

# Interaction balance governs microbial community richness-stability relationship in terrestrial ecosystems

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## Abstract

Richness-stability relationships (RSRs), such as richness-resistance relationship and richness-resilience relationship, are a basic, but controversial, question in ecology. RSRs vary among different communities, with the positive and negative interactions among community members considered as the potential cause of different RSRs. However, there is still no empirical data to support the relationship between these interactions and RSRs. To confirm the potential effect of community interactions on RSRs, we selected soil microbial communities from ecosystems that represented 5 different successional stages and conducted a simulated stress-recovery incubation. Our results showed that soil microbial community RSRs were controlled by the balance of positive and negative interactions. If positive and negative interaction of the microbial community network were balanced, the richness-resistance relationship was significantly positive while the richness-resilience relationship was negative. In contrast, if positive and negative interaction were unbalanced, the richness-resistance relationship was significantly negative while the richness-resilience relationship was positive.

## Introduction

Richness-stability relationships (RSRs) are a basic question of increasing concern in modern ecology (McCann 2000; Dixon *et al.* 2021). RSRs describe the most simplified links between species pool and complex system persistence, and could offer a substantial, convenient, and valuable guide to several ecological fields including artificial community composition (Dixon *et al.* 2021), biological conservation formulation (Griffiths & Philippot 2013), and ecosystem stability assessment (García-Palacios *et al.* 2018). Unfortunately, according to previous community studies, RSRs can vary widely (Sankaran & McNaughton 1999; Naeem *et al.* 2000; Arthur & Dech 2016; Baert *et al.* 2016; O'Brien *et al.* 2017; Pennekamp *et al.* 2018), but the potential cause of these differences has yet to be resolved.

Interactions between community members, both positive (e.g., mutualism and cooperation) and negative interactions (e.g., competition and predation), were predicted as a potential influencer of RSRs (May & MacDonald 1978; Damore & Gore 2012). Positive interactions theoretically benefit to extend the niche width of species and offer them the ability to live under conditions that were originally unfavorable, thus increasing their tolerance to stress (Damore & Gore 2012). Negative interactions were also been predicted as beneficial for community stability in several models (Pinsky 2019). However, there is still no empirical evidence to support whether interactions influence RSRs.

The microbial community is a species rich and functionally important component of ecosystems (Griffiths & Philippot 2013). However, the relatively few studies, primarily in aquatic ecosystems, that have investigated microbial community RSRs, have come to contradictory conclusions. For instance, aquatic micro-cultivations utilizing different combinations of 6 ciliate species (total of 690 incubations) reported a negative relationship

between richness and resistance (Pennekamp *et al.* 2018), while a positive relationship between richness and resistance of microbial community was reported from two lakes in Canada (Hillebrand *et al.* 2018). Yet, the soil microbial community plays an irreplaceable role in decomposition, nutrient cycling, and above-ground community regulation for terrestrial ecosystems (Franciska & Ashley 2013). The variation in community composition caused by environmental stress would threaten the functions relevant to the soil microbial community (Franciska & Ashley 2013). The lack of soil microbial community RSRs research significantly hampers a deeper understanding of terrestrial ecosystem stability and the response to climatic and anthropogenic stresses (Franciska & Ashley 2013).

In order to investigate RSRs of the soil microbial community in terrestrial ecosystems and explore the effect of interactions on RSRs, we selected 5 successional stage ecosystems (bare soil, grass, shrub, deciduous forest, and coniferous forest) from a typical glacial retreat area to compare the microbial community stability components (resistance and resilience) under simulated climatic stress. There were two main reasons for choosing this successional gradient. Firstly, the ecosystems were located in a glacial retreat area of approximately 3km×0.5km with less than 100m difference in elevation, sharing the same regional precipitation and temperature, therefore the types and extents of climatic stress exerted on them could be treated as the same (Li & Xiong 1995). Secondly, the richness and network structure of the microbial community varies among successional stages, offering a natural gradient to analyze how interaction types influence RSRs (Jiang *et al.* 2018). In this study, we found that balanced positive and negative interactions of the community offered a positive richness-resistance relationship, while unbalanced interactions offered a negative relationship.

## Method

### *Sampling and experiment*

The soils were sampled from Gongga Snow Mountain, on the eastern edge of the Tibet plateau, Sichuan province, China. We selected five different ecosystems, bare soil (29°34'37"N, 101°59'25"E, 2961m), grass (29°34'48"N, 101°59'33"E, 2955m), shrub (29°34'60"N, 101°59'42"E, 2934m), deciduous forest (29°34'16"N, 101°59'55"E, 2924m), and coniferous forest (29°34'23"N, 102°00'06"E, 2893m) (Li & Xiong 1995; Jiang *et al.* 2018). Three samples were taken in each type ecosystem (total of 15). All samples were passed through 2mm sieves with large plant litters and small animal bodies (like insects and earthworms) picked out by hand. Samples were transported on ice to Beijing as soon as possible. The main vegetation species and types of the sampling sites were described in detail in previous studies (Li & Xiong 1995; Jiang *et al.* 2018).

Fifteen incubations were set up for each ecosystem (5 per soil sample). For each incubation, 5g (dry weight) of soil were incubated in 50ml centrifuge tubes under 60% water holding capacity and at 20°C. Every 12h the lids of the tubes were opened to allow complete exchange of the air and to adjust water content. Incubations were allowed to acclimate for 3 days before beginning the experiment. At the beginning of the incubation, we sacrificed 3 original samples (O) for each ecosystem, the other incubations were divided into high temperature stress treatment and control groups (6 incubation per group for each ecosystem). The high temperature treatment groups were transferred to 35°C for 3 days while the control groups were incubating under the original temperature condition. We then sampled 3 incubations from each ecosystem for treatment (T1) and control (U1) groups. The remaining temperature stress treatment incubations were returned to the original temperature condition (20°C) and the incubations for both treatment and control groups were incubated an additional 9 days. Then we sampled both treatment (T2) and control (U2) groups at the end 12<sup>th</sup> day.

### *DNA extraction and amplicon sequencing*

Soil DNA was extracted using the FastDNA<sup>TM</sup> SPIN kit (MP Biomedicals) according to the manufacturer's protocol, after which the concentration and quality were checked using a Nano-100, a NanoDrop Spectro-photometer. Primers targeting the V3-V4 region of the 16S rRNA gene of bacteria, 338F (5'-ACTCCTACGGGAGGCAGCA-3') and 806R (5'-GGACTACHVGGGTWTCTAAT-3'). The PCR reaction consisted of 25 µl 2×Primer Taq (Takara, RR902A), 1 µl F-Primer (10 mM) and 1 µl R-Primer (10 mM), 3 µl DNA and 20 µl dd-H<sub>2</sub>O. The PCR program was 94°C 5 min, 31 cycles of (94°C 30 s, 52°C 30

s, 72°C 45 s), 72°C 10 min. The ITS2 region of fungi, 3F (5'-GCATCGATGAAGAACGCAGC-3') and 4R (5'-TCCTCCGCTTATTGATATGC-3'), were chosen for amplification. The PCR reaction consisted of 6 µl 10×E×Taq Buffer, 6 µl dNTP, 0.6 µl BSA, 0.3 µl E×Taq, 1 µl DNA, 1.2 µl F-Primer, 1.2 µl R-Primer, and 43.7 µl dd-H<sub>2</sub>O. The PCR program was 94°C 5 min, 25 cycles of (94°C 30 s, 55°C 30 s, 72°C 30 s), 72°C 7 min. PCR was run on a Biorad 1000, and the ending temperature was 16°C. PCR products was mixed in equimolar ratios according to the GeneTools Analysis Software (Version 4.03.05.0, SynGene). Next, the mix of PCR products was purified using an E.Z.N.A. Gel Extraction Kit (Omega, USA). Sequencing libraries were generated using NEBNext® Ultra II DNA Library Prep Kit for Illumina(r) (New England Biolabs, MA, USA) following manufacturer's recommendations, and index codes were added. The library quality was assessed on the Qubit® 2.0 Fluorometer (Thermo Fisher Scientific, MA, USA). The library was sequenced on an Illumina Nova6000 platform and 250 bp paired-end reads were generated (Guangdong Magigene Biotechnology Co., Ltd. Guangzhou, China).

### *Sequence data preprocessing and bioinformatics approaches*

Fastp (version 0.14.1) was used to assess the quality of the raw sequences using a sliding window (-W4-M20). Primers were removed using cutadapt software (Martin 2011). The Usearch fastq\_mergepairs command was used to merge paired-end clean reads with a minimum of 16 bp overlap, the maximum mismatch allowed in the overlap region was 5 bp, and the spliced sequences were called raw tags. Fastp (version 0.14.1) was then used to assess the quality of the raw tags using a sliding window (-W4-M20) to obtain the paired-end clean reads. Sequences with more than 97% similarity were classified as the same OTU.

### *Statistics*

Resistance was defined as the natural logarithm of the ratio of Bray-Curtis distance between O-U1 to T1-U1, the resilience was defined as natural logarithm of ratios of Bray-Curtis distance between T1-U1 to T2-U2, as shown in Fig. S1.

Network analyses were conducted in a pipeline (<http://www.magichand.online/h5-BioCloud-site/#/>) and visualized by Cytoscape 3.3.0 (<http://cytoscape.org/>). The cutoff threshold was set at 0.9, top 100 relative abundance OTUs of the bacterial and fungal community were selected for network analysis by Spearman correlation matrix. The interaction type ratio was defined as the proportion of positive interactions to all interactions (P%). Thus, a P% of approximately 0.5 indicated relatively equal (balanced) proportions of positive and negative interactions, while a P% near 1 or 0 indicate an exceedingly high proportion of positive or negative interactions, respectively. The significant difference of basic soil properties and diversity indexes among ecosystems were checked using one-way ANOVA test. PCoA analysis were based on Bray-Curtis distance, was performed using a pipeline (<http://www.magichand.online/h5-BioCloud-site/#/>). In order to unify bacterial and fungal richness, we used the standard richness for relative analysis, which was defined as the ratio of richness to the lowest richness from bacterial and fungal samples, here is the fungal community richness of the 3<sup>rd</sup> sample of bare land (only 563).

## **Results**

Our results found that the basic abiotic and biotic properties of the five typical ecosystems studied here showed significant differences. The basic soil environmental conditions are shown in Fig. S2, basic bacterial and fungal community compositions in Fig. S3, and basic  $\alpha$ -diversity in Fig. S4.

### *Differences within stability components among terrestrial ecosystems*

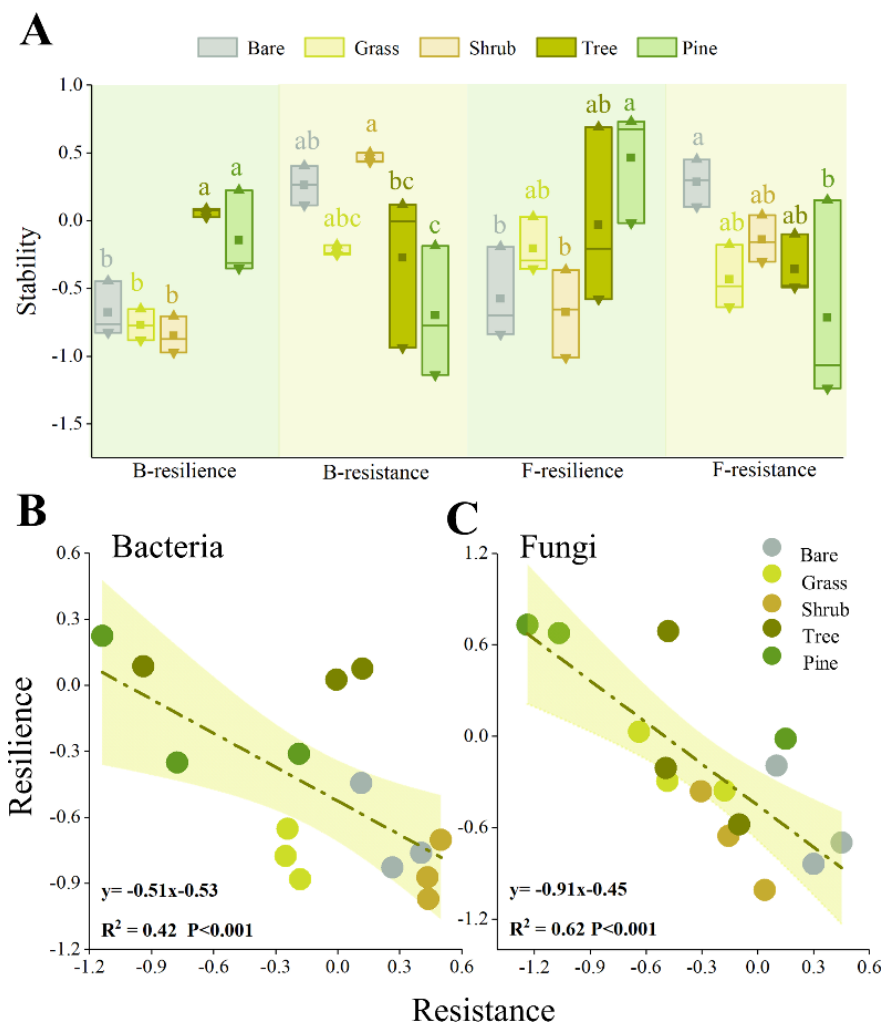


Figure 1 The resistance and resilience of microbial community from different terrestrial ecosystems. Fig. 1A depicts the magnitude of resistance and resilience of the bacterial and fungal communities among bare soil, grass, shrub, deciduous forest, and coniferous forest. Different letters indicate significance ( $P < 0.05$ ; one-way ANOVA Tukey's test). Fig. 1B and 1C depict the negative relationship between resistance and resilience of the bacterial and fungal communities, respectively.

As depicted in Fig. 1, the ecosystem with lowest bacterial resilience was shrub (-0.86), which was not significantly different from grass and bare soil ( $P > 0.05$ ), but was significantly lower than deciduous forest (0.06) and coniferous forest (-0.15,  $P < 0.05$ ). Similarly, fungal resilience was lowest in shrub (-0.68), then bare soil (-0.58), and both were significantly lower than coniferous forest (0.46,  $P < 0.05$ ), but not significantly lower than grass and deciduous forest ( $P > 0.05$ ). Bacterial resistance was highest in shrub (0.46) and lowest in coniferous forest (-0.70), and these two ecosystems were significantly different ( $P < 0.05$ ) from each other while the other 3 showed no significant differences between them ( $P > 0.05$ ). The highest fungal resistance was observed in bare soil (0.28), and was significantly higher than in the coniferous forest (-0.72,  $P < 0.05$ ). Microbial resistance showed a decreasing trend with vegetation types from bare soil, grass, shrub, deciduous forest, to coniferous forest while the microbial resilience showed an increasing trend. Linear regression analysis showed a significantly negative relationship between resistance and resilience in both the bacterial (Fig. 1B,  $P < 0.05$ ,  $R^2=0.42$ , slope=-0.51) and fungal (Fig.1 C,  $P < 0.05$ ,  $R^2=0.62$ , slope=-0.91) communities, which indicated a trade-off between microbial community resistance and resilience and that



fungus communities were less likely to possess both high resistance and resilience.

*The network interaction property*

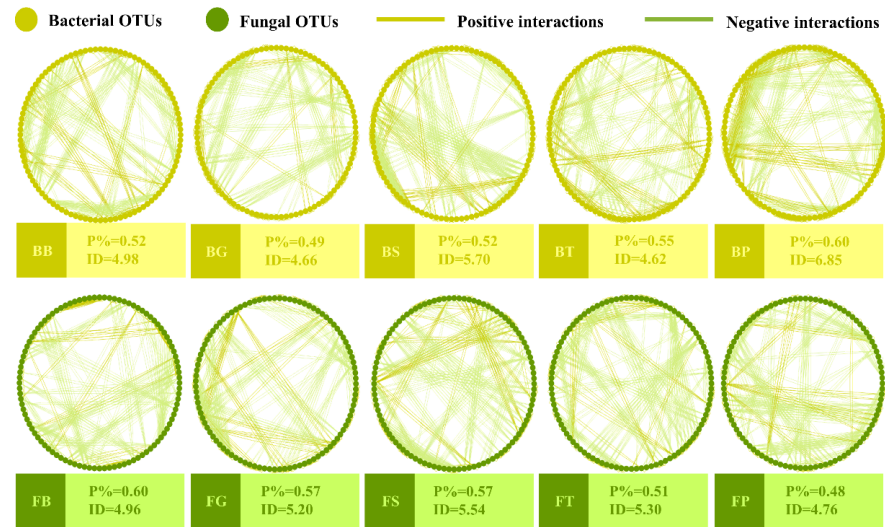


Figure 2 Network visualization of bacterial and fungal communities from different ecosystems. The yellow and green dots indicate bacterial and fungal members, respectively. The yellow and green lines indicate positive and negative interactions, respectively. BB, BG, BS, BT, and BP indicate bacterial community of bare soil, grass, shrub, deciduous forest, and coniferous forest, while FB to FP indicate the corresponding fungal communities. P% indicates the positive interaction proportions while ID (interaction density) indicates number of interactions per unit node.

As shown in Fig. 2, the P% and ID from bacterial and fungal communities of different successional stages varied. The bacterial community P% showed a roughly increasing trend through the successional stages, lowest in grass (0.49) and highest in coniferous forest (0.60). While the fungal community showed a decreasing trend, highest in bare soil (0.60) and lowest in coniferous forest (0.48). Bacterial community ID displayed irregular variation through the different successional stages, ranging from 4.62 (deciduous forest) to 6.85 (coniferous forest). Meanwhile the fungal community ID showed a unimodal trend that was highest in shrub (5.54) and lowest in coniferous forest (4.76).

*The governing of RSRs*

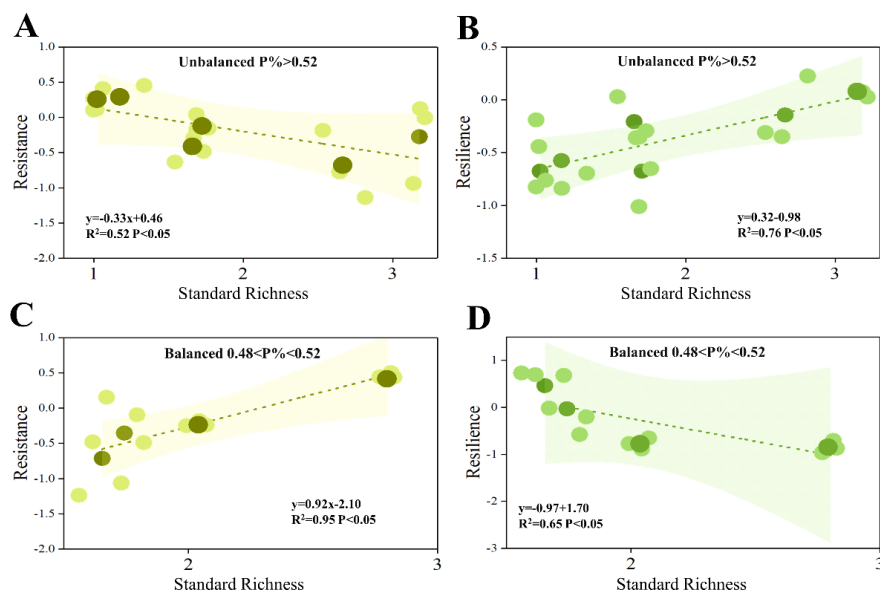


Figure 3 The linear regression of stability and standard richness under different proportions of network positive interactions. The shaded area indicates the 0.95 confidence interval. Fig. 3A and 3B depict the linear relationship of standard richness to resistance and resilience under higher proportions of positive interactions, respectively, while 3C and 3D were under a balanced proportion of positive interactions.  $P\%$  indicate the positive proportion for all interactions. The dark dots indicate the means of bacterial or fungal stability for different ecosystems.

In order to investigate the effect of interactions on RSRs, we chose the richness and stability components (resistance and resilience) for regression analysis. However, we did not find any direct linear relationship between standard richness and stability (Fig. S5), and the  $R^2$  of regression to resistance and resilience were 0.03 and 0.05, respectively, ( $P > 0.05$ ). This indicated potential drivers were governing their relationship. Next, we adopted network analysis to obtain a detailed overview of the microbial community interactions. Interestingly, the results showed that when the proportion of positive interactions was high and unbalanced ( $P\% > 0.52$ ), richness decreased resistance (Fig. 3A, slope=-0.22,  $R^2=0.52$ ), but increased resilience (Fig. 3B, slope=0.32,  $R^2=0.76$ ). When the proportion of positive interactions were balanced ( $0.48 < P\% < 0.52$ ), richness increased resistance (Fig. 3C, slope=0.92,  $R^2=0.95$ ) and decreased resilience (Fig. 3D, slope=-0.97,  $R^2=0.65$ ). These results showed that the relationship between richness and stability was governed by the balance between positive and negative interactions, which highlighted that the organizational pattern of community members plays an important role in influencing the relationship between the size of species pool and system stability.

## Discussion

This study compared microbial community stability components from different successional stages of terrestrial ecosystems and offered direct empirical evidence for the role interactions play in governing RSRs.

We found a rough trend that forests had higher resilience, but lower resistance, than shrub, grassland, and bare soil (Fig. 1A), which was opposite to the trend displayed by plant communities where complex systems were likely to have higher resistance (Isbell *et al.* 2015). We suggest that such differences arise from the reproductive rates, physiological resistance, and differences in richness between plants and microbes (Curtis 2006; Konopka 2006). Compared to microbes, plants have much lower reproductive rates and richness (Curtis 2006; Konopka 2006). When faced with short term high temperature stress, on the order of only several days, the dominant forest plant keystone population was likely to remain unchanged unless large scale regional death occurred, and thus appearing to have high resistance (Curtis 2006; Konopka 2006). However, microbes

have extremely high richness as compared to plants in terrestrial ecosystems, and are able to reproduce in a timespan as short as hours or even minutes (Curtis 2006; Konopka 2006). These indicate that competitive functional groups with different temperature range tolerances could potentially replace the original dominant groups and thus led to lower resistance of the microbial community (Pinsky 2019). However, with keystone species dominated by organisms with high stress tolerance, such as the communities from bare soil (Fig. 1A) that are exposed to high day-night temperature variation, dry-wet alteration, and high ultra-violet, could exhibit high resistance because those keystone species were not likely to change (Remias *et al.* 2012; Harrison & LaForgia 2019).

We found a strong negative linear relationship between microbial community resistance and resilience, which indicated a trade-off between resistance and resilience of microbial communities in the ecosystems studied here (Fig. 1B and Fig. 1C). This is plausible and inevitable from both basic logic and an evolutionary perspective. The essence of resistance and resilience is the ability of altering the relative abundance of species as conditions change. Thus, a microbial community that is more readily prone to change simultaneously has less resistance and higher resilience, and vice versa (Miller & Chesson 2009; Griffiths & Philippot 2013). From an evolutionary perspective, communities need to coordinate the functions of different components to ensure the continuation of key ecological processes for survival of the community under variable environmental conditions. This can be realized by assigning key functions to a few stress tolerant functional species (such as the high resistance community in bare soil) (Craine *et al.* 2013), or to alternative functional groups composed of different stress tolerant members (like the low resistance community in forests) (Whitham *et al.* 2006; Walworth *et al.* 2020), that can be treated as the K-strategy and r-strategy of community evolution or succession. However, to simultaneously possess K- and r-strategy wastes energy and is an evolutionary dead-end (Whitham *et al.* 2006; Liet *et al.* 2020; Walworth *et al.* 2020). Thus, the RSRs varied according to the stability components that we observed.

Most importantly, our results confirmed the role that interaction types play in governing RSRs. Richness offers a basic available species pool from which the community derived, while interactions offer the basic functional organizational patterns for species to form the community (Whitham *et al.* 2006; Montesinos-Navarro *et al.* 2017; Walworth *et al.* 2020). Our results showed that only under approximately balanced proportions of positive and negative interactions did richness increase resistance and decrease resilience, and that an exceedingly high proportion of positive interactions caused richness to decrease resistance and increase resilience (Fig. 3). An extremely high proportion of positive interactions is theoretically unfavorable for resistance because the extinction of one species would threaten the survival of other cooperative or mutualistic species that rely on it, even though they maybe insensitive to the stress (May & MacDonald 1978; Damore & Gore 2012). The higher the richness, the greater the possibility for species co-extinction through positive interaction. Thus, when under exceedingly high proportions of positive interactions, the higher richness and the lower the community resistance (May & MacDonald 1978; Damore & Gore 2012). However, negative interactions compensate for the effect of the positive interactions on RSRs. Negative interactions include predation and competition, with competition the main consideration in bacterial and fungal community networks (Deng & Zhou 2015). Competition indicates an overlap of function and niche among community members (Pianka 1981; Pinsky 2019). Groups which conduct the same functions are capable of replacing species that had been killed off by stress, and protect other members from further extinction due to the disappearance of their functional partner(s) (Montesinos-Navarro *et al.* 2017; Qian & Akçay 2020). Thus, with appropriate proportions of positive and negative interaction, species can coexist in a manner without total dependency. The higher the richness, the higher the functional redundancy and increased community resistance (Pianka 1981; Pinsky 2019).

Theoretical ecologists have considered interaction types as one factor that influence RSRs in models, even though there has been no empirical evidence from previous field and laboratory studies to support this idea. Models constructed based on different constraints and underlying theories generate significantly different results, while our empirical results were supported in part by recent modelling studies which indicated that the appropriate ratio of positive and negative interactions facilitate RSRs (Mougi & Kondoh 2012; Qian & Akçay 2020). The constraints to meet these demands were, firstly, the quantitatively comparable and balanced

effects on community from both positive and negative interactions and, secondly, the decreasing interaction strength with increasing interactions (Kondoh & Mougi 2015). This indicated that interaction strength and distribution were also potential governors of RSRs, and were capable of influencing the effects exerted by the interaction types. However, whether or not such constraints commonly exist in natural ecosystems is still an open question and requires further investigation to test the effect of interaction strength on RSRs. There are also other models that suggest the mixture of appropriate positive and negative interactions of inter-trophic community cannot promote positive RSRs (Suweis *et al.* 2013). Considering that most microbial networks cannot be divided into different trophic groups according to recent methods, further research is needed to test whether our conclusions are applicable to macro communities or not. According to the theoretical predication, exceedingly high proportions of negative interactions are also an unbalanced state and could possibly contribute to a negative richness-resistance relationship, similar to an exceedingly positive unbalanced state (Mougi & Kondoh 2012; Qian & Akçay 2020). Because under an exceedingly negative interaction state, it is possible that a large number of competitors that use similar resources and conduct similar functions may become simultaneously extinct due to environmental stress (Pianka 1981; Pinsky 2019), and thus the higher the richness, the greater the number of species that could potentially become extinct, and the lower the resistance. Unfortunately, microbial communities in our sampling fields, like many terrestrial ecosystems (Shang *et al.* 2018), were dominated by positive interactions, and thus, our results were incapable of directly supporting the conjecture that under an overly negative unbalanced state, richness also reduces resistance. Therefore, we suggest to test the idea in other negative interaction dominated ecosystems, such as aquatic or artificial ecosystems.

## Conclusion

In this study, we selected 5 typical ecosystems in a successional gradient and conducted a short-term climatic stress simulation experiment to determine the role interactions play in governing the RSRs of microbial community stability. The results indicated that the microbial community showed a rough trend of decreasing resistance and increasing resilience through the successional stages, and highlighting the importance of the role of positive and negative interaction balance in governing the microbial community, which could offer valuable and meaningful guidance for artificial community composition, ecosystem stability assessment, and biological conservation formulation.

**Data availability:** The original sequences were up loaded to NCBI (SRA). The bacterial community sequences about O, T1, U1, T2 and U2 were in BioProjects PRJNA721797, PRJNA721832, PRJNA721803, PRJNA721850 and PRJNA721838, respectively. And the fungal community were in BioProjects PRJNA721852, PRJNA721860, PRJNA721854, PRJNA721886 and PRJNA721876, respectively.

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