

Nutrient supply drives concurrent K-to-r strategist shifts and competitive intensification in biocrust bacterial communities

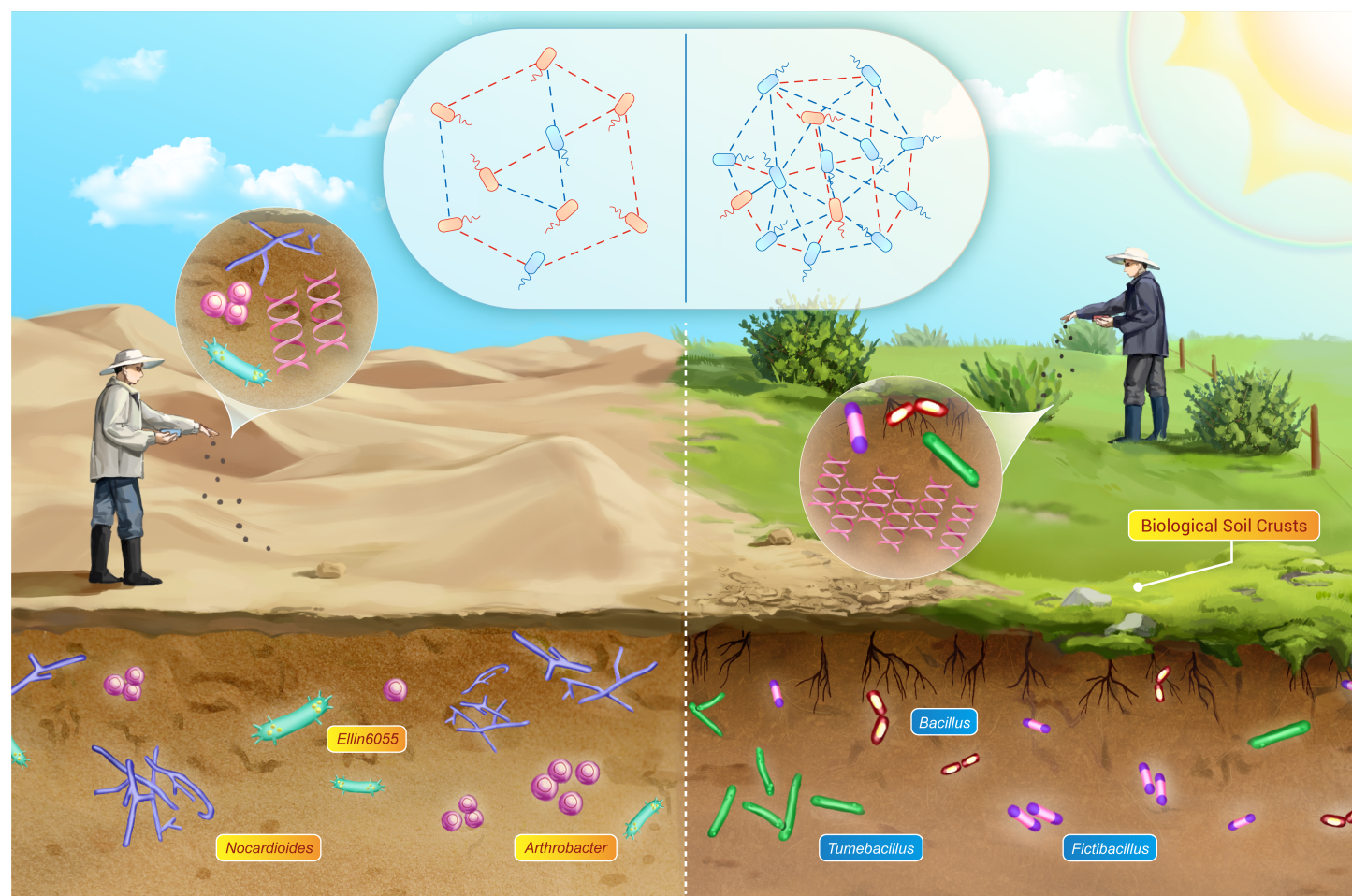
Lina Zhao,¹ Wenjing Zhang,¹ Ning Chen,³ Bettina Weber,⁴ Tianjiao Dai,⁵ Rongliang Jia,⁶ Shaobin Gu,^{1,*} and Xinrong Li^{2,*}

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GRAPHICAL ABSTRACT



PUBLIC SUMMARY

- Increased nutrient supply favored fast-growing, resource-exploiting bacteria.
- Biocrust bacterial complexity and interactions increased with nutrient supply.
- Negative interactions among biocrust bacteria intensified with nutrient supply.
- Six keystone species with different responses to nutrient supply were identified.
- Targeted nutrient and keystone taxa management aids dryland restoration.

Nutrient supply drives concurrent K-to-r strategist shifts and competitive intensification in biocrust bacterial communities

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Biological soil crusts (biocrusts) cover ~30% of global drylands and regulate biogeochemical cycles through bacterial metabolic activities. Although nutrient scarcity profoundly influences biocrust bacterial communities, the general principles governing their nutrient response dynamics remain unclear. Here, we employed controlled microcosms to investigate how differential nutrient supply reshaped bacterial life-history traits and inter-species interactions in both cyanobacteria- and moss-dominated biocrusts. Our findings revealed that with increased nutrient supply, the ribosomal RNA gene operon (*rnn*) copy numbers in bacterial communities significantly increased, while the ratio of oligotrophs to copiotrophs decreased, indicating a shift from K-strategists to r-strategists. Network analysis showed that nutrient supply increased node number, link number, average degree, and negative correlations, indicating stronger interactions within the bacterial community. Keystone taxa analysis identified six keystone taxa, with *Arthrobacter*, *Nocardioides*, and *Ellin6055* responding negatively, and *Bacillus*, *Tumebacillus*, and *Fictibacillus* responding posi-

tively to nutrient supply. Furthermore, bacterial community structure, including life-history strategies, network topology, and keystone taxa, was strongly correlated with soil properties, particularly the contents of available nitrogen and potassium and total phosphorus. Our study establishes a mechanistic framework for nutrient-driven bacterial assembly in dryland ecosystems, providing practical strategies for ecological stabilization through optimized nutrient management and targeted manipulation of bacterial keystone taxa.

INTRODUCTION

Biological soil crusts (biocrusts), which are complex and vital communities of cyanobacteria, fungi, bacteria, archaea, lichens, and bryophytes bound to surface soil particles, cover ~30% of the global dryland surface and play a crucial role in the cycling of nutrients, water, and gases.^{1–4} Biocrust succession, characterized by the transition from the early successional stage dominated

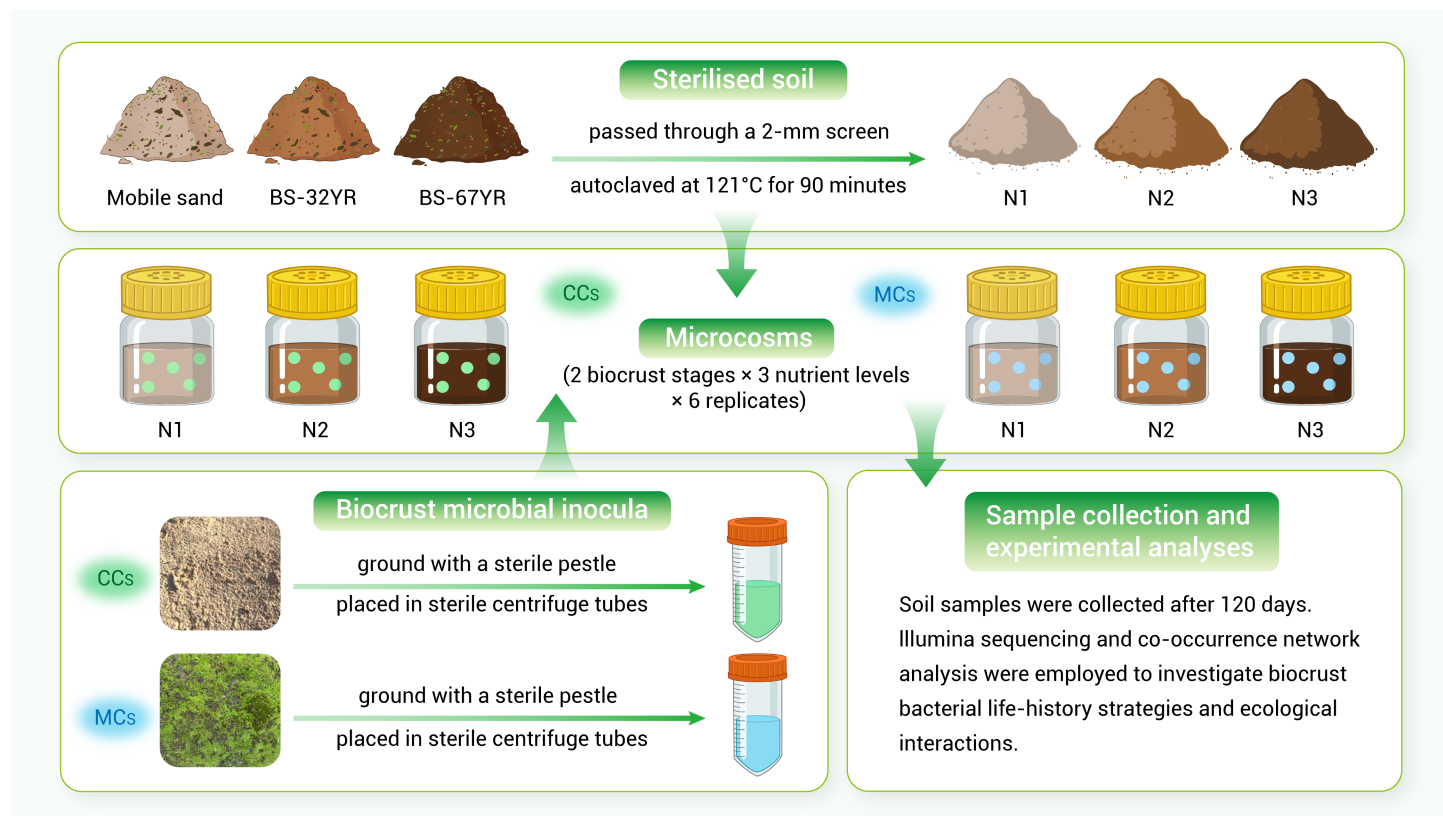


Figure 1. Schematic of the experimental design Biocrust subsoils were sterilized by autoclaving, biocrusts were ground and used as microbial inocula. BS-32YR and BS-67YR represent the biocrust subsoils collected from revegetation sites established in 1991 (32 years of revegetation) and 1956 (67 years of revegetation), respectively. N1, N2, and N3 represent soil types under low, moderate, and high nutrient manipulations, respectively. CCs and MCs represent cyanobacteria- and moss-dominated crusts, respectively.



Figure 2. Biocrust bacterial life-history strategies and taxonomic compositions in soil microcosms under different nutrient levels (n = 6 per treatment) (A) 16S rRNA operon (*rrn*) copy number and (B) Oligo/Copio ratio of biocrust bacterial communities analyzed using Tukey's Honestly Significant Difference test. Different lowercase letters denote significant differences between samples ($P < 0.05$). (C) Biocrust bacterial community composition at the phylum level and (D) at the genus level. (E) Kruskal-Wallis H test results at the genus level showing significant differences in relative abundance among treatments. N1, N2, and N3 represent soil types under low, moderate, and high nutrient manipulations, respectively. CCs and MCs represent cyanobacteria- and moss-dominated crusts, respectively.

by cyanobacteria to later stages dominated by lichens and bryophytes, is accompanied by significant transformations in microbial community structures and substantial increases in soil nutrients.^{1,5–7} Increasing evidence has confirmed the close relationship between soil nutrients and biocrust microbial communities.^{8,9} For example, Illumina MiSeq sequencing of natural biocrust samples at different developmental stages demonstrated the key role of soil phosphorus (P) in explaining the diversity and composition of biocrust bacterial communities.¹⁰ However, the mechanisms by which soil nutrient supply affects biocrust microbial communities remain poorly understood.

The r-K selection theory, originally developed in macroecology, has inspired microbial ecologists to develop soil microorganism classifications based on the trade-off between growth rate and resource utilization efficiency.^{11,12} This theoretical framework provides a valuable approach for understanding linkages between the biocrust bacterial community and nutrient fluctuations. Classically, r-strategists (copiotrophs) are fast-growing, resource-exploitative taxa that dominate nutrient-rich environments, while K-strategists (oligotrophs) are slow-growing, resource-conservative taxa adapted to nutrient scarcity.^{13–15} Another genomic trait that distinguishes bacterial life strategies is the ribosomal RNA gene operon (*rrn*) copy number.^{16,17} The r-strategists typically encode more *rrn* copy numbers to satisfy the higher ribosomal content necessary for maximum growth rates and flexibility in growth rate

adjustments, along with fewer high-affinity transporters, whereas K-strategists, characterized by one or fewer *rrn* copy numbers, are adapted to extract maximum resources out of a limited supply.^{18,19} While genomic traits like *rrn* copy number have been proposed as proxies for trophic strategies in sediments and soil environments,^{20,21} their ecological relevance remains untested in biocrusts—a critical knowledge gap given these ecosystems' unique composition and structure. In addition, taxonomy-based studies are interested in the mining of core r-strategists or K-strategists that are persistently present and/or significantly different across various samples,²² which is essential for understanding restoration success and promoting sustainable management of arid ecosystems.

Soil nutrient supply is generally tied to microbial interactions that affect growth and loss rates of different life-history strategies.^{20,23–25} Recent studies, however, reveal divergent findings on two critical aspects. The first pertains the impact of soil nutrient enrichment on microbial network complexity: while some studies indicate that nitrogen (N) application enhances bacterial interactions and network complexity,^{26,27} others report a downward trend in network complexity with increasing soil carbon (C) and N contents.^{23,28,29} The second concerns the balance of microbial cooperative (positive correlations) and competitive (negative correlations) interactions. Several studies demonstrate that N application enhances cooperative relationships, manifesting as increased

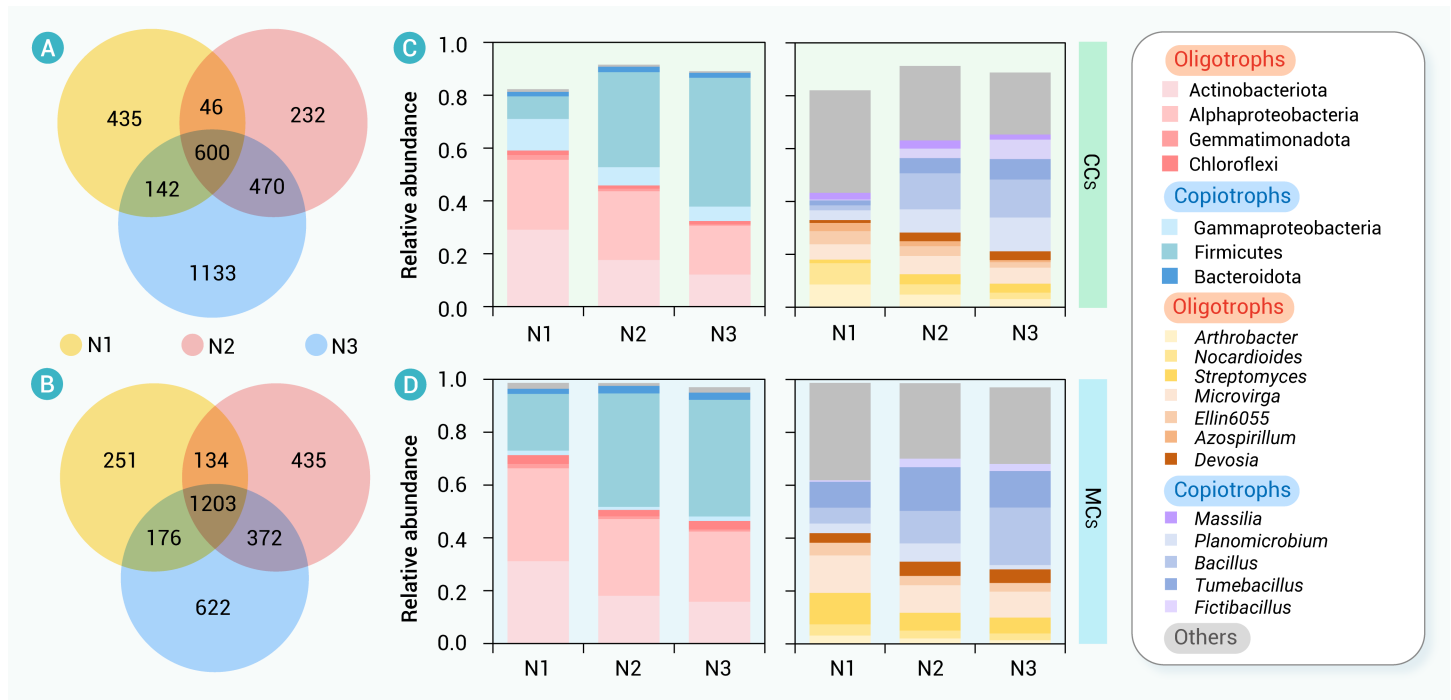


Figure 3. Overview of biocrust bacterial OTUs in soil microcosms under different nutrient levels (A) Venn diagram of the distribution of bacterial OTUs in cyanobacteria-dominated crusts and (B) moss-dominated crusts. (C) Taxonomic composition of shared bacterial OTUs in cyanobacteria-dominated crusts and (D) moss-dominated crusts across soil microcosms under different nutrient levels. N1, N2, and N3 represent soil types under low, moderate, and high nutrient manipulations, respectively.

positive correlations among bacterial taxa.^{17,27} However, other study proposes the “hunger games” hypothesis, suggesting that microbial communities shift from cooperative strategies to competitive behaviors when resources become abundant.²⁰ These conflicting results underscore the complexity of microbial responses to soil nutrient supply and highlight the need for further investigations analyzing into the underlying mechanisms governing microbial growth and interaction dynamics under varying nutrient conditions.^{30,31}

In our study, we conducted microcosm experiments to examine how nutrient supply influences bacterial life-history strategies and potential ecological interactions in cyanobacteria- (CCs) and moss-dominated crusts (MCs). The microcosm approach provides distinct advantages for elucidating nutrient-microbe interactions by utilizing sterilized soil inoculated with defined microbial consortia to address multiple experimental challenges inherent to field studies. This approach effectively decouples nutrient effects from confounding biotic and abiotic variables, while the controlled laboratory environment precisely isolates target nutrient responses through systematic elimination of spatial and temporal heterogeneity characteristic of natural ecosystems.³² These methodological controls collectively enhance reproducibility, signal detection, and causal inference, enabling us to address two pivotal questions: (i) whether bacterial communities of biocrusts shift from K-strategists to r-strategists under elevated nutrient supply, and (ii) how potential ecological interactions between these strategists respond to increasing soil nutrient supply.

MATERIALS AND METHODS

Site description

The study was conducted in the Shapotou region (37°32'N, 105°02'E, 1339 m a.s.l.), located at the southeastern edge of the Tengger Desert in north-central China. The mean annual temperature is 10°C, and the mean annual precipitation is 186 mm.³³ The soil is windborne sand (Eutric Arenosol in the World Reference Base), saline and alkaline, with a pH ranging from 7.5–11.2.³⁴ A 16 km by 0.5 km large non-irrigated revegetation protection system was established in 1956 and expanded in 1964, 1973, 1981, 1991 and 2000 to prevent the Baotou-Lanzhou railway from being buried by sand.^{35,36} These revegetated areas, established in different years, offer ideal experimental sites for studying ecological succession and environmental changes over time.

Field sampling

In June 2023, biocrust and subsoil (0–5 cm) samples were collected for microcosm experiments. Two types of biocrusts were sampled: early-stage cyanobacteria-dominated crusts (CCs) and late-stage moss-dominated crusts (MCs), both exhibiting >80% surface coverage by their respective dominant species. Subsoil samples were collected from three sites representing distinct nutrient levels: mobile sand (initial stage, N1) with low nutrient supply, 32-year revegetated area (established in 1991, N2) with moderate nutrient supply, and 67-year revegetated area (established in 1956, N3) with high nutrient supply.

For each biocrust type and subsoil site, we established five spatially independent 10 × 10 m plots, maintaining a minimum inter-plot distance of 20 m to account for landscape-scale heterogeneity. Within each plot, five subsamples were collected from standardized positions (four vertices and the geometric center) using sterilized tools (ethanol-treated trowel for biocrusts; stainless steel core sampler for subsoils) to prevent cross-contamination. The 25 subsamples (5 positions × 5 plots) were pooled in equal amounts, and thoroughly mixed to form one composite sample. All samples were immediately transported to the laboratory. Biocrust samples were stored at 4°C (for less than two weeks) prior to microcosm preparation. Subsoil samples were kept at room temperature (25 ± 1°C) until microcosm preparation.

Microcosm experiment

To assess biocrust bacterial community development across nutrient levels, we established microcosms using sterilized subsoils (N1–N3) inoculated with either CC or MC microbial communities. All subsoils were passed through a 2 mm screen and autoclaved at 121°C for 90 minutes to achieve sterility while preserving the original nutrient levels (post-sterilization pH values showed no significant differences among treatments: $\Delta\text{pH} < 0.2$, $P > 0.05$; nutrient contents maintained their intended levels: $\text{N1} < \text{N2} < \text{N3}$, $P < 0.05$; Figure 1 & Table S1).^{37,38} Microbial inocula were prepared by aseptically homogenizing CC and MC samples (ground with a sterile pestle and sieved through 0.1 mm mesh), followed by transfer into sterile centrifuge tubes (Figure 1).

Each microcosm was set up in a plastic tissue culture bottle (70 mm diameter and 90 mm height) containing 200 g of sterilized soil. To minimize potential heterogeneity effects from the constrained container size, inoculum (10 g) was carefully and thoroughly homogenized with the sterilized soil in each microcosm. A 0.22 µm filter membrane was placed in each bottle to

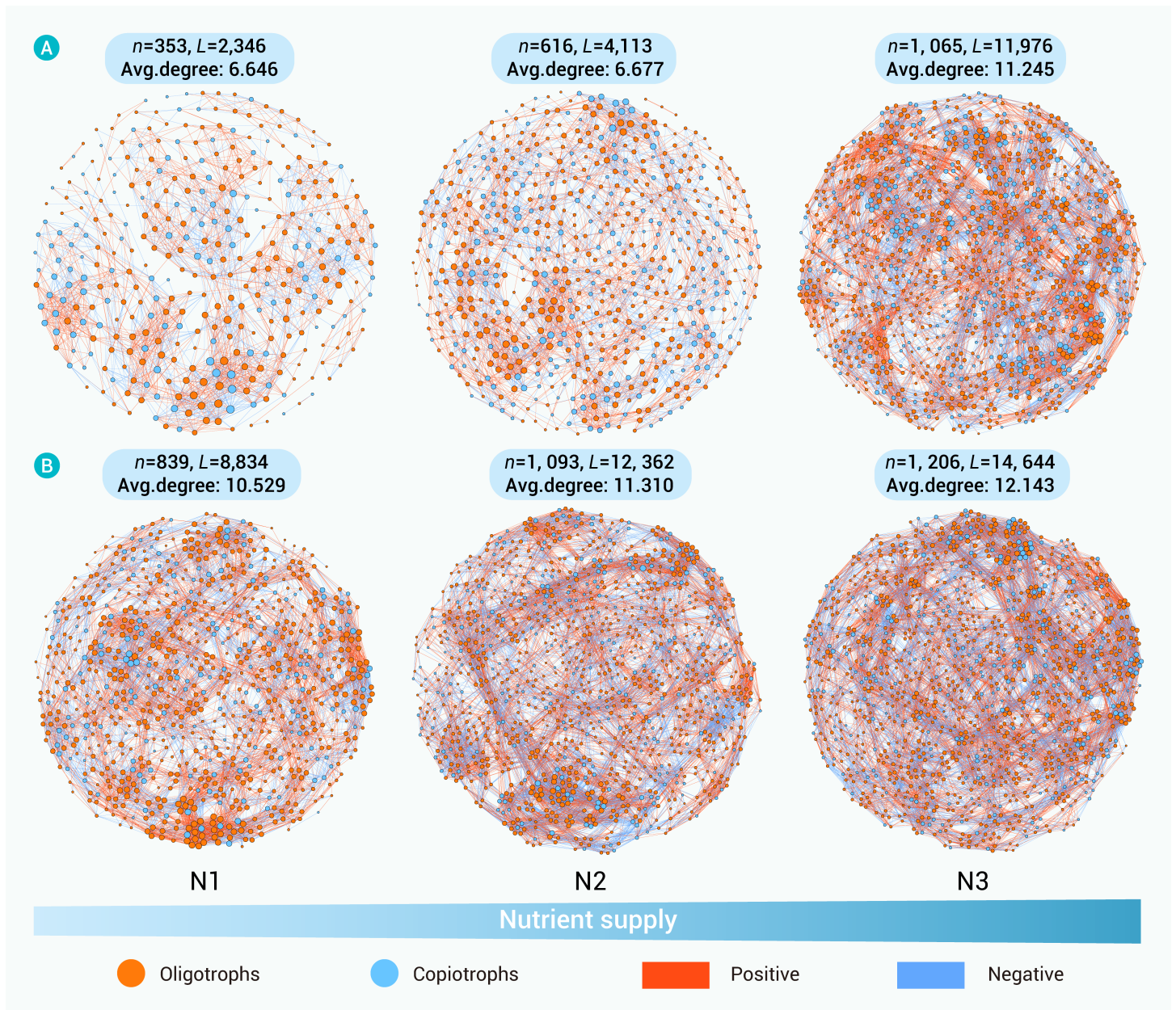


Figure 4. Network associations of biocrust bacterial OTUs in soil microcosms under different nutrient levels (n = 6 per treatment) Co-occurrence networks of (A) cyanobacteria-dominated crusts and (B) moss-dominated crusts constructed using Spearman correlation analysis. Connections represent strong correlations (Spearman's $|\rho| > 0.8$ and $P < 0.01$). Node size is proportional to the number of connections. N1, N2, and N3 represent soil types under low, moderate, and high nutrient manipulations, respectively.

allow gas exchange while preventing cross-contamination. Six replicates per treatment were prepared, totaling 36 samples (2 biocrust stages $\times$ 3 nutrient levels $\times$ 6 replicates). Microcosms were randomly placed in an incubator maintaining 20% field capacity moisture, with 16:8 h light:dark cycles (400 W sodium lamps) and corresponding temperatures of 28°C (day) and 16°C (night). The microcosm experiment lasted for 120 d, then soil samples were collected and stored at -80°C for subsequent molecular analysis.

Soil pH and nutrient analysis

Soil pH was determined using a glass electrode in a soil:water ratio of 1:5 (w/v). Soil organic matter (OM) content was determined by the potassium dichromate oxidation method.³⁹ Soil total N (TN) content was measured with a Vario Macro Cube Elemental (Elementar Analysensysteme, Hanau, Germany). Soil total P (TP) and available P (AP) were measured with the sodium carbonate and Olsen-P methods, respectively.⁴⁰ Soil available N (AN) was determined by the alkaline hydrolysis diffusion method.⁴¹ Available potassium (AK) was measured by flame photometry after extraction with ammonium acetate.⁴² Initial and post-incubation soil characteristics are detailed in Table

S1 (pre-experiment) and Table S2 (post-experiment), respectively.

DNA extraction, amplification and sequencing

Total DNA was extracted using an E.Z.N.A. Soil DNA Kit (Omega Bio-Tek, Norcross, GA, USA) according to the manufacturer's instructions. The concentration and purity of the extracted DNA were tested using a NanoDrop 2000 (Thermo Fisher Scientific, USA). The bacterial 16S rRNA gene was amplified by PCR using 338F (5'-ACTCCTACGGGAGGCAGCA-3') and 806R (5'-GGACTACHVGGGTWTCTAAT-3'). The amplicons were separated by 20 g/L agarose gel electrophoresis, purified using a SanPrep Column DNA Gel Extraction Kit (Sangon Biotech Shanghai Co., Ltd.) and quantified with QuantiFluor™-ST (Promega Corporation, Madison, WI, USA). The purified amplicons were sequenced using the Illumina Nextseq 2000 Platform (Majorbio Bio-Pharm Technology Co., Ltd., Shanghai, China).

Sequence data processing and bacterial community analysis

The raw FASTQ files were multiplexed and filtered using the QIIME pipeline. Subsequently, the sequences were clustered into operational taxonomic units

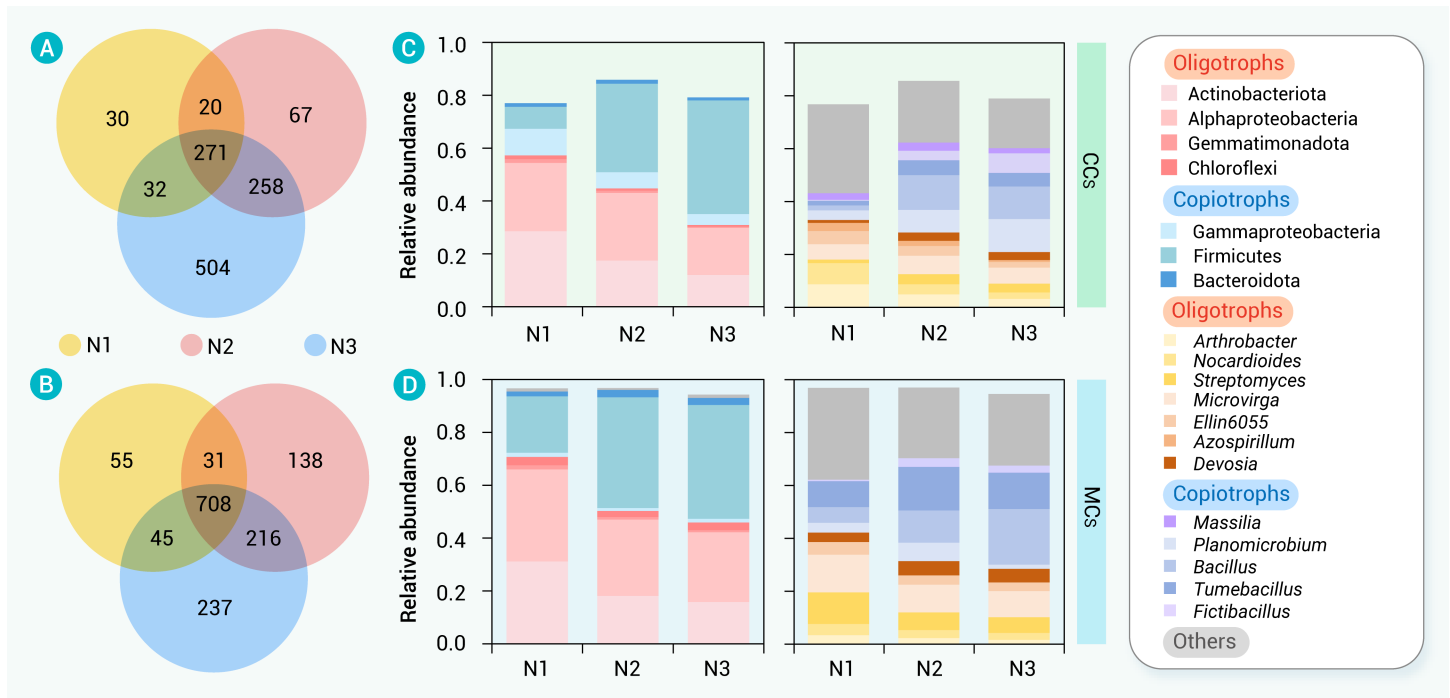


Figure 5. Overview of biocrust bacterial network nodes in soil microcosms under different nutrient levels (A) Venn diagram of the distribution of bacterial network nodes in cyanobacteria-dominated crusts and (B) moss-dominated crusts. (C) Taxonomic composition of shared bacterial network nodes in cyanobacteria-dominated crusts and (D) moss-dominated crusts across soil microcosms under different nutrient manipulation scenarios. N1, N2, and N3 represent soil types under low, moderate, and high nutrient manipulations, respectively.

(OTUs) at 97% sequence identity. The *rrnDB* database (<https://rrndb.umms.med.umich.edu/>) was applied to estimate the *rrn* copy numbers of bacterial OTUs. For each OTU, the *rrn* copy number was estimated based on its phylogenetically closest relative with a known *rrn* copy number. For each sample, the abundance-weighted mean *rrn* copy number was calculated following the method outlined by Dai et al.²⁰

$$rrn\text{ copy number} = \frac{\sum_{i=1}^N S_i}{\sum_{i=1}^N n_i}$$

where N is the number of OTUs in a sample, S_i is the sequence abundance of OTU $_i$, and n_i is the estimated *rrn* copy number of OTU $_i$.

Oligotrophic and copiotrophic bacteria were defined according to previous studies (Table S3).^{14,15} The ratio of oligotrophs to copiotrophs (Oligo/Copio ratio) was calculated as the sum of the oligotrophs divided by the sum of the copiotrophs. The Tukey's Honestly Significant Difference test was performed using SPSS 16.0 (SPSS, Inc., Chicago, IL, USA) to assess differences in *rrn* copy numbers and the Oligo/Copio ratio across soil treatments. The Kruskal-Wallis H test was used to compare differences in taxa between the three levels (Majorbio Cloud Platform). The "Hmisc" R package was used to construct the bacterial network based on the Spearman correlation matrix, and correlations with Spearman's $|\rho| > 0.8$ and $P < 0.01$ were visualized as a co-occurrence network using "Gephi".⁴³ The heatmap correlation analysis was generated using the Spearman methods. Figures were generated using Origin 8.0 (Origin Lab Corporation, Northampton, MA, USA).

RESULTS

Bacterial life-history strategies and taxonomic compositions

The *rrn* copy numbers of bacterial communities increased with increasing nutrient supply (Figure 2A), while the Oligo/Copio ratio decreased (Figure 2B). Actinobacteriota (12.72% to 29.90% in CCs, 16.11% to 31.42% in MCs) and Alphaproteobacteria (18.99% to 27.33% in CCs, 26.80% to 35.32% in MCs) represented dominant oligotrophs, showing a decrease in relative abundance with increasing nutrient supply, whereas Firmicutes were dominant copiotrophs that increased (10.65% to 52.78% in CCs, 21.52% to 45.35% in MCs) (Figure 2C). At the genus level, *Arthrobacter*, *Nocardioidea*, *Streptomyces*,

Microvirga, *Ellin6055*, *Azospirillum* and *Devosia* were dominant oligotrophs, and *Massilia*, *Planomicrobium*, *Bacillus*, *Tumebacillus* and *Fictibacillus* were dominant copiotrophs (Figure 2D). Moreover, the Kruskal-Wallis H test was applied to assess differences in the relative abundance of bacterial genera across nutrient levels. In CC bacterial communities, the relative abundance of *Planomicrobium*, *Tumebacillus*, *Fictibacillus*, and *Devosia* significantly increased, while that of *Arthrobacter*, *Nocardioidea*, and *Ellin6055* significantly decreased (Figure 2E). In MC bacterial communities, the relative abundance of *Bacillus* significantly increased, whereas that of *Microvirga*, *Streptomyces*, *Ellin6055*, *Nocardioidea*, and *Arthrobacter* significantly decreased (Figure 2E).

Moreover, we identified shared bacterial OTUs across nutrient levels (Figure 3). A total of 600 OTUs in the CC bacterial community and 1,203 OTUs in the MC bacterial community were common to all three levels (Figures 3A-B). These OTUs primarily belonged to *Arthrobacter*, *Nocardioidea* and *Streptomyces* (Actinobacteriota), *Microvirga*, *Ellin6055* and *Devosia* (Alphaproteobacteria), and *Planomicrobium*, *Bacillus*, *Tumebacillus* and *Fictibacillus* (Firmicutes) (Figures 3C-D).

Bacterial co-occurrence networks

To better understand the co-occurrence patterns of oligotrophs and copiotrophs with increasing nutrient supply, network analysis based on Spearman's rank correlations ($|\rho| > 0.8$ and $P < 0.01$) was performed, and the results were visualized (Figure 4). However, it should be emphasized that these correlation-based associations represent potential ecological relationships rather than confirmed direct interactions, and may be influenced by shared environmental preferences or indirect ecological effects.

In bacterial networks, both the number of nodes and links, as well as the average degree, increased with nutrient supply (Figure 4). Specifically, the number of nodes in CC bacterial networks increased from 353 to 1,065, and in the MC bacterial networks increased from 839 to 1,206 with increasing nutrient supply (Figure 4). The number of links in CC bacterial networks increased from 2,346 to 11,976, and in MC bacterial networks increased from 8,834 to 14,644 (Figure 4). The average degree also increased, from 6.646 to 11.245 in CC bacterial networks, and from 10.529 to 12.143 in MC bacterial networks (Figure 4). Additionally, the proportion of negative correlations in the CC bacterial networks increased from 39.60% to 42.48%, and in MC networks,

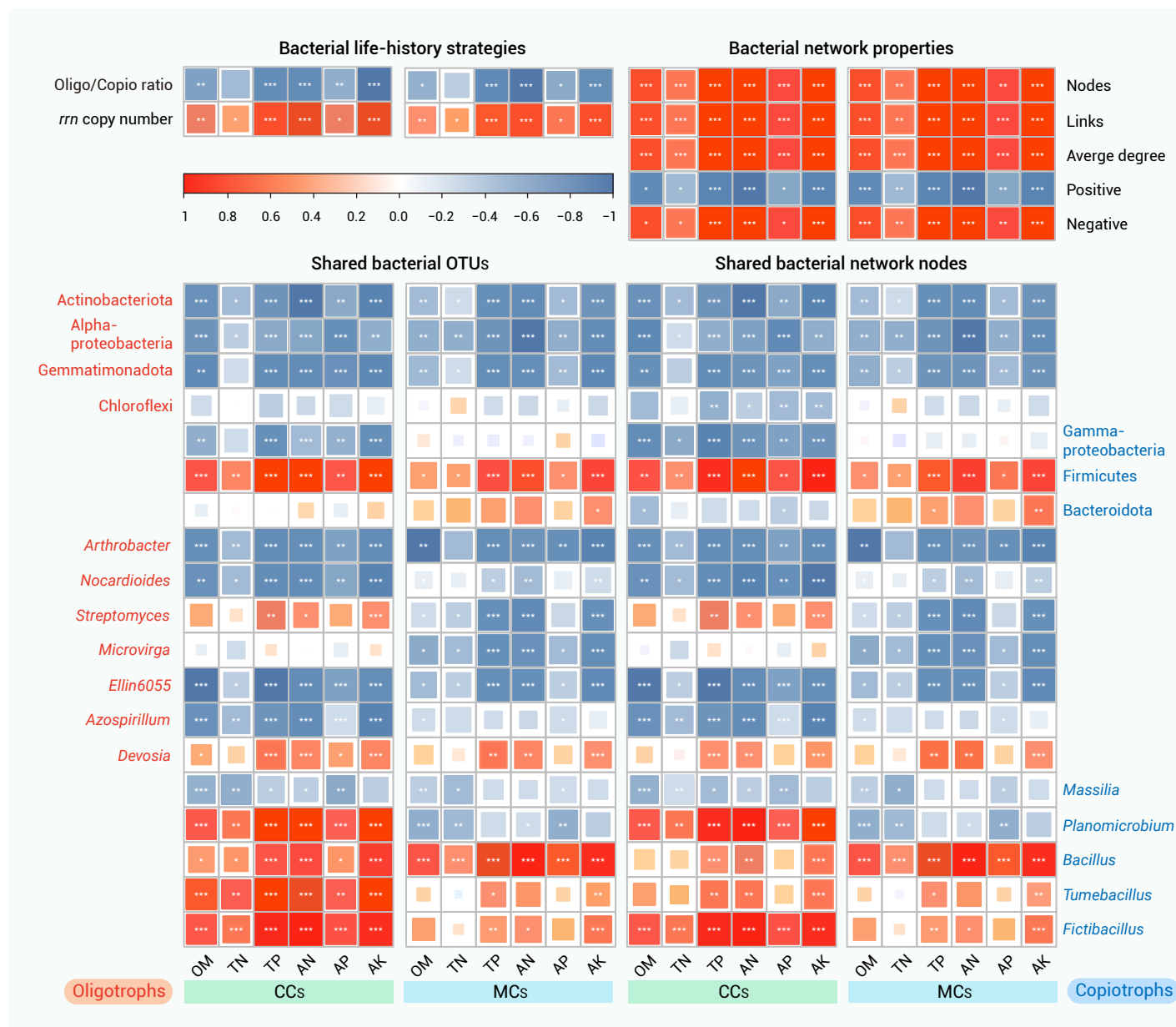


Figure 6. Spearman correlation analysis between bacterial community structures and soil properties The color intensity of each cell is proportional to the value of Spearman's correlation coefficient. Red indicates a positive correlation; blue indicates a negative correlation. Statistical significance levels: * $0.01 < P \leq 0.05$, ** $0.001 < P \leq 0.01$, *** $P \leq 0.001$. CCs and MCs represent cyanobacteria- and moss-dominated crusts, respectively. OM, TN, TP, AN, AP and AK represent organic matter, total nitrogen, total phosphorus, available nitrogen, available phosphorus and available potassium, respectively.

from 40.17% to 48.14%, with increasing nutrient supply (Figure S1).

Moreover, we identified shared nodes in bacterial networks across nutrient levels (Figure 5). A total of 271 nodes in the CC bacterial network and 708 nodes in the MC bacterial network were common to all three levels (Figures 5A-B). These nodes primarily belonged to *Arthrobacter*, *Nocardioides* and *Streptomyces* (Actinobacteriota), *Microvirga*, *Ellin6055* and *Devosia* (Alphaproteobacteria), and *Planomicrobium*, *Bacillus*, *Tumebacillus* and *Fictibacillus* (Firmicutes) (Figures 5C-D).

Relationships between bacterial community structures and soil properties

As shown in Figure 6, the bacterial community structure (including bacterial life-history strategies, network topological properties, shared OTUs, and shared network nodes) of CCs and MCs was closely associated with soil properties. Detailed correlation analyses revealed that the Oligo/Copio ratio correlated negatively with AN ($r = -0.89$ in CCs, $r = -0.87$ in MCs), AK ($r = -0.92$ in CCs, $r = -0.83$ in MCs), and TP ($r = -0.88$ in CCs, $r = -0.81$ in MCs) (all $P < 0.001$), whereas bacterial *rrn* copy numbers showed positive correlations (AN: $r = 0.87$ in CCs, $r = 0.83$ in MCs; AK: $r = 0.90$ in CCs, $r = 0.80$ in MCs;

TP: $r = 0.83$ in CCs, $r = 0.76$ in MCs; all $P < 0.001$) (Figure 6 & Table S4). Nodes, links, average degree, and negative correlations of bacterial networks in CCs and MCs were positively associated with soil properties ($|r| > 0.90$; $P \leq 0.001$), while positive correlations of bacterial networks were negatively associated with soil properties ($|r| > 0.90$; $P \leq 0.001$) (Figure 6 & Table S4). Additionally, all oligotrophic phyla exhibited negative correlations with nutrient supply, whereas the copiotrophic phylum (only Firmicutes) showed significant positive correlations (Figure 6, Tables S5 & S6). The shared bacterial OTUs and network nodes in CCs and MCs, predominantly derived from *Arthrobacter*, *Nocardioides* and *Ellin6055* in oligotrophs, and *Bacillus*, *Tumebacillus* and *Fictibacillus* in copiotrophs, were strongly correlated with AN, AK, and TP (Tables S5 & S6).

DISCUSSIONS AND CONCLUSIONS

Soil-microbial interactions are crucial for ecosystem health and resilience, supporting nutrient cycling, organic matter decomposition, soil structure formation, and plant health.^{44,45} Recent scientific results highlight the close relationship between soil nutrient supply and bacterial communities,¹⁰ but

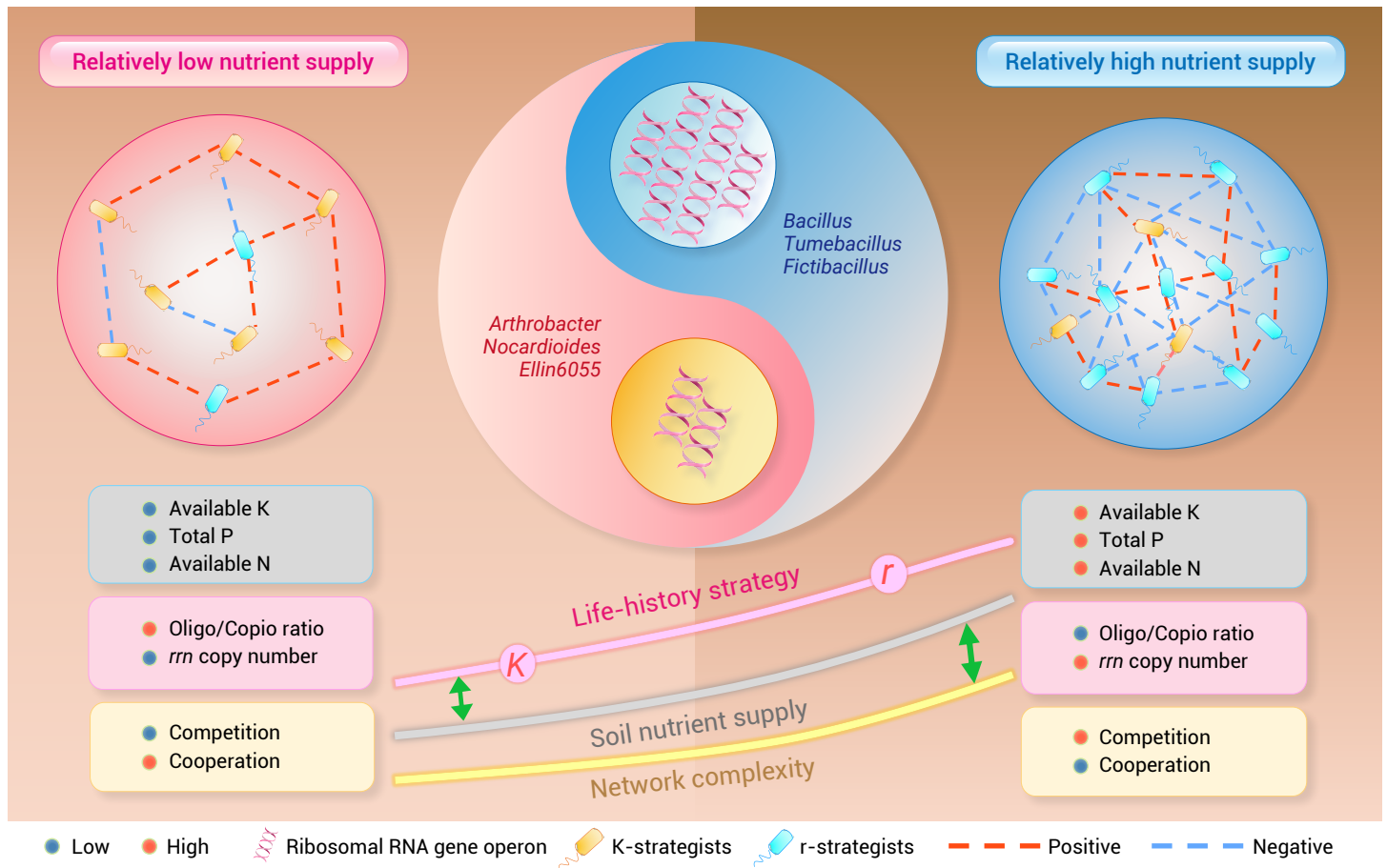


Figure 7. Conceptual model of nutrient-driven shifts in biocrust bacterial life-history strategies and ecological interactions Under relatively low-nutrient supply (left panel), K-strategists characterized by lower *rrn* copy numbers dominate, where cooperative behaviors are favored to mitigate resource limitations. In contrast, under relatively high-nutrient supply (right panel), r-strategists with higher *rrn* copy numbers become prevalent. Here, the ecological dynamics shift toward intensified interspecific interactions, with competition emerging as a dominant force, as organisms vie for increasingly abundant (but still limited) resources. Blue dots (low values) and orange dots (high values) represent parameter levels under relatively low and high nutrient supply conditions, respectively. Yellow and blue bacterial icons represent K-strategists and r-strategists, respectively. Red and green dashed lines denote positive and negative interactions between bacterial taxa, respectively.

gaps remain in understanding how bacterial life-history strategies and ecological interactions adapt to nutrient fluctuations, especially in biocrusts. Therefore, integrative models that combine bacterial life-history strategies, genetic traits (*rrn* copy numbers), ecological interactions, and nutrient supply are urgently needed to predict the complex interactions between soil nutrient conditions and biocrust bacterial community dynamics.

Our first major finding was that elevated nutrient supply shifts biocrust bacterial communities from K-strategists to r-strategists, characterized by: (i) an increase in the *rrn* copy numbers of bacterial communities, and (ii) a decrease in the Oligo/Copio ratio (Figure 2). Trait-based studies are crucial for forecasting and comprehending the effects of environmental shifts on ecological functions.⁴⁶ While previous researches have highlighted the close relationship between *rrn* copy number and nutrient supply in ecosystems,^{20,47,48} nutrient supply patterns vary across ecosystems, particularly in less-disturbed solid systems, resulting in differing community metabolic levels.²¹ The observed transition in life-history strategies strongly supports the r-K selection theory and can be attributed to the rate–yield trade-off in bacterial metabolism, which requires cells to make strategic resource allocation decisions.⁴⁹ In nutrient-rich environments, metabolic resources are preferentially allocated to ribosome production rather than metabolic enzyme synthesis, facilitating increased protein synthesis and promoting rapid growth rates and biomass accumulation.¹⁹ Conversely, nutrient-scarce environments promote the allocation of resources towards metabolic enzyme synthesis over ribosome production, allowing bacteria to maximize resource utilization efficiency to sustain growth.^{50,51} Our findings extend the current understanding of bacterial life-history strategies in desert ecosystems by highlighting *rrn* copy number as a pivotal genomic trait, demonstrating that the adaptive transition of bacterial communities from K-strategists to r-

strategists may enhance their ability to respond to increased nutrient supply.

Our second major finding was that nutrient supply substantially influenced ecological interactions of K-strategists and r-strategists in biocrust bacterial communities, primarily by intensifying interactions and competition. The influence of nutrient supply on microbial community dynamics has long been a subject of interest in microbial ecology, with several studies indicating that nutrient levels can shape the competitive balance between different microbial groups.⁵² In this study, we delved into the intricate relationship between nutrient supply and the ecological interactions within biocrust bacterial communities, specifically focusing on the dichotomy between K- and r-strategists. Our results underscored that nutrient supply not only drives the relative abundance of K-strategists and r-strategists (Figures 2C–D) but also fundamentally alters the nature of their interactions (Figures 4 & S1), reinforcing the idea that biotic interactions are closely tied to resource availability in microbial ecosystems (Figure 6, Tables S4 & S6). We observed a significant increase in both the number of nodes and links within bacterial networks as nutrient supply increased (Figure 4), indicating heightened interspecies engagement. Concurrently, there was an increased proportion of negative correlations, which directly reflected intensified competitive interactions (Figures 4 & S1). These findings provide empirical support for the “hunger games” hypothesis, which posits those microbial interactions transition from cooperation under nutrient scarcity to competition under resource enrichment.²⁰ Specifically, our results corroborate the hypothesis’s prediction that nutrient limitation encourages metabolic cooperation to mitigate resource constraints,⁵³ while increased nutrient supply fosters competition for newly available resources. Moreover, the increased competition driven by nutrient supply is not only a direct consequence of resource competition but also reflects the complex interplay of environmental selections, evolutionary

strategies, and microbial niche construction.^{54–56} Our network analysis reveals how nutrient conditions shape competitive interactions between bacterial life-history strategies, providing insights into ecosystem stability under climate change and land degradation where nutrient dynamics are frequently altered.⁵⁷ However, several methodological limitations warrant consideration when interpreting these findings. First, our correlation-based approach may detect indirect associations driven by unmeasured environmental factors or shared habitat preferences rather than direct microbial interactions. Second, the compositional nature of sequencing data could potentially generate spurious correlations, possibly inflating the perceived strength or significance of certain microbial relationships. Future studies should incorporate time-series data, experimental manipulations, or alternative methods (e.g., SparCC, mutual information, or machine learning approaches) to better distinguish direct from indirect associations and validate these ecological relationships.

Moreover, we identified keystone taxa in biocrust bacterial communities, including *Arthrobacter*, *Nocardioides* and *Ellin6055* (oligotrophs), as well as *Bacillus*, *Tumebacillus* and *Fictibacillus* (copiotrophs), which exhibit distinct responses to nutrient supply. Dominant taxa with high relative abundance, along with biomarker taxa, are commonly identified as keystone taxa.⁵⁸ Recent studies have highlighted the critical role of taxa shared across different treatment groups in soil systems.⁵⁹ Based on the data mining approach outlined above, we identified three keystone oligotrophs and three keystone copiotrophs in biocrust bacterial communities (Figures 2–3 & 5). Oligotrophs, such as *Nocardioides*, play pivotal roles in nutrient-scarce environments by leveraging accommodative genomic features and facilitating nutrient cycling, particularly nitrogen fixation and the degradation of complex organic matter.⁶⁰ On the other hand, *Bacillus* as a copiotrophic taxon that utilizes environmental resources quickly for growth has historically been associated with plant growth promotion and disease protection. It has been identified by multiple studies as a core group of soil ecosystems.^{61–63} Our findings underscore the importance of keystone taxa in biocrust bacterial communities and their response to nutrient supply. These taxa not only contribute to the overall functioning of the soil ecosystem but also serve as potential indicators of ecosystem health and resilience. Understanding their dynamics is crucial for predicting how soil ecosystems will respond to environmental changes and for developing strategies for soil management and conservation.

To conceptualize the effects of nutrient supply on biocrust bacterial communities, we propose a model (Figure 7) in which increased nutrient levels trigger a shift in bacterial life-history strategies from K-strategists to r-strategists, intensifying competitive relationships among these strategies. This shift is critical because K-strategists typically contribute to stable, long-term nutrient cycling through mechanisms such as organic matter decomposition and nutrient retention, whereas r-strategists are more effective at rapidly exploiting available resources, leading to increased nutrient turnover.^{13–15} This fundamental difference may ultimately influence ecosystem resilience and nutrient cycling dynamics in biocrust habitats. For instance, as r-strategists dominate in nutrient-rich conditions, we may observe enhanced rates of N mineralization and C release, potentially altering the availability of these essential nutrients in the ecosystem.⁶⁴ Conversely, the decline of K-strategists could reduce the stability and resilience of biocrust ecosystems, impacting their ability to retain nutrients and respond to environmental fluctuations.^{14,15} In conclusion, our study elucidates the dynamics of biocrust bacterial communities and their responses to environmental fluctuations, establishing a mechanistic framework for nutrient-driven bacterial assembly in drylands. These insights translate into actionable strategies for ecological stabilization, including optimized N, K, and P inputs to balance nutrient supply, as well as targeted manipulation of keystone taxa to bolster ecosystem resilience. Such nutrient- and keystone bacteria-based management strategies may provide highly relevant approaches for preserving biocrust ecosystems and controlling desertification under the impact of rapidly changing environmental conditions.

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AUTHOR CONTRIBUTIONS

Lina Zhao: Conceptualization, Formal analysis, Investigation, Methodology, Visualization, Writing – original draft, Writing – review & editing. Wenjing Zhang: Formal analysis, Investigation, Visualization, Writing – review & editing. Ning Chen: Writing – review & editing. Bettina Weber: Writing – review & editing. Tianjiao Dai: Writing – review & editing. Rongliang Jia: Writing – review & editing. Shaobin Gu: Writing – review & editing, Supervision. Xinrong Li: Writing – review & editing, Conceptualization. All authors contributed to the manuscript and approved the final version.

DECLARATION OF INTERESTS

The authors declare no competing interests.

DATA AND CODE AVAILABILITY

All sequence data were submitted to the NCBI Sequence Read Archive (SRA) under accession number PRJNA1137544.