nonsignificantly, sustaining a high threshold level of multifunctionality tends to require more particular species with beneficial identity than expected by chance. The bimodal distribution of multifunctional importance (SES) further demonstrates that functional effects are nonrandom among species and thus not simply cumulative (Figure 4b), thereby underlining the role of species identity, instead of the stochastic effect of richness (Bender et al., 2016), on driving ecosystem functioning.

As noted previously, because different diversity components are context-dependent, disentangling the variety of alternative metrics and precisely evaluating which measure of diversity is most appropriate is an important step towards practical application of the knowledge about the biodiversity effects on ecosystem functioning (Bender et al., 2016; Mori et al., 2013). Abundance-weighted phylogenetic distance represents the degree of evolutionary relatedness among the individuals of phototrophic microbiota and presumably indicates the integrated phenotypic difference and ecological uniqueness (Cadotte et al., 2010; Valiente-Banuet & Verdu, 2007). Therefore, in our case of biocrusts, high phylogenetic dissimilarity of phototrophs is supposed to maximize trait diversity, facilitate potential complement by capturing resources differentially in the spatial-temporal scale, and ultimately ensures the response variability of biocrusts to stabilize soil multifunctionality against environmental erosion (Cadotte, Cardinale, & Oakley, 2008; Elmqvist et al., 2003). Our results demonstrate that phototrophic compositional identity (species idiosyncrasy and MPD) is a stronger predictor of the multifunctional performance of biocrusts, rather than how many species are present. It gives theoretical support for current restoration practices by using cyanobacterial inoculation in degraded soils, highlighting the importance of inoculum selection (Rossi, Li, Liu, & De Philippis, 2017).

Nevertheless, recent syntheses argued that microbial diversity may not necessarily be informative or sensitive enough to predict functional consequences of ambient perturbation, but species interaction matters (Harvey, Gounand, Ward, & Altermatt, 2017; Karimi et al., 2017). To summarize the association trait of species, we evaluated the degree of keystoneness of nodes in the co-occurrence network based on major topological parameters. This metric detected the property to what extent that one species could impact the rest members disproportionately (Berry & Widder, 2014; Valiente-Banuet et al., 2015). Thus, higher averaged keystoneness of a given microbial assemblage indicated a more highly connected and centrally clustering pattern, which was used to predict community-wide interaction strength. We found that the strength of interspecies facilitation explained more 20% of the variance (adjusted R^2) in soil multifunctionality than phototrophic multifaceted diversity did, after accounting for the influence of microhabitat change. The effect of facilitation approached saturation until a significantly higher threshold (99%) than diversity achieved (71%), suggesting that maintaining interspecies links could be equally considerable to promote the resilience of biocrusts and the stability of their functioning. This association has also been observed in other terrestrial ecosystems; for example, anthropogenic N deposition may alter carbon cycling of hardwood forest via changes in the nature of biotic interactions among saprotrophic soil bacteria (Freedman & Zak, 2015). However, understanding how microbial interaction network determines specific ecosystem functioning remains elusive (Karimi et al., 2017). Despite that, we reveal a crucial positive association between multifunctional importance and synthetic topological characteristic (keystoneness) of phototrophic microbes within the co-occurrence network (Figure 5). Our finding provides empirical evidence that changes in network architecture could translate into changes in functional performance. Given the observed neutral or even negative effect of richness, the results show that species turnover is likely to be decoupled from the dynamics of association network (Li, Poisot, Waller, & Baiser, 2018); in other words, soil multifunctionality maintained by phototrophic microbiota in biocrusts can be lost despite certain species remaining present (Valiente-Banuet et al., 2015).

Biocrusts have been proven to be often dominated by a limited suite of cyanobacterial species (e.g., *Microcoleus* spp.) (Freeman et al., 2009; Garcia-Pichel, Loza, Marusenko, Mateo, & Potrafka, 2013), alongside the majority of the rest with low abundance. We found that abundant, moderate and rare species, as the subcommunities of phototrophic microbiota in biocrusts, have stepwise changes of their ecological relevance with the difference of rarity (Figure 2c; Table S3). For multiple biodiversity components, it is the richness of abundant species that determined an overall negative effect on soil multifunctionality, whilst averaged keystoneness of both moderate and rare species positively associated (Figure 3c). It means that a higher level of multiple functioning of biocrusts relies on fewer abundant phototroph dominant with a closely connected set of rare species, which reflects the stark differentiation of their roles in maintaining soil multifunctionality. Additionally, we also found that, as the belowground producer, rare phototrophic species are less likely to negatively affect soil multifunctionality than abundant species (Figure 4). This difference was explained to be derived from the frequency of functional trade-offs between species in previous studies, where functional roles of abundant and rare species are

driven by density and presence, respectively (Soliveres, Manning, et al., 2016). In grasslands across Germany, they observed that rare species of productive plants had significantly more positive, rather negative, relationships with multifunctionality than common species did, but not found in belowground heterotrophic organisms (Soliveres, Manning, et al., 2016), thereby implying a trophic level-dependent balance of functional trade-offs within abundant and rare species.

It is noteworthy that different cyanobacterial species were observed to inhabit different vertical layers of topsoil under a gradient of abiotic stresses (Belnap & Lange, 2003; Lan, Wu, Zhang, & Hu, 2011). It has been supposed that species more exposed to ambient perturbation tend to be poorly linked to other species whereas the more connected species tend to be less exposed (Araujo, Rozenfeld, Rahbek, & Marquet, 2011). As proof, our finding indeed shows that almost all of the abundant species were relatively isolated and merely interacted within small topological structures, but the majority of rare species were tightly connected in complicated network modules (Figure 2b; Table S5). Accordingly, we infer that different subcommunities of phototrophic microbiota probably distribute in different vertical layers of biocrusts, such that abundant species inhabit topmost and rare species below. Meanwhile, given that the extent of modularity in a network was verified to be positively correlated with stability and negatively correlated with resilience (Eldridge et al., 2015; Ruiz-Moreno, Pascual, & Riolo, 2006), we speculate that abundant species could determine the resilience of biocrust whereas rare species ensure multifunctional stability. However, the consequence of network alteration in abundant and rare species for ecosystem functionality is just an emerging field (Harvey et al., 2017). While our correlative study does not investigate the exact mechanisms behind, the results provide a novel insight into a deeper understanding of spatial assemblage and stress resistance of biocrusts in drylands.

In conclusion, by evaluating the biocrusts across a subcontinental scale, we uncover the underlying associations between a general family of multiple biodiversity components and maximized multifunctionality in dryland soils. While phototrophic richness is not positively related to the maxima of multifunctional performance, interspecies facilitation and compositional identity are particularly stronger but often neglected predictors. We also reveal a significant positive correlation of species functional importance with its topological feature in co-occurrence networks, highlighting a potential mechanism by which species interaction promotes multifunctionality. Furthermore, abundant species tend to isolate and merely interact within small topological structures, but rare species were tightly connected in complicated network modules. These results suggest that subcommunities of phototrophic microbiota with different rarity impact soil functionalities of biocrusts through distinctive ways. Collectively, our findings give a comprehensive view of how soil constructive species drive multifunctionality and contribute to guiding management efforts of ecological restoration according to the theory of biodiversity-functionality relationship (Bender et al., 2016; Bommarco, Kleijn, & Potts, 2013).

AUTHOR CONTRIBUTIONS

H.L. and R.-H.L. designed this research in consultation with W.-B.W., X.-L.C., and G.-L.Y.; H.L. and D.H. took the samples in the field; H.L., Y.-X.C., and W.-B.W. conducted laboratory measurement; H.L. and D.H. conducted statistical analyses; H.L. wrote the manuscript with contributions from all coauthors.

DATA AVAILABILITY STATEMENT

Soil physicochemical and community composition data that support the findings of this study are deposited in Dryad (https://doi.org/10.5061/dryad.51qq0b4). Sequencing data sets are available on the NCBI website under the accession numbers SRR9694426 through SRR9694487. The climatic data are available from the database Worldclim (http://www.worldclim.org/).

ORCID

Hua Li https://orcid.org/0000-0002-9476-0830

REFERENCES

Araujo, M. B., Rozenfeld, A., Rahbek, C., & Marquet, P. A. (2011). Using species co-occurrence networks to assess the impacts of climate change. *Ecography*, *34*(6), 897–908. https://doi.org/10.1111/j.1600-0587.2011.06919.x

Barabasi, A. L., & Oltvai, Z. N. (2004). Network biology: Understanding the cell's functional organization. *Nature Reviews Genetics*, *5*(2), 101–115. https://doi.org/10.1038/nrg1272

Barberan, A., Bates, S. T., Casamayor, E. O., & Fierer, N. (2012). Using network analysis to explore co-occurrence patterns in soil microbial communities. *The ISME Journal*, *6*(2), 343–351. https://doi.org/10.1038/ismej.2011.119

Bardgett, R. D., & van der Putten, W. H. (2014). Belowground biodiversity and ecosystem functioning. *Nature*, *515*(7528), 505–511. https://doi.org/10.1038/nature13855

Baveye, P. C., Berthelin, J., & Munch, J.-C. (2016). Too much or not enough: Reflection on two contrasting perspectives on soil biodiversity. *Soil Biology and Biochemistry*, *103*, 320–326. https://doi.org/10.1016/j.soilbio.2016.09.008

Belnap, J. (2003). The world at your feet: Desert biological soil crusts. *Frontiers in Ecology and the Environment*, *1*(4), 181–189. https://doi.org/10.2307/3868062

Belnap, J., & Lange, O. L. (2003). *Biological soil crusts: Structure, function, and management*. Berlin Heidelberg, Germany: Springer-Verlag.

Bender, S. F., Wagg, C., & van der Heijden, M. G. (2016). An underground revolution: Biodiversity and soil ecological engineering for agricultural sustainability. *Trends in Ecology and Evolution*, *31*(6), 440–452. https://doi.org/10.1016/j.tree.2016.02.016

Berry, D., & Widder, S. (2014). Deciphering microbial interactions and detecting keystone species with co-occurrence networks. *Frontiers in Microbiology*, *5*, 219. https://doi.org/10.3389/fmicb.2014.00219

Bommarco, R., Kleijn, D., & Potts, S. G. (2013). Ecological intensification: Harnessing ecosystem services for food security. *Trends in Ecology and Evolution*, 28(4), 230–238. https://doi.org/10.1016/j.tree.2012.10.012

Bowker, M. A. (2007). Biological soil crust rehabilitation in theory and practice: An underexploited opportunity. *Restoration Ecology*, 15(1), 13–23.

Bowker, M. A., Maestre, F. T., Eldridge, D., Belnap, J., Castillo-Monroy, A., Escolar, C., & Soliveres, S. (2014). Biological soil crusts (biocrusts) as a model system in community, landscape and ecosystem ecology. *Biodiversity and Conservation*, 23(7), 1619–1637. https://doi.org/10.1007/s10531-014-0658-x

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, 923–933. https://doi.org/10.1007/s10021-013-9644-5

Bradford, M. A., Wood, S. A., Bardgett, R. D., Black, H. J., Bonkowski, M., Eggers, T., ... Jones, T. H. (2014). Discontinuity in the responses of ecosystem processes and multifunctionality to altered soil community composition. *Proceedings of the National Academy of Sciences of the United States of America*, 111(40), 14478–14483.

Büdel, B. (2002). Diversity and ecology of biological crusts. In K. Esser, U. Luttge, W. Beyschlag, & W. Hellwig (Eds.), *Progress in botany. Genetics, physiology, ecology* (pp. 386–404). Berlin, Germany: Springer.

Byrnes, J. E. K., Gamfeldt, L., Isbell, F., Lefcheck, J. S., Griffin, J. N., Hector, A., ... Freckleton, R. (2014). Investigating the relationship between biodiversity and ecosystem multifunctionality: Challenges and solutions. *Methods in Ecology and Evolution*, 5(2), 111–124. https://doi.org/10.1111/2041-210x.12143

Cadotte, M. W., Cardinale, B. J., & Oakley, T. H. (2008). Evolutionary history and the effect of biodiversity on plant productivity. *Proceedings of the National Academy of Sciences of the United States of America*, 105(44), 17012–17017. https://doi.org/10.1073/pnas.0805962105

Cadotte, M. W., Jonathan Davies, T., Regetz, J., Kembel, S. W., Cleland, E., & Oakley, T. H. (2010). Phylogenetic diversity metrics for ecological communities: Integrating species richness, abundance and evolutionary history. *Ecology Letters*, 13(1), 96–105. https://doi.org/10.1111/j.1461-0248.2009.01405.x

Carey, J. (2016). Crucial role of belowground biodiversity. *Proceedings of the National Academy of Sciences of the United States of America*, 113(28), 7682–7685. https://doi.org/10.1073/pnas.1609238113

Cernansky, R. (2017). The biodiversity revolution. *Nature*, 546(14), 22–24.

Colica, G., Li, H., Rossi, F., Li, D., Liu, Y., & De Philippis, R. (2014). Microbial secreted exopolysaccharides affect the hydrological behavior of induced biological soil crusts in desert sandy soils. *Soil Biology and Biochemistry*, 68, 62–70. https://doi.org/10.1016/j.soilbio.2013.09.017

de Vries, F. T., Griffiths, R. I., Bailey, M., Craig, H., Girlanda, M., Gweon, H. S., ... Bardgett, R. D. (2018). Soil bacterial networks are less stable under drought than fungal networks. *Nature Communications*, 9, 3033. https://doi.org/10.1038/s41467-018-05516-7

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

Edgar, R. C. (2018). Updating the 97% identity threshold for 16S ribosomal RNA OTUs. *Bioinformatics*, 34(14), 2371–2375. https://doi.org/10.1093/bioinformatics/bty113

Eldridge, D. J., Woodhouse, J. N., Curlevski, N. J., Hayward, M. W., Brown, M. V., & Neilan, B. A. (2015). Soil-foraging animals alter the composition and co-occurrence of microbial communities in a desert shrubland. *The ISME Journal*, 9(12), 2671–2681. https://doi.org/10.1038/ismej.2015.70

Elmqvist, T., Folke, C., Nystrom, M., Peterson, G., Bengtsson, J., Walker, B., & Norberg, J. (2003). Response diversity, ecosystem change, and resilience. *Frontiers in Ecology and the Environment*, 1(9), 488–494. https://doi.org/10.2307/3868116

Faust, K., & Raes, J. (2012). Microbial interactions: From networks to models. *Nature Reviews Microbiology*, 10(8), 538–550. https://doi.org/10.1038/nrmicro2832

Freedman, Z. B., & Zak, D. R. (2015). Atmospheric N deposition alters connectance, but not functional potential among saprotrophic bacterial communities. *Molecular Ecology*, 24(12), 3170–3180. https://doi.org/10.1111/mec.13224

Freeman, K. R., Pescador, M. Y., Reed, S. C., Costello, E. K., Robeson, M. S., & Schmidt, S. K. (2009). Soil CO_2 flux and photoautotrophic community composition in high-elevation, 'barren' soil. *Environmental Microbiology*, 11(3), 674–686. https://doi.org/10.1111/j.1462-2920.2008.01844.x

Friedman, J., Hastie, T., & Tibshirani, R. (2010). Regularization paths for generalized linear models via coordinate descent. *Journal of Statistical Software*, 33(1), 1–22. https://doi.org/10.18637/jss.v033.i01

Garcia-Pichel, F., Loza, V., Marusenko, Y., Mateo, P., & Potrafka, R. M. (2013). Temperature drives the continental-scale distribution of key microbes in topsoil communities. *Science*, 340(6140), 1574–1577. https://doi.org/10.1126/science.1236404

Gobet, A., Quince, C., & Ramette, A. (2010). Multivariate cutoff level analysis (MultiCoLA) of large community data sets. *Nucleic Acids Research*, 38(15), e155. https://doi.org/10.1093/nar/gkq545

Gonzalez, A., & Loreau, M. (2009). The Causes and consequences of compensatory dynamics in ecological communities. *Annual Review of Ecology Evolution and Systematics*, 40, 393–414. https://doi.org/10.1146/annurev.ecolsys.39.110707.173349

Gotelli, N. J., & McCabe, D. J. (2002). Species co-occurrence: A meta-analysis of J. M. Diamond's assembly rules model. *Ecology*, 83(8), 2091–2096. https://doi.org/10.2307/3072040

Gotelli, N. J., Ulrich, W., & Maestre, F. T. (2011). Randomization tests for quantifying species importance to ecosystem function. *Methods in Ecology and Evolution*, 2(6), 634–642. https://doi.org/10.1111/j.2041-210X.2011.00121.x

Green, L. E., Porras-Alfaro, A., & Sinsabaugh, R. L. (2008). Translocation of nitrogen and carbon integrates biotic crust and grass production in desert grassland. *Journal of Ecology*, 96(5), 1076–1085. https://doi.org/10.1111/j.1365-2745.2008.01388.x

Gross, N., Bagousse-Pinguet, Y. L., Liancourt, P., Berdugo, M., Gotelli, N. J., & Maestre, F. T. (2017). Functional trait diversity maximizes ecosystem multifunctionality. *Nature Ecology & Evolution*, 1(5), 132. https://doi.org/10.1038/s41559-017-0132

Harris, D. J. (2016). Inferring species interactions from co-occurrence data with Markov networks. *Ecology*, 97(12), 3308–3314. https://doi.org/10.1002/ecy.1605

Harvey, E., Gounand, I., Ward, C. L., & Altermatt, F. (2017). Bridging ecology and conservation: From ecological networks to ecosystem function. *Journal of Applied Ecology*, 54(2), 371–379. https://doi.org/10.1111/1365-2664.12769

Hastie, T., Tibshirani, R., & Friedman, J. (2009). *The elements of statistical learning: Data mining, inference, and prediction*. New York, NY: Springer-Verlag.

Hector, A., Schmid, B., Beierkuhnlein, C., Caldeira, M. C., Diemer, M., Dimitrakopoulos, P. G., ... Lawton, J. H. (1999). Plant diversity and productivity experiments in European grasslands. *Science*, 286(5442), 1123–1127.

Hijmans, R. J., Cameron, S. E., Parra, J. L., Jones, P. G., & Jarvis, A. (2005). Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology*, 25(15), 1965–1978. https://doi.org/10.1002/joc.1276

Hooper, D. U., Chapin, F. S., Ewel, J. J., Hector, A., Inchausti, P., Lavorel, S., ... Wardle, D. A. (2005). Effects of biodiversity on

ecosystem functioning: A consensus of current knowledge. *Ecological Monographs*, 75(1), 3–35. https://doi.org/10.1890/04-0922

Janatkova, K., Rehakova, K., Dolezal, J., Simek, M., Chlumska, Z., Dvorsky, M., & Kopecky, M. (2013). Community structure of soil phototrophs along environmental gradients in arid Himalaya. *Environmental Microbiology*, 15(9), 2505–2516. https://doi.org/10.1111/1462-2920.12132

Jing, X., Sanders, N. J., Shi, Y. U., Chu, H., Classen, A. T., Zhao, K. E., … He, J.-S. (2015). The links between ecosystem multifunctionality and above- and belowground biodiversity are mediated by climate. *Nature Communications*, 6, 8159. https://doi.org/10.1038/ncomms9159

Jousset, A., Bienhold, C., Chatzinotas, A., Gallien, L., Gobet, A., Kurm, V., … Hol, W. H. G. (2017). Where less may be more: How the rare biosphere pulls ecosystems strings. *The ISME Journal*, 11(4), 853–862. https://doi.org/10.1038/ismej.2016.174

Karimi, B., Maron, P. A., Boure, N.-C.-P., Bernard, N., Gilbert, D., & Ranjard, L. (2017). Microbial diversity and ecological networks as indicators of environmental quality. *Environmental Chemistry Letters*, 15(2), 265–281. https://doi.org/10.1007/s10311-017-0614-6

Kembel, S. W., Cowan, P. D., Helmus, M. R., Cornwell, W. K., Morlon, H., Ackerly, D. D., … Webb, C. O. (2010). Picante: R tools for integrating phylogenies and ecology. *Bioinformatics*, 26(11), 1463–1464. https://doi.org/10.1093/bioinformatics/btq166

Kirwan, L., Lüscher, A., Sebastià, M. T., Finn, J. A., Collins, R. P., Porqueddu, C., … Connolly, J. (2007). Evenness drives consistent diversity effects in intensive grassland systems across 28 European sites. *Journal of Ecology*, 95(3), 530–539. https://doi.org/10.1111/j.1365-2745.2007.01225.x

Krause, S., Le Roux, X., Niklaus, P. A., Van Bodegom, P. M., Lennon, J. T., Bertilsson, S., … Bodelier, P. L. E. (2014). Trait-based approaches for understanding microbial biodiversity and ecosystem functioning. *Frontiers in Microbiology*, 5, 251. https://doi.org/10.3389/fmicb.2014.00251

Kurtz, Z. D., Muller, C. L., Miraldi, E. R., Littman, D. R., Blaser, M. J., & Bonneau, R. A. (2015). Sparse and compositionally robust inference of microbial ecological networks. *PLOS Computational Biology*, 11(5), e1004226. https://doi.org/10.1371/journal.pcbi.1004226

Lan, S., Wu, L., Zhang, D., & Hu, C. (2011). Successional stages of biological soil crusts and their microstructure variability in Shapotou region (China). *Environmental Earth Sciences*, 65(1), 77–88. https://doi.org/10.1007/s12665-011-1066-0

Lan, S., Wu, L., Zhang, D., & Hu, C. (2013). Assessing level of development and successional stages in biological soil crusts with biological indicators. *Microbial Ecology*, 66(2), 394–403. https://doi.org/10.1007/s00248-013-0191-6

Li, D., Poisot, T., Waller, D. M., & Baiser, B. (2018). Homogenization of species composition and species association networks are decoupled. *Global Ecology and Biogeography*, 27(12), 1481–1491. https://doi.org/10.1111/geb.12825

Li, H., Colica, G., Wu, P. P., Li, D., Rossi, F., De Philippis, R., & Liu, Y. (2013). Shifting species interaction in soil microbial community and its influence on ecosystem functions modulating. *Microbial Ecology*, 65(3), 700–708. https://doi.org/10.1007/s00248-012-0171-2

Liao, J., Cao, X., Wang, J., Zhao, L., Sun, J., Jiang, D., & Huang, Y. (2017). Similar community assembly mechanisms underlie similar biogeography of rare and abundant bacteria in lakes on Yungui Plateau, China. *Limnology and Oceanography*, 62(2), 723–735. https://doi.org/10.1002/lno.10455

Liu, L., Yang, J., Yu, Z., & Wilkinson, D. M. (2015). The biogeography of abundant and rare bacterioplankton in the lakes and reservoirs of China. *The ISME Journal*, 9(9), 2068–2077. https://doi.org/10.1038/ismej.2015.29

Logares, R., Lindström, E. S., Langenheder, S., Logue, J. B., Paterson, H., Laybourn-Parry, J., … Bertilsson, S. (2013). Biogeography of

bacterial communities exposed to progressive long-term environmental change. *The ISME Journal*, 7(5), 937–948. https://doi.org/10.1038/ismej.2012.168

Lyons, K. G., & Schwartz, M. W. (2001). Rare species loss alters ecosystem function – Invasion resistance. *Ecology Letters*, 4(4), 358–365. https://doi.org/10.1046/j.1461-0248.2001.00235.x

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. https://doi.org/10.1111/j.1365-2745.2011.01918.x

Maestre, F. T., Eldridge, D. J., Soliveres, S., Kéfi, S., Delgado-Baquerizo, M., Bowker, M. A., … Berdugo, M. (2016). Structure and functioning of dryland ecosystems in a changing world. *Annual Review of Ecology, Evolution and Systematics*, 47, 215–237. https://doi.org/10.1146/annurev-ecolsys-121415-032311

Maier, S., Tamm, A., Wu, D., Caesar, J., Grube, M., & Weber, B. (2018). Photoautotrophic organisms control microbial abundance, diversity, and physiology in different types of biological soil crusts. *The ISME Journal*, 12(4), 1032–1046. https://doi.org/10.1038/s41396-018-0062-8

Mallen-Cooper, M., Bowker, M. A., Antoninka, A. J., & Eldridge, D. J. (2019). A practical guide to measuring functional indicators and traits in biocrusts. *Restoration Ecology*. https://doi.org/10.1111/rec.12974

Meyer, S. T., Ptacnik, R., Hillebrand, H., Bessler, H., Buchmann, N., Ebeling, A., … Weisser, W. W. (2018). Biodiversity–multifunctionality relationships depend on identity and number of measured functions. *Nature Ecology & Evolution*, 2(1), 44–49. https://doi.org/10.1038/s41559-017-0391-4

Mori, A. S. (2016). Resilience in the studies of biodiversity-ecosystem functioning. *Trends in Ecology and Evolution*, 31(2), 87–89. https://doi.org/10.1016/j.tree.2015.12.010

Mori, A. S., Furukawa, T., & Sasaki, T. (2013). Response diversity determines the resilience of ecosystems to environmental change. *Biological Reviews of the Cambridge Philosophical Society*, 88(2), 349–364. https://doi.org/10.1111/brv.12004

Mori, A. S., Isbell, F., Fujii, S., Makoto, K., Matsuoka, S., & Osono, T. (2016). Low multifunctional redundancy of soil fungal diversity at multiple scales. *Ecology Letters*, 19(3), 249–259. https://doi.org/10.1111/ele.12560

Nielsen, U. N., Ayres, E., Wall, D. H., & Bardgett, R. D. (2011). Soil biodiversity and carbon cycling: A review and synthesis of studies examining diversity-function relationships. *The European Journal of Soil Science*, 62(1), 105–116. https://doi.org/10.1111/j.1365-2389.2010.01314.x

Pedros-Alio, C. (2012). The rare bacterial biosphere. *Annual Review of Marine Science*, 4, 449–466. https://doi.org/10.1146/annurev-marine-120710-100948

Peter, H., Beier, S., Bertilsson, S., Lindström, E. S., Langenheder, S., & Tranvik, L. J. (2010). Function-specific response to depletion of microbial diversity. *The ISME Journal*, 5, 351. https://doi.org/10.1038/ismej.2010.119

Pointing, S. B., & Belnap, J. (2012). Microbial colonization and controls in dryland systems. *Nature Reviews Microbiology*, 10(8), 551–562. https://doi.org/10.1038/nrmicro2831

Rath, K. M., Fierer, N., Murphy, D. V., & Rousk, J. (2019). Linking bacterial community composition to soil salinity along environmental gradients. *The ISME Journal*, 13(3), 836–846. https://doi.org/10.1038/s41396-018-0313-8

Reynolds, R., Belnap, J., Reheis, M., Lamothe, P., & Luiszer, F. (2001). Aeolian dust in Colorado Plateau soils: Nutrient inputs and recent change in source. *Proceedings of the National Academy of Sciences of the United States of America*, 98(13), 7123–7127. https://doi.org/10.1073/pnas.121094298

Rossi, F., Li, H., Liu, Y., & De Philippis, R. (2017). Cyanobacterial inoculation (cyanobacterisation): Perspectives for the development of a standardized multifunctional technology for soil fertilization and

desertification reversal. *Earth-Science Reviews*, *171*, 28–43. https://doi.org/10.1016/j.earscirev.2017.05.006

Rottjers, L., & Faust, K. (2018). From hairballs to hypotheses-biological insights from microbial networks. *FEMS Microbiology Reviews*, *42*(6), 761–780. https://doi.org/10.1093/femsre/fuy030

Ruiz-Moreno, D., Pascual, M., & Riolo, R. (2006). Exploring network space with genetic algorithms: Modularity, resilience and reactivity. In M. Pascual & J. A. Dunne (Eds.), *Ecological networks: Linking structure to dynamics in food webs*. Oxford, UK: Oxford University Press.

Schmid, B., Balvanera, P., Cardinale, B. J., Godbold, J., Pfisterer, A. B., & Raffaelli, D. (2009). Consequences of species loss for ecosystem functioning: Meta-analyses of data from biodiversity experiments. In S. Naeem, D. E. Bunker, A. Hector, M. Loreau, & C. Perrings (Eds.), *Ecosystem functioning, and human wellbeing: An ecological and economic perspective of data from biodiversity experiments*. Oxford, UK: Oxford University Press.

Selmants, P. C., Zavaleta, E. S., Pasari, J. R., & Hernandez, D. L. (2012). Realistic plant species losses reduce invasion resistance in a California serpentine grassland. *Journal of Ecology*, *100*(3), 723–731. https://doi.org/10.1111/j.1365-2745.2011.01949.x

Shannon, P., Markiel, A., Ozier, O., Baliga, N. S., Wang, J. T., Ramage, D., … Ideker, T. (2003). Cytoscape: A software environment for integrated models of biomolecular interaction networks. *Genome Research*, *13*(11), 2498–2504. https://doi.org/10.1101/gr.1239303

Smith, M. D., & Knapp, A. K. (2003). Dominant species maintain ecosystem function with non-random species loss. *Ecology Letters*, *6*, 509–517. https://doi.org/10.1046/j.1461-0248.2003.00454.x

Soliveres, S., Manning, P., Prati, D., Gossner, M. M., Alt, F., Arndt, H., … Allan, E. (2016). Locally rare species influence grassland ecosystem multifunctionality. *Philosophical Transactions of the Royal Society of London. Series B. Biological Sciences*, *371*(1694), 20150269. https://doi.org/10.1098/rstb.2015.0269

Soliveres, S., van der Plas, F., Manning, P., Prati, D., Gossner, M. M., Renner, S. C., … Allan, E. (2016). Biodiversity at multiple trophic levels is needed for ecosystem multifunctionality. *Nature*, *536*(7617), 456–459. https://doi.org/10.1038/nature19092

Valiente-Banuet, A., Aizen, M. A., Alcántara, J. M., Arroyo, J., Cocucci, A., Galetti, M., … Zamora, R. (2015). Beyond species loss: The extinction of ecological interactions in a changing world. *Functional Ecology*, *29*(3), 299–307. https://doi.org/10.1111/1365-2435.12356

Valiente-Banuet, A., & Verdu, M. (2007). Facilitation can increase the phylogenetic diversity of plant communities. *Ecology Letters*, *10*(11), 1029–1036. https://doi.org/10.1111/j.1461-0248.2007.01100.x

Wagg, C., Bender, S. F., Widmer, F., & van der Heijden, M. G. A. (2014). Soil biodiversity and soil community composition determine ecosystem multifunctionality. *Proceedings of the National Academy of Sciences of the United States of America*, *111*(14), 5266–5270.

Wen, C., Wu, L., Qin, Y., Van Nostrand, J. D., Ning, D., Sun, B. O., … Zhou, J. (2017). Evaluation of the reproducibility of amplicon sequencing with Illumina MiSeq platform. *PLoS ONE*, *12*(4), e0176716. https://doi.org/10.1371/journal.pone.0176716

Winfree, R., Fox, J. W., Williams, N. M., Reilly, J. R., & Cariveau, D. P. (2015). Abundance of common species, not species richness, drives delivery of a real-world ecosystem service. *Ecology Letters*, *18*(7), 626–635. https://doi.org/10.1111/ele.12424

Yachi, S., & Loreau, M. (1999). Biodiversity and ecosystem productivity in a fluctuating environment: The insurance hypothesis. *Proceedings of the National Academy of Sciences of the United States of America*, *96*(4), 1463–1468. https://doi.org/10.1073/pnas.96.4.1463

Yoon, J., Blumer, A., & Lee, K. (2006). An algorithm for modularity analysis of directed and weighted biological networks based on edge-betweenness centrality. *Bioinformatics*, *22*(24), 3106–3108. https://doi.org/10.1093/bioinformatics/btl533

Zavaleta, E. S., Pasari, J. R., Hulvey, K. B., & Tilman, G. D. (2010). Sustaining multiple ecosystem functions in grassland communities requires higher biodiversity. *Proceedings of the National Academy of Sciences of the United States of America*, *107*(4), 1443–1446. https://doi.org/10.1073/pnas.0906829107

SUPPORTING INFORMATION

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